

CHEMICAL AND BEHAVIORAL ECOLOGY OF PALM WEEVILS
(CURCULIONIDAE: RHYNCHOPHORINAE)

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ABSTRACT

Palm weevils in the subfamily Rhynchophorinae (Curculionidae) (*Rhynchophorus* spp., *Dynamis borassi*, *Metamasius hemipterus*, *Rhabdoscelus obscurus*, and *Paramasius distortus*) use male-produced aggregation pheromones for intraspecific chemical communication. Pheromones comprise 8, 9, or 10 carbon, methyl-branched, secondary alcohols. (4*S*,5*S*)-4-Methyl-5-nonanol (ferrugineol) is the major aggregation phero-

none for *R. ferrugineus*, *R. vulneratus*, *R. bilineatus*, *M. hemipterus*, and *D. borassi* and a minor component for *R. palmarum*. (5*S*,4*S*)-5-Methyl-4-octanol (cruentol), (3*S*,4*S*)-3-methyl-4-octanol (phoenicol), and (4*S*,2*E*)-6-methyl-2-hepten-4-ol (rhynchophorol) are the main aggregation pheromones for *R. cruentatus*, *R. phoenicis*, and *R. palmarum*, respectively. Plant kairomones strongly enhance pheromone attractiveness but none of the identified volatiles, such as ethyl acetate, ethyl propionate, or ethyl butyrate are as synergistic as fermenting plant (palm or sugarcane) tissue. Studying orientation behavior of foraging weevils to semiochemical devices helped to design and test traps for weevil capture. Generally, 3 mg per day of synthetic pheromone (with non-natural stereoisomers being benign) plus insecticide-treated plant tissue constitute highly attractive trap baits. Potential exists for pheromone-based mass-trapping of weevils to reduce their populations and the spread of the weevil-vectored red ring disease, for monitoring their population dynamics to facilitate pest management decisions, and for detection and possible interception of non-native weevils at ports of entry.

Key Words: Aggregation pheromones, behavior, *Bursaphelenchus cocophilus*, chemical ecology, *Dynamis borassi*, kairomones, *Metamasius hemipterus*, nematode, *Paramasius distortus*, red ring nematode, *Rhabdoscelus obscurus*, *Rhynchophorus* spp.

RESUMEN

Los picudos de la palma pertenecientes a la familia Rhynchophorinae (Curculionidae) (*Rhynchophorus* spp., *Dynamis borassi*, *Metamasius hemipterus*, *Rhabdoscelus obscurus*, y *Paramasius distortus*) utilizan feromonas de agregación de los machos en la comunicación química intraespecífica. Las feromonas comprenden alcoholes secundarios con ramas de methyl de 8, 9 o 10 carbonos. (4*S*,5*S*)-4-Methyl-5-nonanol (ferrugineol) es la feromona de agregación principal para *R. ferrugineus*, *R. vulneratus*, *R. bilineatus*, *M. hemipterus* y *D. borassi* y un componente menor para *R. palmarum*. (5*S*,4*S*)-5-Methyl-4-octanol (cruentol), (3*S*,4*S*)-3-methyl-4-octanol (phoenicol) y (4*S*,2*E*)-6-Methyl-2-hepten-4-ol (rhynchophorol) son las feromonas de agregación principales para *R. cruentatus*, *R. phoenicis*, and *R. palmarum*, respectivamente. Las kairomonas vegetales incrementan fuertemente la atractividad de la feromona pero ninguno de los volátiles identificados, tales como acetato de etilo, propionato de etilo, o burtirato de etilo, son tan sinérgicos como el tejido de una planta (palma o caña de azúcar) en estado de fermentación. El estudio del comportamiento de la orientación de los picudos forrajeando hacia dispositivos semioquímicos ayudó a diseñar y probar trampas para la captura de los mismos. Generalmente, 3 mg por día de feromona sintética (con estereoisómeros no naturales) más tejido vegetal tratado con insecticida constituye un cebo muy atractivo. Existe el potencial para la captura masiva de picudos con feromonas para reducir sus poblaciones y contener la diseminación de la enfermedad que ellos transmiten, enfermedad del anillo rojo, así como para muestrear su dinámica de población y facilitar las decisiones de manejo de la plaga, y para la detección y posible intercepción de picudos no nativos en los puertos de entrada.

The observation that adults of *Rhynchophorus cruentatus* Fab. were attracted to nitrocellulose lacquer-based automobile paint in Sanford, FL (Bare 1929) led to research in the last few years on semiochemical-based communication of palm weevils in the subfamily Rhynchophorinae. Semiochemicals are defined as chemicals that act as signals between organisms (Dusenbery 1992). Aggregation or sex pheromones serve as intraspecific transitory signals, whereas kairomones, such as host-plant volatiles, act interspecifically with the receiver benefiting (Dusenbery 1992). As we now know, several possible components or contaminants of lacquer paints of the 1920s act

as semiochemicals for foraging *R. cruentatus*. For example, 5-methyl-4-octanol and ethyl acetate, both possible constituents of lacquer paint, function as aggregation pheromone and host kairomone, respectively, for *R. cruentatus* (Giblin-Davis et al. 1994b). Thus, the freshly painted automobiles standing outside Kent's garage during the summer of 1928 (Bare 1929), superficially resembling behemoth beetles in the sweltering heat and humidity, sent a clear "come hither" message to all palmetto weevils that could detect them and fly.

For the purpose of this paper, the discussion is limited to palm weevils in the subfamily Rhynchophorinae, including *Rhynchophorus* spp., *Dynamis borassi* Fab., *Metamasius hemipterus* L., *Rhabdoscelus obscurus* (Boisduval), and *Paramasius distortus* (Gemminger & Harold) (= *Metamasius inaequalis* [Gyllenhal 1838]). Palm weevils are defined here as weevils that use palms as a major host for larval development, even though they may colonize other monocots such as sugarcane and banana (Giblin-Davis et al. 1989, Napompeth et al. 1972, Peña et al. 1995, Vaurie 1966, Wattanapongsiri 1966). Other species of weevils that are associated with palms, such as the small pollinators of the African oil palm, *Elaeidobius* spp. (subfamily: Eriirrhinae) (O'Brien & Woodruff 1986), *Parisoschoenus* spp. (Baridinae) (O'Brien pers. comm.), *Homalinotus* spp. (Cholinae) (Vaurie 1973), and *Rhinostomus* spp. (Rhynchophorinae) (Vaurie 1970) will not be discussed.

BIOLOGY OF PALM WEEVILS

The basic life cycles of *Rhynchophorus* spp., *D. borassi*, *M. hemipterus*, *R. obscurus*, and *P. distortus* are similar. Adult female weevils are attracted to, and oviposit 30-400 eggs in, damaged (pruning or chain saw wounds), stressed, or healthy palms (Napompeth et al. 1972, Wattanapongsiri 1966, Weissling & Giblin-Davis 1994). Larvae bore into the palms and after several instars develop into adults in about 2 months (Giblin-Davis et al. 1989, Napompeth et al. 1972, Wattanapongsiri 1966). Larvae of *Rhynchophorus* spp., *D. borassi*, *M. hemipterus*, *R. obscurus*, and *P. distortus* appear to inhabit slightly different niches in palms, with *Rhynchophorus* spp. preferring the crown and/or stem (Wattanapongsiri 1966, Giblin-Davis & Howard 1989, Giblin-Davis et al. 1995b); *D. borassi* living tissue of coconut inflorescence and stem (Gerber et al. 1990, Wattanapongsiri 1966); and *M. hemipterus*, *R. obscurus*, and *P. distortus* petioles and stem periphery, sometimes entering the crown (Giblin-Davis et al. 1995b, R.M.G-D. & C.M.C., unpublished observation, Halfpapp & Story 1991). The last instar larvae of these weevils move to the petioles or to the rind of the stem to prepare a cocoon from coarse fibers and become a prepupa, pupa, and adult within several weeks (Wattanapongsiri 1966, Vaurie 1966). As borer damage from most of these species accumulates, fermentation volatiles increase rendering the host more apparent to adults of con- and heterospecifics.

Fermented sap exuding from dead or wounded palms (*Sabal palmetto* [Walter] and *Phoenix canariensis* Hortorum ex Chabaud) is highly attractive to *R. cruentatus* (Chittenden 1902). Attractiveness of chopped, fermenting, *S. palmetto* crown and stem tissue peaks 24-72 hours after cutting, whereas cut surfaces of felled palms remain attractive for 35 days (Weissling et al. 1992). Moist fermenting (stem) tissues from various palm species, fruits, sugarcane, pineapple, and molasses (plus water) are similarly attractive to palm weevils (Diegado & Moreno 1986, Giblin-Davis et al. 1994a,b, 1995a). Plant tissue [*Serrenoa repens* (Bartram) stem] or molasses with minimal moisture content are significantly less attractive to *R. cruentatus* and *M. hemipterus*, respectively (Giblin-Davis et al. 1994b, 1995a). Early fermentation volatiles of moist and stressed, damaged, or dying host plant tissues with high sugar content ob-

vously provide olfactory cues to attract palm weevils. *Dynamis borassi*, in contrast, usually prefers fresh tissue (R.M.G-D. unpublished observation).

WEEVIL-PRODUCED SEMIOCHEMICALS

Laboratory and field work with *R. obscurus* provided the first evidence that males of palm weevils produce male and female-attracting aggregation pheromones (Chang et al. 1971, Chang & Curtis 1972). Subsequently, male-produced aggregation pheromones have been demonstrated for many species in the subfamily Rhynchophorinae [i.e., *R. palmarum* (L.) (Moura et al. 1989, Rochat et al. 1991a), *R. cruentatus* (Weissling et al. 1993), *R. phoenicis* (Fab.) (Gries et al. 1993), *R. ferrugineus* (Olivier) and *R. vulneratus* (Panzer) (Hallett et al. 1993b), *M. hemipterus* (Giblin-Davis et al. 1994a, Rochat et al. 1993b), *Cosmopolites sordidus* Germar (Budenberg et al. 1993), *Sitophilus* spp. (Walgenbach et al. 1983)].

Successful elucidation of pheromones and host kairomones for palm weevils has required collaboration between field entomologists, chemists, and physiologists. For semiochemical identification, 10-50 male or female weevils with different mating, rearing and/or feeding status are placed in modified 9-liter Nalgene polycarbonate desiccators with a source of moisture (2 Petri dishes filled with 40 ml of deionized water and tissue paper each) or with plant tissue (e.g., 250 g of chopped palm stem or sugarcane). Charcoal prefiltered air is drawn (1.5 cm³ per min) for 5-7 days through the desiccator and downstream through a glass tube filled with an adsorbent matrix (Porapak Q). Volatile chemicals are eluted from the Porapak Q with redistilled pentane, concentrated by distillation (Oehlschlager et al. 1988,1992) and subjected to gas chromatographic (GC) analyses [Hewlett Packard (HP) 5885B gas chromatograph] employing both flame ionization (FID) and electroantennographic detection (EAD) (Arn et al. 1975). A variety of GC-columns and GC-temperature programs are used for separation of semiochemicals (Perez et al. 1994). In GC-EAD recordings, volatiles eliciting responses by male or female weevil antennae are analyzed by GC-mass spectrometry (GC-MS) in both electron impact (EI; 70 eV) and chemical ionization (CI) modes [HP 5985B GC-mass spectrometer (MS) equipped with the same column as used in GC-EAD recordings]. If required, Kratos MS80RFA high resolution MS and/or nuclear magnetic resonance (NMR) spectroscopy is used to elucidate chemical structure(s).

Enantioselective pheromone production and response are common in the Coleoptera and help fine-tune intra- and interspecific semiochemical communication (Seybold 1993). Because non-weevil-produced stereoisomers in synthetic pheromones may cause interruption in response (Seybold 1993), enantiomer(s) and/or stereoisomers of the weevil-produced pheromone are determined on a chiral, isomer separating column (Perez et al. 1994). Weevil-produced and EAD-active isomers in synthetic stereoisomeric mixtures are stereoselectively synthesized and tested for behavioral activity in field experiments (Gries et al. 1993, Oehlschlager et al. 1992, 1995b, Perez et al. 1994, 1995a,b). Methods of synthesis depend upon the chemical structure of the semiochemical (Gries et al. 1993, Mori et al. 1993a,b, Oehlschlager et al. 1992, 1995b, Perez et al. 1994, 1995a, Rochat et al. 1991b, Weissling et al. 1994b).

Major and minor male-produced aggregation pheromones for palm weevils (Table 1) are 8, 9, or 10 carbon, methyl-branched, secondary alcohols. Only the pheromone for *R. palmarum*, (2*E*)-6-methyl-2-hepten-4-ol, is unsaturated. Typically, the (*S*)-enantiomer or (*S,S*) stereoisomer is produced by the weevils and elicits a behavioral response [(*R. palmarum*, Oehlschlager et al., 1992) (*R. bilineatus* (Montrouzier) (Oehlschlager et al. 1995b), *R. cruentatus* and *R. phoenicis* (Perez et al. 1994, Rochat et al. 1995), *R. ferrugineus* and *R. vulneratus* (Perez et al. 1995b), and *M. hemipterus*

(Perez et al. 1995a)]. Synergistic behavioral activity of (4*S*), (4*R*), or (±) 2-methyl-4-heptanol in *M. hemipterus* constitutes the only exception to this general rule (Perez et al. 1995a). Non-natural occurring (non-weevil-produced) stereoisomers in synthetic pheromones are behaviorally benign (non-interruptive) thus allowing application of racemic blends for operational use.

Lethal traps baited only with aggregation pheromones or host kairomones are not very attractive to palm weevils, but in combination synergize attractiveness 8-20 fold [*R. palmarum* (Oehlschlager et al. 1992), *R. phoenicis* (Gries et al. 1993, Perez et al. 1994, Roach et al. 1995), *R. vulneratus* and *R. ferrugineus* (Hallett et al. 1993a,b) *R. bilineatus* (Oehlschlager et al. 1995b), *R. cruentatus* (Giblin-Davis et al. 1994b, Weissling et al. 1993, 1994b, Perez et al. 1994), and *M. hemipterus* (Giblin-Davis et al. 1995a, Perez et al. 1995a)]. These weevils appear to be opportunistic oligophages, responding to early fermentation volatiles from wounded or stressed hosts and recruiting conspecifics over long distances with male-produced aggregation pheromones (Jaffé et al. 1993, Weissling et al. 1994b).

Ferrugineol [(4*S*,5*S*)-4-methyl-5-nonanol] is the major aggregation pheromone for Asian *R. ferrugineus*, *R. vulneratus*, and *R. bilineatus* and for the neotropical *M. hemipterus* and *D. borassi* (Oehlschlager et al. 1995b, Perez et al. 1995a,b) and a possible minor component for *R. palmarum* (Hallett et al. 1993a). Other members of the Rhynchophorinae, i.e. *Sitophilus* spp., use the same stereoisomer of their major male-produced aggregation pheromone (Walgenbach et al. 1987). Identical male-produced aggregation pheromones have also been reported for geographically isolated African and Asian rhinoceros beetles (*Oryctes* spp.; Scarabaeidae) (Gries et al. 1994b, Hallett et al. 1995).

Production of, and response to, ferrugineol which is present in many of the palm weevils may be pleisomorphic, whereas other pheromones such as (5*S*,4*S*)-5-methyl-4-octanol (cruentol; *R. cruentatus*), (3*S*,4*S*)-3-methyl-4-octanol (phoenicol; *R. phoenicis*), and (4*S*,2*E*)-6-methyl-4-hepten-2-ol (rhynchophorol; *R. palmarum*) may represent a more derived (apomorphic) character. Alternatively, *M. hemipterus* may represent a more primitive form because males produce a larger number of alcohols and corresponding ketones (Table 1) than most *Rhynchophorus* species which typically produce one or two male produced volatiles. The premise that *R. palmarum* might have speciated from Asian weevils (Griffith 1987, Oehlschlager et al. 1995b) with the movement of coconut, *Cocos nucifera* L., from Melanesia to the Neotropics is not tenable because of the recency (< 1000 years ago) of coconut introduction by man, and the fact that *Rhynchophorus* species do not appear to have greatly expanded their ranges until very recently (Wattanapongsiri 1966). Fossil evidence suggests that there was a diverse and widespread palm flora during the early to mid-Cretaceous at about the time when Laurasia and Gondwanaland separated (Uhl & Dransfield 1987). Early protopalm weevils might have been associated with early palms (Thrinacinae-like). Radiation of different palm groups and their associated protopalm weevils might have begun prior to the separation of Laurasia and Gondwanaland. Continued continental drift may have prevented gene flow between African, North and South American, and Asian palm weevils resulting in the contemporary pattern of reproductive behavior and aggregation pheromones. Knowledge about pheromone biosyntheses and dissemination for palm weevils will be important for testing evolutionary hypotheses.

The role of minor EAD-active, male-produced volatiles in palm weevils is not well understood. High doses of the four ketones in males of *M. hemipterus* (Giblin-Davis et al. 1994a, Perez et al. 1995) reduce attractiveness of the main pheromone. In contrast, low doses of (±) 2-methyl-4-heptanol in *M. hemipterus* (Perez et al. 1995a), slightly enhance pheromonal attractiveness. 3-Pentanol and 2-methyl-4-octanol in *M. hemi-*

TABLE 1. AGGREGATION PHEROMONES (AP)¹ AND MINOR COMPONENTS IDENTIFIED FROM AERATIONS OF MALES OF PALM-ASSOCIATED WEEVILS.

Genus:	<i>Rhynchophorus</i>			<i>Dynamis</i>	<i>Metamasius</i>	<i>Paramasius</i>
	<i>bilineatus</i>	<i>cruentatus</i>	<i>palmarum</i>			
Species:	New Guinea	N. America	Asia	Asia	Neotropics	Neotropics
Distribution:						
3-pentanol						Minor ⁶
3-pentanone						Minor ⁶
(4 <i>S</i> ,2 <i>E</i>)-6-methyl-2-hepten-4-ol			AP ^{8,10}			
(±)-2-methyl-4-heptanol						Minor ^{6,12}
2-methyl-4-heptanone						Minor ⁶
2,3-epoxy-6-methyl-4-heptanol			Minor ^{8,11,12}			
2-methyl-4-octanol						Minor ^{6,12}
2-methyl-4-octanone						Minor ⁶
(3 <i>S</i> ,4 <i>S</i>)-3-methyl-4-octanol				AP ^{1,3,5,12,13}	Minor ^{12*}	
(5 <i>S</i> ,4 <i>S</i>)-5-methyl-4-octanol		AP ^{5,14}				
5-nonanol						Minor ¹²
(4 <i>S</i> ,5 <i>S</i>)-4-methyl-5-nonanol	AP ⁹	AP ^{2,7}	Minor ^{2*}	AP ^{4,7,12}	AP ⁶	AP ^{4,5,12}
4-methyl-5-nonanone		Minor ^{2,7}		Minor ^{2,7}		Minor ⁶

¹AP = main aggregation pheromone, Minor = minor component with unknown or small effect on weevil behavior. Citations for chemical and behavioral elucidation are in superscript; 1) Gries et al. 1993, 2) Hallett et al. 1993a, 3) Mori et al. 1993a, 4) Mori et al. 1993b, 5) Mori et al. 1994, 6) Perez et al. 1995a, 7) Perez et al. 1995b, 8) Oehlschlager et al. 1992, 9) Oehlschlager et al. 1995b, 10) Rochat et al. 1991, 11) Rochat et al. 1993a, 12) Rochat et al. 1993b, 13) Rochat et al. 1995, and 14) Weissling et al. 1994b.

*Active stereoisomers not determined.

pterus (Perez et al. 1994) and 2,3-epoxy-6-methyl-4-heptanol (Rochat et al. 1993a) and 4-methyl-5-nonanol in *R. palmarum* (Hallett et al. 1993a) are behaviorally benign. Aeration of many confined weevils for long periods may have induced atypical production of compounds or distorted ratios thereof. For example, 24-hour aerations of 5-12 *M. hemipterus* (subspecies *M. h. hemipterus*?) from Guadeloupe revealed 5 male-specific compounds (Rochat et al. 1993b), whereas 96 hour aerations of 38 males of *M. h. sericeus* from Florida disclosed 8 male-specific volatiles (Table 1) (Perez et al. 1995a). The question remains whether these chemical differences represent divergence in the chemical ecology of the two subspecies or artifacts from different methodology.

Capture of neotropical palm weevils in lethal traps baited with aggregation pheromones of heterospecifics suggests synomonal pheromone activity. For example, *D. borassi*, *M. hemipterus*, and *P. distortus* are attracted to the aggregation pheromone of *R. palmarum* (Chinchilla et al. unpublished data, Giblin-Davis et al. unpublished data) and *P. distortus* also responds to the aggregation pheromone of *M. hemipterus* (Chinchilla et al. unpublished data). Cross-attraction of sympatric weevils may have evolved because of its adaptive significance in overcoming a palm's defense and time-efficient use of a temporarily suitable resource. Minor volatile components may serve as intra- or interspecific semiochemicals mediating resource partitioning. Niche divergence and larval cannibalism in *R. palmarum*, *M. hemipterus*, *D. borassi*, and *P. distortus* may reduce interspecific competition in an occupied host. Further work with pheromone combinations in palm weevils, such as has been done for *Carpophilus* species (Bartelt et al. 1995), could simplify the use of pheromones for monitoring or mass-trapping palm weevils in the Neotropics.

In dose response trapping experiments, 3-7 mg per d of synthetic pheromone cost-effectively attracts palm weevils (Gries et al. 1994a, Hallett et al. 1993b, Oehlschlager et al. 1992, 1993b, Weissling et al. 1994b). In the presence of plant tissue, 0.3, 20, or 200 mg per d of (\pm)-rhynchophorol (Oehlschlager et al. 1993b), 0.3, 1, or 3 mg per d of (\pm)-ferrugineol (Hallett et al. 1993b), 0.4 or 4 mg per d of (\pm)-cruentol (Weissling et al. 1994b) equally attract their respective weevils. Release rates of 3-4 mg per d rather than 0.3-0.4 mg per d of pheromone effectively attract *R. phoenicis*, *R. ferrugineus*, and *R. bilineatus* (Gries et al. 1993, Hallett et al. 1993b, Oehlschlager et al. 1995b). Release rates exceeding 3 mg per d of (\pm)-ferrugineol reduced attraction of *R. bilineatus* (Oehlschlager et al. 1995b). Ten-fold increase in the binary pheromone blend of (\pm)-4-methyl-5-nonanol and (\pm)-2-methyl-4-heptanol (8:1 ratio; "metalure"; 30 mg per d) plus sugarcane only doubled trap captures of *M. hemipterus* in Costa Rica (Oehlschlager et al. unpublished data), thus not justifying the increased lure costs. For experimental and commercial use, racemic pheromone (about 90 mg total) with an indicator dye is hermetically sealed in a polymer membrane release device (ChemTica International, San Jose, Costa Rica) for slow and constant pheromone dissemination [about 3 or 7 mg per d at 25°C for 2-3 months (Oehlschlager et al. 1995a,b)].

Some of the palm weevils seem to respond to cuticle-bound courtship pheromones of conspecific females (Rochat & Zagatti 1993). Male *R. palmarum* exhibit precopulatory behavior (a jerky swinging motion of the body) after antennating dead females but not dead male decoys or decoys that had been washed with hexane (Rochat & Zagatti 1993). As part of their precopulatory behavior, male *R. cruentatus* antennate the pronotum of live conspecifics and mount males and females with equal aplomb (Weissling unpublished observation). Cuticular lipids in hexane or methylene chloride extracts of *R. cruentatus* adults lack sex-specific differences when analyzed by GC-MS or thin layer chromatography (Giblin-Davis et al. unpublished data). Interspecific mating pairs of *R. ferrugineus* and *R. vulneratus* suggest that these weevils have similar or identical precopulatory behavior, rely on postzygotic reproductive isolating mechanisms, or are conspecifics (Hallett et al. 1993b).

HOST KAIROMONES

Early research provided evidence that general fermentation volatiles, such as ethanol, appeared attractive to *Rhynchophorus* weevils (Gunatilake & Gunawardena 1986, Hagley 1965). The recent discovery of aggregation pheromones which greatly enhance attractiveness of plant tissues facilitated identification of individual palm kairomones (Giblin-Davis et al. 1994b, 1995a, Gries et al. 1994a, Jaffé et al. 1993, Perez et al. 1995a).

Kairomones identified by GC-EAD and GC-MS include the "palm esters" ethyl acetate, ethyl propionate, ethyl butyrate, and ethyl isobutyrate for *R. phoenicis*, *R. cruentatus*, *R. palmarum*, *R. bilineatus*, *R. ferrugineus*, and *R. vulneratus* (Gries et al. 1994a). Ethyl propionate (30 mg per d) was the only "palm ester" tested that synergized attraction of *R. phoenicis* to (\pm)-phoenicol (Gries et al. 1994a). Ethyl acetate, ethyl propionate, ethyl butyrate, ethyl isobutyrate, ethyl (*S*)-(-)-lactate, and ethanol at various release rates synergized attraction of *R. cruentatus* to (\pm)-cruentol (Giblin-Davis et al. 1994b, Giblin-Davis, unpublished), and ethyl acetate of unknown release rate enhanced attraction of *R. palmarum* to (\pm)-rhynchophorol (Jaffé et al. 1993). Each of the fermenting sugarcane volatiles, ethyl acetate (30 mg per d), ethyl propionate (20 mg per d), and ethyl butyrate (20 mg per d) equally enhanced attraction of *M. hemipterus* to metalure (Perez et al. 1995a). None of the "palm esters" tested to date with pheromone has been as effective as palm or sugarcane tissue in enhancing pheromonal attractiveness (Giblin-Davis et al. 1994b, 1995a, Gries et al. 1994a, Jaffé et al. 1993, Perez et al. 1995a), suggesting additional as yet unknown palm kairomones or improper ratios of tested components. Peak field attraction of chopped palm or sugarcane tissue within 2 to 5 days indicates proportional changes in volatile chemicals from fermentation over time, affecting optimal attraction of weevils to traps (Gries et al. 1993, Hallett et al. 1993a, Weissling et al. 1992). Proportional changes in volatile chemicals from fermenting or fermented palm sap can be attributed to the abiotic conditions and microflora present (Nagnan et al. 1992, Samara-jeewa et al. 1981).

Ethyl acetate released at 400-900 mg per d significantly enhanced attraction of *M. hemipterus* to metalure, sugarcane, or both (Giblin-Davis et al. 1995a). Because ethyl acetate at 400-1600 mg per d is not repellent to *R. cruentatus* or *M. hemipterus* (Giblin-Davis et al. 1994b, 1995a), it may be used to increase the "active space" of a trap, improve short range orientation towards, or arrest weevils near traps. Ethyl acetate release rates of 400-1600 mg per d may seem high, but may be competitive with levels produced by large damaged palms (Giblin-Davis et al. 1995a). Ethyl acetate perceived by male *R. palmarum* also stimulates pheromone production (Jaffé et al. 1993). If true for *M. hemipterus* or other palm weevils, high rather than low relative release of ethyl acetate from traps should induce pheromone production by nearby weevils.

Sugarcane is one of the cheapest and best sources of kairomones to enhance attraction of palm weevils to pheromone-baited traps. Other tissues such as pineapple, *S. palmetto*, or molasses plus water were equally synergistic in trapping trials with *R. cruentatus* and *M. hemipterus* (Giblin-Davis et al. 1994a,b, 1995a). African oil palm stem cubes, molasses on a sponge, or molasses-impregnated mesocarp were not as effective as sugarcane for *R. palmarum* (Oehlschlager et al. 1993b). Increasing quantities of sugarcane or host tissue generally increase attractiveness of the pheromone-baited trap (Giblin-Davis et al. 1994a, 1995a, Oehlschlager et al. 1993a,b), but optimal quantities should be based on a cost-benefit analysis.

Endemic *R. cruentatus*, together with the recently introduced *M. hemipterus* are more effective in attacking and colonizing the introduced *P. canariensis* palm in Florida than either weevil by itself (Giblin-Davis et al. unpublished observation). Feeding

by *M. hemipterus* in the petioles causes intense kairomone production, attracting the crown-dwelling *R. cruentatus* which kills the tree. Palm weevils may mutually benefit by "cross-responding" to kairomones of their hosts. *Rhynchophorus* spp., *M. hemipterus*, *R. obscurus*, and *P. distortus* appear to respond to identical or similar host kairomones (Chang & Curtis 1972, Giblin-Davis et al. 1994a,b, Gries et al. 1994a, Hallett et al. 1993b). *Dynamis borassi*, in contrast, may occupy a more specific "feeding" niche (coconut palm inflorescences), and may respond to host kairomones different than those of other palm weevils (Gerber et al. 1990, Giblin-Davis unpublished observation, Wattanapongsiri 1966).

Palms appear to have defenses that must be overcome by weevils or weevil-associated organisms such as the red ring nematode, *Bursaphelenchus cocophilus*. Stressed, unlike healthy *S. palmetto* palms, become infested with larval progeny when bagged with *R. cruentatus* adults (Giblin-Davis & Howard 1989). Even healthy *P. canariensis* palm, in contrast, is a susceptible and suitable host for *R. cruentatus* (Giblin-Davis et al. 1995b), suggesting that there are differential physical and/or chemical defenses conveying host suitability and susceptibility (Giblin-Davis et al. unpublished data, Schuiling & Dinther 1981).

Association of *R. palmarum* (Gerber & Giblin-Davis 1990, Giblin-Davis 1993), *D. borassi* (Gerber et al. 1990), and *M. hemipterus* (Toquica 1993) in the Neotropics with the red ring nematode may affect the population dynamics of the weevils. Deposition of nematodes into wounds of healthy palms can cause a lethal wilt (red ring disease; RRD) within 2-4 months (Giblin-Davis 1993). Palms dying from RRD, in turn, produce kairomones that attract palm weevils. Thus, red ring nematode is a lethal agent that increases the potential number of hosts for palm weevils. Their cross-attraction to host kairomones and aggregation pheromones increases the probability of associating with and vectoring the dispersal stage of the nematode. *Rhynchophorus* spp. and *M. hemipterus* are also associated with, or even rely on, other microorganisms in dead or dying hosts (Giblin-Davis et al. 1989, Griffith 1987). Diets lacking debittered yeast, e.g., are not suitable for rearing *R. cruentatus* (Weissling & Giblin-Davis 1995). In addition, various potential fungal and bacterial plant and weevil pathogens may contaminate and affect behavior and population dynamics of palm weevils (Griffith 1987).

BEHAVIOR AND A "BETTER MOUSE TRAP"

The abundance of adult palm weevils is affected by seasonal changes. *R. palmarum* populations appear to peak at the end of the rainy season and throughout most of the dry season in coconut plantations in Trinidad (Hagley 1963), and in the dry season in oil palm plantations in Brazil (Schuiling & Dinther 1981), Costa Rica (Morales & Chinchilla 1990), and Honduras (Chinchilla et al. 1990). In Florida, *R. cruentatus* (Weissling et al. 1994a) and *M. hemipterus* (Peña et al. 1995) are more abundant in spring, before the onset of the rainy season. *Rhynchophorus palmarum* (Rochat 1987) and *M. hemipterus* (Giblin-Davis et al. unpublished observation) have crepuscular flight patterns. Flight of *R. cruentatus* in the laboratory was not correlated with time of day and feeding status but increased with increasing temperature and decreasing relative humidity (Weissling et al. 1994a).

Rhynchophorus spp. seek harborage in leaf axils of healthy palms (Weissling & Giblin-Davis 1993) and moist fermenting garbage (Chittenden 1902). Cryptic behavior of *R. cruentatus* may help to conserve water because this weevil has high cuticular permeability which causes desiccation in dry environments (Weissling & Giblin-Davis 1993). In a bioassay with choices between low and high relative humidity environments, *R. cruentatus* preferred high relative humidity, suggesting that this weevil possesses hygroreceptors to locate moist harborage sites (Weissling & Giblin-Davis

1993). High relative humidity in semiochemical-baited traps can be provided by use of soapy water or by pesticide-treated sugarcane or palm, or wet sponges or towels.

Different trap designs have been tested to optimize capture of palm weevils (Giblin-Davis et al. 1994a,b, 1995a, Oehlschlager et al. 1992, 1993a,b, Weissling et al. 1992, 1993). Large bucket traps with good surface area placed on the ground or attached to palm trunks are available (Oehlschlager et al. 1993b). Captured weevils are killed with pesticide-treated (i.e., carbaryl, carbofuran, lannate) sugarcane (Oehlschlager et al. 1993a) or with soapy water in the bottom of traps (Weissling et al. 1994b). *Rhynchophorus* species usually fly into the vicinity of a trap to land on leaves, the tree trunk, or ground and then walk into the trap (Oehlschlager et al. 1993b). The proportionally smaller *M. hemipterus* is agile in flight and, unlike large species of *Rhynchophorus*, may not require a large landing surface or trap placement on the ground (Giblin-Davis et al. 1995a). A lethal pitfall trap (Giblin-Davis et al. 1994a) appears to work best for *P. distortus* (Chinchilla et al. unpublished data), suggesting that these weevils may occupy pruned or fallen leaves or petioles at the base of the stem at or below the soil surface.

In trap height studies with *R. palmarum* (Oehlschlager et al. 1993a,b) and *M. hemipterus* (Giblin-Davis et al. 1995a), traps associated with possible landing areas were superior. Traps on the ground, e.g., captured more *R. palmarum* than those pole-suspended 1.7 or 3.3 m above ground. In contrast, traps attached to palm trunks at 0, 1.7, and 3.3 m heights were equally effective (Oehlschlager et al. 1993a,b). Unlike *R. palmarum*, *M. hemipterus* was captured equally well in ground traps and pole-suspended traps (1 m) (Giblin-Davis et al. 1995a). Open "ground" traps can be problematic in areas where raccoons (*Procyon* sp.) occur and eat captured weevils (Giblin-Davis et al. 1995a).

Trap silhouette and color as potential visual cues for foraging palm weevils have not yet been intensively studied. In field tests using sugarcane and synthetic pheromone as trap bait, all trap colors tested equally attracted *M. hemipterus* to ground-mounted bucket traps (Giblin-Davis et al. 1995a) and *R. palmarum* to tree-mounted bucket traps (Oehlschlager et al. 1993b). These data suggest that color in the human-perceived spectrum is not a critical parameter for an optimal trap design.

APPLIED CHEMICAL AND BEHAVIORAL ECOLOGY

Semiochemical-based mass trapping of beetles may offer a viable pest management alternative (Borden 1993, Hardee 1982). *Rhynchophorus* weevils are suitable for mass trapping because of their long life cycle and adult longevity, low fecundity, and reliance on aggregation pheromones and host kairomones.

The viability of semiochemical-based mass trapping for management of palm weevils has been evaluated in a commercial African oil palm (*Elaeis guineensis*) plantation in Costa Rica infested with *R. palmarum* and red ring nematode (Chinchilla et al. 1993, Oehlschlager et al. 1995a). Continuous mass trapping over 17 months at densities of about 6 traps per ha, together with good phytosanitation practices, reduced *R. palmarum* trap counts over time and lowered RRD incidence (Chinchilla et al. 1993, Oehlschlager et al. 1995a). At mass trapping onset, most *R. palmarum* were captured in "border" traps of the test site, suggesting removal of potential immigrants into the study area (Oehlschlager et al. 1995a). A combination of perimeter and "internal" traps is most effective for mass trapping (Chinchilla et al. 1993). More than 62,500 weevils (about 94 weevils per ha per month) were captured during the study, with RRD incidence decreasing by a factor of > 2 (Oehlschlager et al. 1995a).

Success of semiochemical-based *R. palmarum* management in Costa Rica is based on: 1) autocratic control over a large *R. palmarum*-infested area (> 100 ha), 2) monoculture of African oil palm that is not as suitable and susceptible for *R. palmarum* and

red ring nematode as is coconut palm, and 3) implementation of mass trapping in concert with intense phytosanitation (aggressive removal of any palm with early symptoms of RRD, little leaf, or palm weevil damage). The same criteria are applicable for *R. ferrugineus* in date palm, *P. dactylifera*, in the United Arab Emirates (Hallett et al. 1993b), *R. cruentatus* in *P. canariensis* in Florida (Giblin-Davis et al. 1994a), and *R. phoenicis* in African oil palm in Africa (Gries et al. 1993), except that RRD does not occur in these locations.

In the Neotropics, small (<5 ha) coconut palm plantings may be less suitable for mass trapping of *R. palmarum* and reduction of RRD incidence. Coconut is more suitable and susceptible to *R. palmarum* and red ring nematode than is African oil palm. Moreover, small farm holders may not be able to purchase the pheromones for mass trapping and are not easily organized to consistently rogue trees at the onset of RRD symptoms.

More research is needed to demonstrate the potential of semiochemical-based mass trapping for other palm weevils. Semiochemical-based monitoring can already be implemented to track population dynamics of palm weevils and to facilitate pest management decisions (Giblin-Davis et al. 1995B). In ports of entry, pheromone-baited survey traps may help to detect and possibly intercept introduction of foreign weevils.

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