

Pheromones as management tools for non-Scolytinae Curculionidae: development and implementation considerations

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Abstract

For the large family Curculionidae, the number of species considered pests is expected to increase due to global movement of plant and soil material, as well as climate change. Pheromones are increasingly popular for use in pest management programmes, either as stand-alone tactics or with other management tactics. Biological differences between Curculionidae species often require species-specific optimization of methodologies to successfully collect, identify and integrate pheromones into management programmes. This review aims to provide an overview of current knowledge on non-Scolytinae Curculionidae pheromones and their use in strategies to manage these insects where they are pests. Throughout, we highlight the importance of understanding the chemical ecology of target pests and related species to direct pheromone sampling and the development of pheromone-based management tactics.

Keywords: chemical ecology, Integrated Pest Management, pheromone-baited trap, pheromone development, weevil pheromone

Introduction

Species in the family Curculionidae are phytophagous as adults or larvae or both. Their feeding on plants, predominately fruits, inner phloem and roots, can result in economic damage (Tewari et al. 2014; Garnas et al. 2016). Species that attack woody plants include South African pests like *Gonipterus* sp. 2 (Schröder et al. 2019), *Rhynchophorus phoenicis* (Prinsloo and Uys 2015), *Phlyctinus callosus* (Barnes and Capatos 1989; Bredenhand et al. 2010) and *Pissodes nemorensis* (Gebeyehu and Wingfield 2003; Wondafrash et al. 2018). Integrated Pest Management (IPM) programmes for weevils, and insects in general, often incorporate or rely exclusively on behaviour-modifying semiochemicals (Pickett et al. 1997). These programmes often target pheromone communication because the high level of specificity minimizes non-target impacts (Nadel et al. 2012; Larsson 2016). Successful implementation of such pheromone-based management tactics, however, relies on a thorough understanding of the biology and chemical ecology of target pests. We exclude the Scolytinae subfamily (bark beetles), as their biology and pheromone functionality forms part of a specialized group which have been reviewed elsewhere (Wood 1982; Gitau et al. 2013). We included species in the subfamily Dryophthorinae that have recently been elevated to the family level, Dryophthoridae, in some (Dosunmu et al. 2014; Köhler et al. 2020; Malo et al. 2020), but not all literature (Hazzouri et al. 2020).

The first pheromone from species of non-Scolytinae Curculionidae was isolated and identified for the boll weevil, *Anthonomus grandis* Boheman, a serious pest of cotton in the USA (Tumlinson et al. 1969). The isolation process required solvent extraction and distillation of 54.7 kg of frass obtained from 4.5 million weevils of mixed sex. The discovery of the boll weevil pheromone stimulated studies into the pheromones of many other economically important species in the Curculionidae family (Hardie and Minks 1999; Ambrogi et al. 2009; Tewari et al. 2014). To date, pheromones have been identified from 45 species of non-Scolytinae Curculionidae and some of these pheromones are being used in management programmes. However, successful elucidation of new effective pheromone formulations for species where pheromone blends are unknown, remains a major challenge.

Studies of non-Scolytinae Curculionidae beetle pheromones are usually initiated in response to economic loss (Szmedra et al. 1991; Palacio-Cortés et al. 2015; Drmić et al. 2017). For example, the boll weevil caused severe crop damage for years in the USA, despite considerable effort to control population levels including the application of systemic insecticides that were subsequently banned (Szmedra et al. 1991; Haney et al. 2009). Tumlinson et al. (1969) identified the boll weevil pheromone and a pheromone trapping and monitoring system was subsequently developed (Hardee et al. 1974; Hedin et al. 1979). An IPM programme with systemic and conventional insecticides combined with pheromone-based trapping was implemented during 1987-1990 in Georgia (Haney et al. 2009). In short, insecticides were used to kill most of the boll weevil population in one season, and surviving weevils in diapause were captured with a single pheromone trap per acre in the following season. The effect of this programme was quickly evident as yield increased from \$482 per acre (average between 1971-1986) to \$733 per acre (average between 1991-1995) and acreage increased from 228 000 to 770 000. In addition, the number of costly insecticide applications could be reduced by 60% (Szmedra et al. 1991; Haney et al. 2009). Reduction of insecticide applications also resulted in resumed biological control of other pests (Haney et al. 2009). Even though the current dominant control strategy of the boll weevil is the use of transgenic cotton (Ribeiro et al. 2017), existing boll weevil pheromone-based applications include lure-and-kill, mass-trapping and monitoring which continues to inform decisions on insecticide application (Hardee et al. 1974; Hedin et al. 1979; Ambrogi et al. 2009; Haney et al. 2009).

Pheromones identified from species in the non-Scolytinae Curculionidae that are used in pest management have been primarily identified from adults (Ambrogi et al. 2009; Tewari et al. 2014). Male-produced pheromones are generally aggregation pheromones (Ambrogi et al. 2009; Tewari et al. 2014), whereas female-produced pheromones are usually short-range sex pheromones (Heath et al. 1986; Ravi and Palaniswami 2002; Cork and Lobos 2003). Non-volatile contact pheromones have also been identified from both adults and larvae (Mody et al. 1975; Mutis et al. 2009). There have been few studies of larval pheromones, most likely because of their limited application in pest management.

In the light of the expected increase of Curculionidae pests worldwide (Wingfield et al. 2008), the need for fast development of pest management tools is higher than ever. Here we review the literature on weevil pheromones and identify several lessons learned. Our hope is that this will facilitate future weevil pheromone identifications. We also review the methods used for pheromone identification and consider reasons that may explain why these procedures

were successful. Finally, a concise overview of successfully implemented IPM strategies is provided.

Weevils are important pests globally

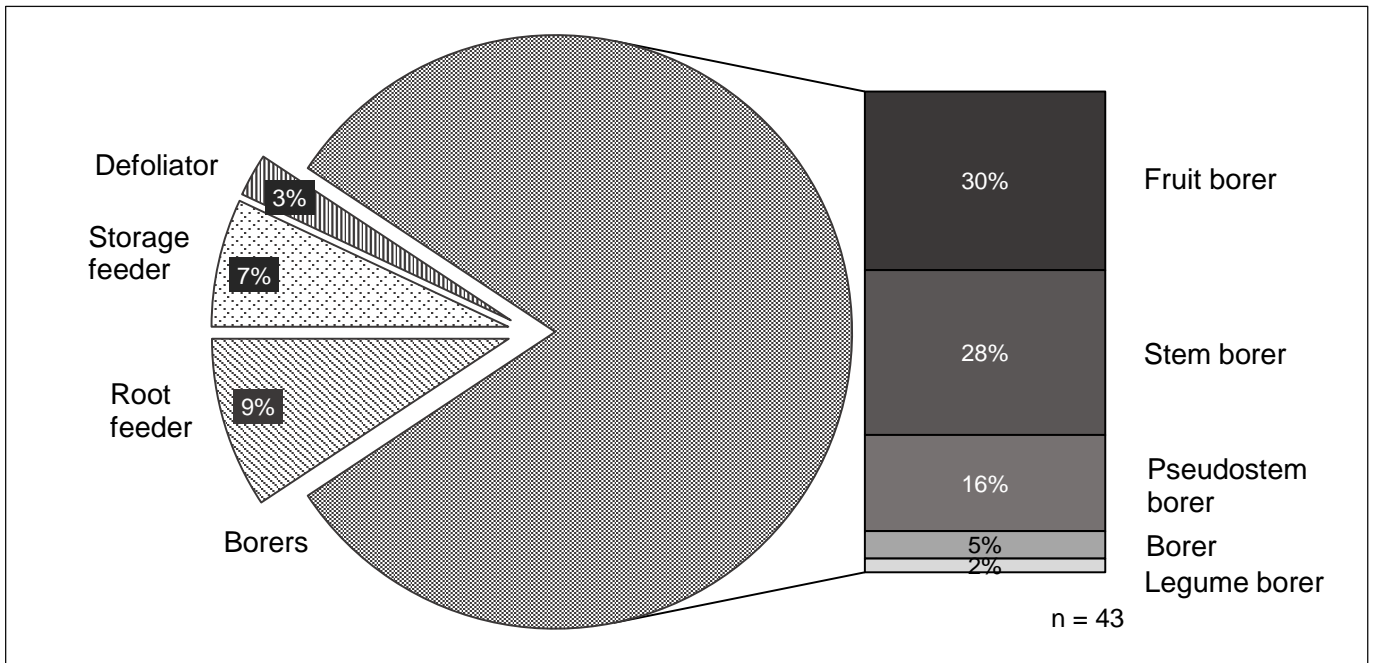
An extensive range of commodities suffer economic loss due to damage caused by non-Scolytinae Curculionidae including orchard crops, forestry and grain and stored products (Supplementary Table 1). The way in which weevils cause damage varies among species. For example, adults may damage hosts directly by feeding on phloem or bark (i.e. *Pissodes* spp.) (Booth et al. 1983), plant roots (i.e. *Sphenophorus* spp.) or foliage (i.e. *Gonipterus* spp.) (Lapointe et al. 2012). Direct damage caused by different life stages of the same species may also vary. For example, adult weevils may defoliate while larvae feed on roots (i.e. *Phlyctinus sulcatus*) (Kamiya et al. 2015; Bredenhand et al. 2010) or other internal parts of the same host (Zarbin et al. 2003; Silva et al. 2018).

Indirect damage may also occur due to weevils that vector important plant pathogens (Supplementary Table 1). These include palm weevils which vector the nematode, *Bursaphelenchus cocophilis* Cobb., which causes red ring disease in palm trees (Giblin-Davis et al. 1997; Alpizar et al. 2002; Oehlschlager et al. 2002) and palm weevils which vector the fungus, *Fusarium circinatum*, the causal agent of pitch canker disease (Gebeheyu and Wingfield 2003). Agave weevils vector a gram positive bacterium, *Pseudomonas fluorescens*, that causes petrification of the agave plant (Ruiz-Montiel et al. 2003, 2008), and citrus root weevil larvae create galleries which increases host susceptibility to *Phytophthora* infections (Graham et al. 1996). In these scenarios it is more cost-effective to control the weevil vectors with the objective of preventing, rather than controlling, the diseases that they transfer to their hosts.

More than three-quarters of the weevils for which pheromones have been described are borers (35 out of 43 species). As a group the borers are diverse and include fruit-borers (13 out of 43 species), stem-borers (12 out of 43 species), pseudostem-borers (7 out of 43 species), two ‘borers’, and one legume-borer species. Pheromones are also known for one defoliator species, stored products weevils (n = 3) and root-feeders (n = 4) (Figure 1, Supplementary Table 1).

Weevil biology: impact on identification and implementation of pheromones into IPM programmes

The process of identifying pheromones and implementing them in weevil management programmes is complex and requires a good understanding of the biology and chemical



•Figure 1: The types of host damage caused by non-Scolytinae Curculionidae for which pheromones have been described (n = 43, Supplementary Table 1). Borers represent 81% of all the species with known pheromone, and are subdivided into groups including fruit-, stem-, pseudostem and legume borers and a catch-all term of 'borers' for weevils that feed on miscellaneous host tissues.

ecology of the target species. In general, the life cycle of most Curculionidae involves female oviposition on the host plant or in the soil. Eggs then develop into larvae and these larvae go through a number of instars before they are ready to pupate. Pupation occurs either in or on the host, or in the soil. In some species, adult weevils have a maturation feeding period before mating (Ruiz-Montiel et al. 2009) and in others this does not occur (Giblin-Davis et al. 2000; Kamiya et al. 2015).

Variations of the life cycle exist (Supplementary Table 2). For example, the time required for larval development can range from as little as five months for the citrus root weevil, *Diaprepes abbreviatus* Linnaeus (Wolcott 1936), to up to five years for the large pine weevil, *Hylobius abietis* Linnaeus (Langstrom 1982). The number of larval instars may also differ between species. For example, the *Eucalyptus* snout beetle, *Gonipterus* sp. complex has four larval instars (Tooke 1953), while the citrus root weevil has sixteen (Wolcott 1936).

Developmental time of different life stages varies among species and this impacts how control measures should be implemented (Supplementary Table 2). For instance, the larvae of the pecan weevil may enter a diapause period that lasts up to two years before they develop into pupae (Teddars and Wood 1994). Adults of this species often emerge synchronously and, within a relatively short time frame of four to six days, mate and lay eggs (Hall 2018). This results in huge larval populations approximately one month later when eggs hatch. Control measures can be difficult to implement for univoltine weevil species such as these (Simpson et al. 1996), because they emerge in short time windows, which are often difficult to predict. Sensitive pheromone-based population monitoring strategies have been implemented for species like this to aid with timing of control activities, and these have had variable success (Teddars and Wood 1994).

Polyphagous species can be more difficult and expensive to control than monophagous species. The citrus root weevil, *D. abbreviatus*, the plum curculio, *Conotrachelus nenuphar*, the palm weevil, *Rhynchophorus* spp. (Hallett et al. 1993) and the maize weevil, *Sitophilus zeamais* (Walgenbach et al. 1983; Hallett et al. 1993) (Supplementary Table 2) are all polyphagous. Control of these weevils is difficult because they have multiple hosts that can serve as population reservoirs in the vegetation surrounding the commodity of interest (Simpson et al. 1996). Area-wide applications of pheromone-based control measures are usually advised in such circumstances (Haney et al. 2009; Reddy et al. 2012; Drmić et al. 2017). In contrast, weevils that feed on a single host plant species, like the banana weevil,

Cosmopolites sordidus, can be simpler to control because the area treated can be restricted to the planted area (Budenberg et al. 1993; Rannestad et al. 2011) (Supplementary Table 2).

For many weevils, the majority of the life cycle (i.e. pupae and/or larvae and/or adult) is spent concealed within host tissues and consequently it is protected from most control tactics (Supplementary Table 2). Adults of some species have periods where they are exposed and periods where they are concealed, primarily in host tissues (Booth et al. 1983; Phillips et al. 1984; Giblin-Davis et al. 1996; Illescas-Riquelme et al. 2016; Reis et al. 2018). Approximately half of the species of non-Scolytinae Curculionidae for which pheromones have been described, are inconspicuous as adults (21 out of 43 species) and another nine species are hidden to some extent as adults (Supplementary Table 2). These are adults like the sugar beet weevil, *Bothynoderes punctiventris*, that are hidden in the soil during overwintering, and exposed during defoliation (Drmić et al. 2017), or cactus weevil adults, *Metamasius spinolae*, that feed on young stems internally or externally (Tafuya et al. 2003).

Implementation of pheromone-based management tactics that target adults rely on time periods where weevils are exposed and vulnerable to intervention. This period may be a short interval during a weevil's adult life stage. For example, adult grain-, maize-, bearded- and corkwood weevils typically move around outside their host plant in search of mates and are easiest to target and capture with pheromones at this developmental stage (Faustini et al. 1982; Walgenbach et al. 1983; Kamiya et al. 2015; Reis et al. 2018). Despite the reasoning that pheromones might only be useful for weevils that are exposed throughout the adult life stage, pheromones have been identified and incorporated into IPM programmes for several species that are mostly concealed as adults. In fact, less than a quarter (12 out of 43 species) of the Curculionidae for which pheromones have been described are exposed and vulnerable to control measures throughout the adult life stage (Supplementary Table 2). This finding illustrates the potential for pheromone identification and use for any weevil species in IPM.

Pests that develop concealed within host tissues are often not detected until high levels of damage occur (Chambers et al. 1996). For example, the banana pseudostem weevil adults may live up to 200 days concealed in fallen or rotten banana stems and infestations are only noticed from the damage they cause (Ravi and Palaniswami 2002) (Supplementary Table 2). Conversely, larvae of the citrus root weevil also feed concealed in host tissue but can cause severe root damage in as little as five weeks (CABI 2019). Sensitive pheromone-based monitoring strategies that detect adults may aid in these cases, as surveillance or detection of

hidden larvae typically require manual inspection which is time-consuming and expensive (Chambers et al. 1996; Ravi and Palaniswami 2002; Lapointe et al. 2012).

The biology of the weevil being targeted can affect trapping success rates. For example, adults of some weevil species require a period of maturation feeding to become sexually mature and responsive to pheromone signals (Booth et al. 1983). Ideally, pheromone-induced behaviours are confirmed in the field, because behaviours observed *in situ* are not always observed in field conditions (Hedin et al. 1979). In addition, correct placement of traps along environmental gradients and the timing of trapping interventions is crucial (Tooke 1953; Hallett et al. 1993; Piñero and Prokopy 2003; Reddy et al. 2012; Drmić et al. 2017). In some cases, the efficacy of pheromone-based pest management can also depend on the population density of the pest (Alpizar et al. 2002; Oehlschlager et al. 2002; Drmić et al. 2017).

Knowledge of the biology of a novel pest may not be available, which complicates predicting when, where and how to sample for pheromones. Researchers thus depend on knowledge from other, often related, systems that may not be applicable (Giblin-Davis et al. 1996; Ramirez-Lucas et al. 1996; Unelius et al. 2013). After the initial pheromone identification, the next challenge is the correct formulation and presentation of synthetic pheromone to achieve the desired release rate and ratio of components from the lure matrix. Lures have to release pheromones in blend ratios (Phillips et al. 1989; Hibbard and Webster 1993; Zarbin et al. 2003; Unelius et al. 2013) and at rates (Hardee et al. 1974; Hallett et al. 1993; Piñero and Prokopy 2003) that are biologically active for their target species.

The Pheromone identification process

Behaviour guides sampling

Most successful pheromone studies are preceded by behavioural studies that confirm or suggest the existence of pheromone-mediated behaviours. Some of these behavioural studies observe and describe mating behaviour in controlled laboratory assays [e.g., *Sitophilus granarius* (Faustini et al. 1982), *Cyrtomon luridus* (Kamiya et al. 2015) and *Odoiporus longicollis* (Ravi and Palaniswami 2002)]. Others use bioassays to provide evidence for pheromone-mediated reproduction. Female *O. longicollis* have been observed to expose their ovipositor, rub them on a surface and knock on the substrate with their rostrum (Ravi and Palaniswami 2002). In response, conspecific males were observed to lift their heads, extend their antennae and move rapidly towards the calling female; probe females with their antennae and mount them (Ravi and Palaniswami 2002). This sexual interaction implies the existence of

a female-produced sex pheromone. Pheromone-mediated mate location has also been demonstrated with field trapping tests. For example, traps baited with males or females can be used to demonstrate pheromone-mediated mate location and which sex is responsible for pheromone production.

Behaviours that potentially suggest the utilization of pheromones can be observed in the field without trapping trials. For example, it was observed that male red sunflower seed weevils, *Smicronyx fulvus* LeConte, were always present on sunflowers before females. This suggested that males may use volatile chemicals to attract females to sunflowers for mating (Roseland et al. 1990). *Rhyncophorus cruentatus* was observed to aggregate on newly painted cars (Bare, 1929, as cited in Giblin-Davis et al. 1996). One potential explanation for this behavior was that *R. cruentatus* has pheromone-mediated aggregation and the paint contained volatile constituents that mimicked the aggregation pheromone. This hypothesis was later confirmed when the aggregation pheromone was identified and aggregations induced with synthetic pheromone and host volatiles (Weissling et al. 1994; Giblin-Davis et al. 1996).

If behaviours are reproducibly associated with pheromone production, this can facilitate sampling (Patrock 1986; Roseland et al. 1990). For example, timing of collection of pheromone from guava weevil males was facilitated through observation that mounting behaviour only occurs at night (Zarbin et al. 2007; Palacio-Cortés et al. 2015). Similarly, pheromone production periodicity was identified for red pine weevils, which were investigated for pheromone presence multiple times throughout the year. Pheromone production was shown to be seasonal and pheromone was only isolated during spring and summer when females were sexually mature (Booth et al. 1983).

In addition to providing evidence for pheromone-mediated behaviours, preliminary bioassays can elucidate functionality (sex, aggregation). For example, the angle of approach toward an odour source has been used to discriminate between sex (approach from the back leading to mounting and copulation) and aggregation (approach from the side, no mounting and copulation) functions (Collins 1996; Ravi and Palaniswami 2002; Zarbin et al. 2007; Kayima et al. 2015). They can also facilitate the development of bioassays critical to demonstrating activity of identified putative pheromones (Palacio-Cortés et al. 2015).

In some species, adult weevils must feed to become sexually mature and produce pheromone. One such example is the agave weevil, *Scyphophorus acupunctatus* (Smith et al. 2012), which starts producing pheromone when they are a month old. When a study is initiated,

it is not always known if maturation feeding is required for pheromone production. Investigations may need to systematically explore which factors are necessary for pheromone production if pheromones are not identified in the initial sampling endeavours (Appendix 1) (Ruiz-Montiel et al. 2009).

In some species mating status can influence production and response to pheromone (Dickens and Wiygul 1987; Piñero et al. 2001) and both mated and unmated weevils can be used for pheromone sampling. For example, red pine- (Booth et al. 1983), plum- (Eller and Bartelt 1996) and New Guinea sugarcane weevils (Giblin-Davis et al. 2000) were sampled for pheromone as virgins (Supplementary Table 3). Virgin male pecan weevils, *Curculio caryae*, were found to produce pheromone when they mount virgin females (Hedin et al. 1997). In contrast, boll weevil, *A. grandis* pheromone production was diminished when females were present in a sampling chamber (Dickens and Wiygul 1987). In other studies, both mated and virgin male maize weevils were determined to produce the same amount of pheromone (Walgenbach et al. 1983).

Pheromone production may occur only under specific conditions, and these can vary among species (Supplementary Table 3). For example, pheromone production may be dependent on the presence of appropriate host plant material, as in the case of guava- (Zarbin et al. 2007) and agave weevils (Ruiz-Montiel et al. 2003; Smith et al. 2012). In these species, host-derived precursors may be necessary for pheromone biosynthesis, as previously observed in other Curculionidae (Hughes 1974; Byers 1981; Jurenka 2004). Male pheromone production often coincides with sexual maturity of responding conspecifics, as for pine weevils *Pissodes strobi* and *P. approximatus* (Booth et al. 1983).

Although knowledge of beetle age and mating status can be critical to successful pheromone sampling in some species (Giblin-Davis et al. 2000; Azuara-Domínguez et al. 2013), field-collected weevils of unknown physiological state and age are often used for sampling (Oehlschlager et al. 1995) (Supplementary Table 3). This was done for weevils including banana- (Budenberg et al. 1993); cactus- (Tafoya et al. 2004); and cranberry weevils (Szendrei et al. 2011). Sampling beetles from different developmental stages or in large cohorts may improve the likelihood of having some individuals of the correct physiological state to produce pheromone during the sampling process. Alternatively, beetles can be reared in captivity in order to know their exact age and mating status (Ehounou and Ouali-N'goran 2018). However, development of laboratory rearing techniques can be time-consuming and is not always successful (Ambrogi et al. 2012).

Like in bark beetles (Borden et al. 1969; Vanderwel 1994), weevil pheromone production is suspected to be hormone regulated. The regulation of pheromone biosynthesis is not fully understood, as only a few studies have been conducted on pheromone biosynthesis in non-Scolytinae Curculionidae. Increased production of pheromone constituents has been shown in *S. humeralis* (Imrei et al. 2017) and *A. grandis* (Hedin et al. 1982) upon topical treatment with juvenile hormone III (JHIII), with 20 and threefold increases, respectively.

Weevils do not always produce pheromones during sampling, and it is not always clear why. For example, a comprehensive study of variation among agave weevil males manipulated photoperiod, male age, the presence of host material and starvation to test the hypotheses that these were factors affecting pheromone release by males (Ruiz-Montiel et al. 2009). These factors could not explain why there were always some males that did not produce pheromone.

There are examples where pheromones of non-Scolytinae Curculionidae were successfully isolated and identified without knowledge of mating behaviour (Oehlschlager et al. 1995; Palacio-Cortés et al. 2015). In these studies, GC-EAD analyses of dynamic headspace extracts of field collected *Rhynchophorus bilineatus* (Oehlschlager et al. 1995) and *Conotrachelus psidii* weevils (Palacio-Cortés et al. 2015) showed responses to single chromatographic peaks. These peaks were identified as 4-methyl-5-nonanol and papayanol and behavioural assays confirmed activity in each species. Such cases are the exception rather than the rule.

Pheromone identification

Various methods of pheromone sampling have been used for species of non-Scolytinae Curculionidae. Samples are generally screened with electrophysiological (e.g., GC-EAD) assays to identify putative pheromone components, the activity of which must subsequently be confirmed behaviorally. Most pheromone identification methods are general for insects (Appendix 1), but some aspects of the pheromone identification process are specific to non-Scolytinae Curculionidae.

Antennal preparations from species in the Curculionidae often give noisy signals (Branco et al. 2019). Therefore, true responses are difficult to detect. Different antennal preparation methods have been explored to reduce noise in signals. The recording electrode is generally attached to the club-shaped terminal tip of the antenna, and a grounding electrode is attached to the base of the antenna. In some studies, authors pierce the antennal tip with the recording electrode (Chambers et al. 1996; Giblin-Davis et al. 1997) and in others they simply touch the recording electrode to the tip of the antenna (Van Tol and Visser 2002). Sometimes it is

necessary to remove the distal part of the flagellum to expose the neurons in the antenna to improve the signal to noise ratio (Unelius et al. 2013). The antennae can be cut near the scape (Giblin-Davis et al. 1997) or pedicel (Budenberg et al. 1993) or the grounding electrode can be coupled by inserting it through the ventral surface of the insect head (Chambers et al. 1996; Unelius et al. 2013). At the processing level, the signal-to-noise ratios can be enhanced with analysis algorithms (Slone and Sullivan 2007).

Once putative pheromone structures have been identified, behavioural activity must be demonstrated with laboratory and/or field bioassays (Supplementary Table 4). In addition to confirming behavioural activity these trials are designed to determine the impact of component ratios (Supplementary Table 4). These bioassays can also demonstrate the biological function of the identified pheromone (Supplementary Table 4), although this might already be known if behavioural studies preceded pheromone identification.

Laboratory bioassays have the advantage of being easier to implement and are generally less expensive than field bioassays (Hedin et al. 1979). However, results may depend on the ability to mimic natural conditions in laboratory. Despite the increased logistical challenges and expense, field-based pheromone trials have been more common than laboratory-based assays for species of non-Scolytinae Curculionidae. Some of the challenges associated with field bioassays include weather and variation in population densities. Like all insects, weevils are exotherms and rainy or cold weather usually leads to decreased activity, which may result in low captures in pheromone-baited traps (Eller et al. 1994). In addition, weevil population densities fluctuate from one year to the next. Even though the same fraction of a population may be captured in different seasons, the number of weevils captured may differ due to differences in population densities (Alpizar et al. 2002; Walgenbach and Burkholder 1986). These fluctuations can be confounded by the effect of trap colour, design or placement on weevil behaviour, and together may lead to incorrect conclusions (Heuskin et al. 2011).

In addition to abiotic factors that challenge the success of field bioassays, several programmatic considerations can have significant impacts on field studies. For example, the absence of an effective trap design can result in field bioassays providing false negatives (i.e., no attraction to correctly identified pheromone compounds). The optimal trap design depends on the target species and how they interact with the trap (Laurent and Frérot 2007; Piñero et al. 2011; Silva et al. 2018). Knowing the behaviour of the target pest can therefore help with the selection and development of trap designs. For example, the trap developed for the rice weevil, *Sitophilus oryzae*, exploits its tendency to hide or crawl into enclosed spaces (Trematerra and

Girgenti 1989). A floor trap was developed from corrugated cardboard with a center hole from which pheromones and host volatiles are released and beetles can crawl into (Trematerra and Girgenti 1989). An added advantage of this trap design is that captured weevils are not killed and also release pheromone, which enhances trap performance (Trematerra and Girgenti 1989).

Trap design and use optimization

Various elements of trap design can influence captures of target insects. Black and green pyramidal traps consistently captured more plum curculio weevils than white, yellow or clear traps of the same shape (Leskey 2006). Similarly, pecan weevils, *C. caryae*, were more attracted to brown than white pyramidal traps (Teddens and Wood 1994), and yellow sticky traps were consistently more attractive to cranberry weevils, *A. musculus*, than white sticky traps (Silva et al. 2018). In terms of trap shape, pyramid-shaped traps were superior for plum curculio weevil capture compared to cylindrical traps (Leskey 2006), and sticky traps were best for cranberry weevils, *A. musculus* (Silva et al. 2018). How weevils interact with the trap can also be important. Some species prefer to enter traps through holes at the top (El-Shafie and Faleiro 2017), and others through holes in the bottom (Van Tol et al. 2012; Silva et al. 2018). Horizontal and vertical orientation of traps has also been shown to affect capture rates of the strawberry blossom weevil, *A. rubi* (Innocenzi et al. 2001).

Trap placement both relative to other traps (i.e., intertrap distance) and along environmental gradients can influence field bioassays. The odour plumes of traps that are too close together will coalesce downwind and consequently adjacent traps may interfere with each other. For example, plum curculio weevils, *C. nenuphar*, seemed to avoid each other due to confusion in high pheromone concentrations when traps were placed 1 m apart, but not when traps were 10 meters apart (Piñero and Prokopy 2003).

Trap location along both horizontal and vertical gradients can also influence trap captures. The underlying mechanisms for these gradient effects include resource availability, microclimate and interspecific interactions. If the effects of horizontal and vertical gradients on weevil distribution are unknown, randomization of traps along gradients can avoid biased results (Piñero et al. 2001, 2003). Effects of gradients on weevil distribution can be exploited in IPM programmes. For example, traps can be concentrated in areas along gradients with high weevil activity to optimize the sensitivity of monitoring programmes (Trematerra and Girgenti 1989).

Timing of trap deployment may depend on seasonal progression that may change how weevils respond to pheromone signals. For instance, mated female maize weevils, *S. zeamais*, are less responsive to pheromone. This could result in decreased trapping efficiency when more mated females are in the environment later in the season (Walgenbach et al. 1983; Walgenbach and Burkholder 1986). The sex ratio of captured strawberry blossom weevil, *A. musculus*, varies seasonally (Innocenzi et al. 2001). In contrast, activity of plum curculio (*C. nenuphar*) pheromone lures were independent of host fruit development, mating status, and density of mated females in the vicinity (Piñero et al. 2001, 2003). Consideration of the impact of these factors on trap capture can facilitate programme optimization and interpretation of results.

Pheromone deployment optimization

The amount and ratio of components released from lures can affect weevil captures in field bioassays (Hardee et al. 1974). The natural release rate of pheromone from an adult weevil ranges among species, from as low as 2.8 ng/male/day for *A. musculus* (Szendrei et al. 2011) to as high as 6 µg/male/day for *A. rubi* (Innocenzi et al. 2001). It may be necessary to adjust release rates of synthetic pheromone from traps, either to make pheromone release last longer between lure replacements (Hardee et al. 1974), or to enhance capture efficiency. To reduce the release rate, pheromones have been diluted with mineral oil (Eller et al. 1994; Piñero et al. 2001), and higher release rates can be created by using more than one dispenser on a trap. However, trap captures can be reduced if release rates become too high (Ravi and Palaniswami 2002; Piñero and Prokopy 2003). Often the most effective lures release pheromone consistently and at low rates [<10 mg/day] (Hardee et al. 1974; Heuskin et al. 2011) even though these rates may be orders of magnitude higher than natural release rates from weevils. For example, Giblin-Davis et al. (2000) used high density polyethylene in black buckets that released 3 mg of pheromone per day. Ruiz-Montiel et al. (2008) used polypropylene microcentrifuge tubes with two or three pinholes in the caps and they released pheromone at a rate of 2.6 to 3 mg/day.

When the ratios of pheromone components are similar between closely-related species of non-Scolytinae Curculionidae (i.e., major pheromone components do not differ), inter-specific attraction can occur. For example, even though the amount of pheromone released by pepper weevil males, *A. eugenii*, is approximately three times greater than that released by boll weevil males, *A. grandis* (Tumlinson et al. 1969), their similar blend compositions causes interspecific attraction to the same pheromone blend (Eller et al. 1994). In this case, both species are considered pests, making the interspecific capture a welcome occurrence. A similar trend was

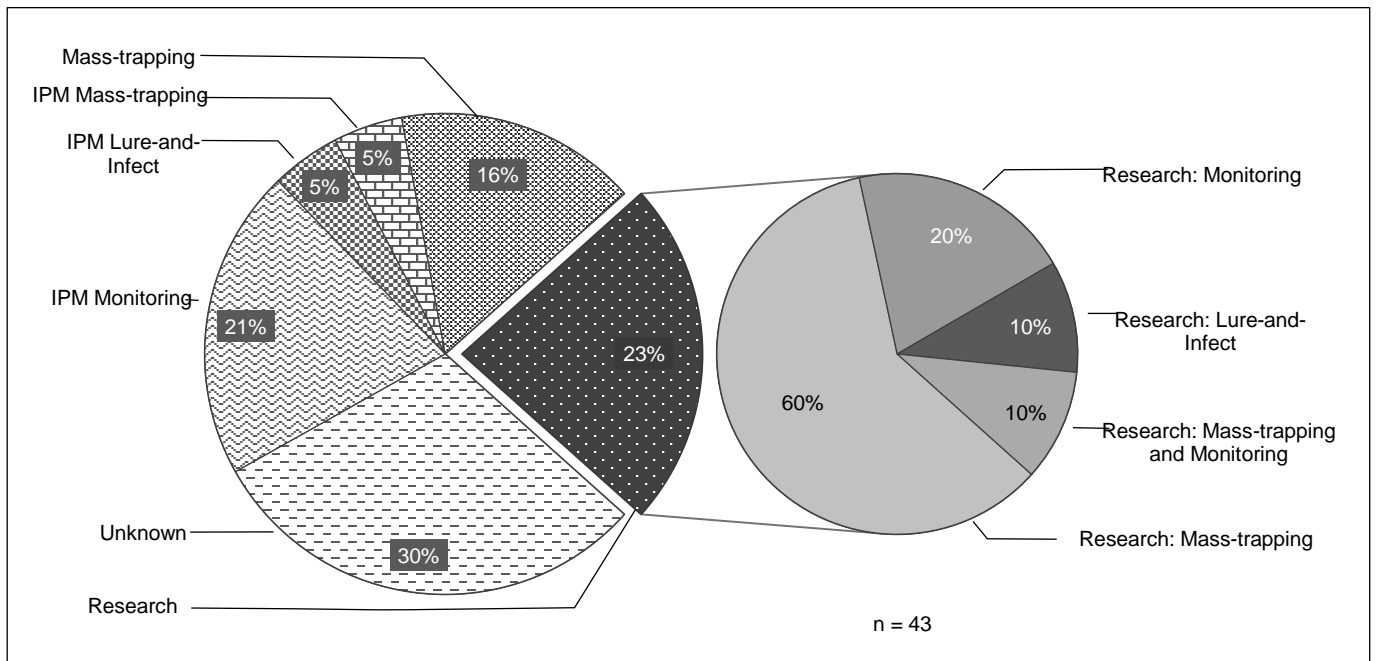
also seen in *Sitophilus* species, where rice and maize weevils, *S. oryzae* and *S. zeamais*, are attracted to the same pheromone components in very similar blend ratios (Walgenbach et al. 1983). Because high release rates often increase trap captures, pheromone dispensers usually have higher release rates than calling insects (Allison and Cardé 2016).

Release of component ratios from lures that differ from those released by weevils can result in skewed sex ratios or failure of trapping programmes (Ramirez-Lucas et al. 1996). For example pure 2*S*,3*R*-sitophilate is less attractive to the grain weevil, *S. granarius* than natural extracts from conspecifics (Faustini et al. 1982). This was due to the absence of another pheromone component that was yet to be identified (Phillips et al., 1989; Chambers et al., 1996). The inclusion of a positive control (i.e., live weevils) can facilitate quantification of how much the sex ratio is skewed with synthetic attractants (Mitchell and Hardee 1974; Hallett et al. 1993).

Some compounds are sensitive to environmental conditions and may degrade during trials. Researchers have developed several strategies to prevent this from happening. For example, inverted green plastic cups were used to protect grandisoic acid in plum curculio, *C. nenuphar*, pheromone lures from UV radiation and rain (Piñero and Prokopy 2003). Similarly, the use of white, rather than non-attractive low density polyethylene vials as lure dispensers for trapping of plum curculios, *C. nenuphar*, have been reported to minimize the UV radiation and polymerization of benzaldehyde (Piñero et al. 2001, 2003). Ultra violet absorbers like TinuvinTM and SongsorbTM are also used in commercial insect traps to protect pheromones from degradation, although we are not aware of examples where these or similar products have been used in research or operational trials targeting non-Scolytinae Curculionidae. Pheromone components within a blend may also interfere with the stability of other components. Strawberry blossom weevil, *A. rubi* pheromone lures contain aldehyde components which cause formation of alcohol breakdown products that can alter the pheromone blend (Innocenzi et al. 2001). These scenarios have to be considered when choosing the appropriate pheromone release device for field-based pest management applications.

Pheromones in weevil IPM

Several pheromone-based tactics exist and these are integrated into IPM strategies, often with other non-pheromone tactics. Pheromone-mediated tactics can be grouped based on how they affect pest populations. Direct pheromone-based management tactics directly affect weevil population levels. Indirect tactics do not impact population levels, rather they are used



•Figure 2: Development of pheromone-based pest management tactics for non-Scolytinae Curculionidae pests for which pheromones have been described (n = 43, Supplementary Table 1). Integrated pest management (IPM) methods imply that pheromones are used together with insecticide or biocontrol. 'Unknown': studies where pheromones communication has been proven, but pheromones have not been reported as successful attractants in field trials. Mass-trapping implies effective capture and control with only pheromone-baited traps without reported necessity of using other control mechanisms. Studies were classified as 'Research' if studies did not mention current application of pheromone traps in commercial plots.

to inform the timing and/or necessity for other tactics that do impact population levels (e.g., insecticide applications). Direct pheromone-based tactics include mass-trapping, mating-disruption or lure-and-kill/infect. The use of pheromones for survey and detection is an indirect application.

Mass-trapping and monitoring are the most common applications of pheromones in weevil IPM programmes. Pheromone monitoring tactics are often used to inform insecticide applications (Blight and Wadhams 1987; Phillips et al. 1989; Palanichamy et al. 2011) (Figure 2, left). Lure-and-infect applications are more common in recent literature, and involve a pheromone-baited lure to attract insects to a capture and release trap where they are inoculated with an infectious biocontrol agent (Padilla-Cubas et al. 2010; Lapointe et al. 2012) (Figure 2, left).

Mass-trapping, Lure-and-kill, and Lure-and-infect

Pest management tactics such as mass trapping, lure-and-kill, and lure-and-infect use attractants (often from more than one modality) to increase the density of a target pest in an area to facilitate control (e.g., in a trap) (Cork 2016). Olfactory attractants are by far the most commonly used and among these, host volatiles and pheromones are most common. Pheromones have the advantage of high specificity, low doses are required to attract target species, and being non-toxic to nontarget organisms (Cork 2016). The main difference between these three tactics is how the target pest is controlled (killed). Mass trapping kills target insects by confining them in a trap where they either are exposed to a toxicant (Silva et al. 2018), drowned or expire from heat exhaustion or dehydration. Lure-and-infect attracts insects to a location (often a trap) where they are inoculated with a pathogen and subsequently released or allowed to escape. Ideally after release or escape these insects spread inoculum to conspecifics and initiate an epizootic. The lure-and-kill tactic differs in that it does not require a trap and insects are attracted to a substrate that contains a traditional killing agent [e.g., synthetic insecticide in studies on *R. ferrugineus* and *R. palmarum* (Oehlschlager et al. 2002; El-Shafie and Faleiro 2017)]. As with other tactics, these techniques can be successful without killing attracted insects if they prevent or delay mating (Cork 2016).

Pheromone-based mass-trapping aims to capture as many individuals as possible to reduce total pest population levels. Capture of females is preferred because in most insects, males are able to mate multiple times. When pheromone lures only attract males, trapping efforts may have no effect on population levels in the next generation despite the capture of large numbers

of males, especially when males mate more than once and fertilize multiple females and females lay large clutches of eggs (Innocenzi et al. 2001; Kamiya et al. 2015). For example, the female sex pheromone of the sweet potato weevil, *C. formicarius*, can attract many males (Yasuda 1999), but this does not reduce population levels in subsequent generations (Yasuda 1995). In cases like this, pheromone-trapping would be more successful as an indirect monitoring strategy.

The lure-and-infect tactic was attempted for the banana weevil, *C. sordidus* (Tinzaara et al. 2007). For this study, two treatments were compared. The blank treatment involved manual application of an entomopathogenic fungus, *Beauveria bassiana*, on field-collected weevils which were later released in the infested plot. This fungus was previously shown as an effective killing agent of weevils in a lure-and-kill trial (Tinzaara et al. 2005). For the other treatment, weevils were lured with pheromone into specialized infection traps, which were laced with the same fungus. Infected *C. sordidus* weevils were then allowed to escape from these traps in order to spread the entomopathogen among other banana weevils. The number of dead and living weevils with and without mycosis were counted two weeks later from surrounding areas. Results showed that manual fungus applications were significantly less effective than pheromone-baited infection traps to infect, and ultimately kill weevils (Tinzaara et al. 2007). Similar traps were also developed for sweet potato weevils, *C. formicarius* (Yasuda 1999) and citrus root weevils, *D. abbreviatus* (Rivera et al. 2017).

Mass-trapping has been used in individual weevil infested plots (Alpizar et al. 2002; Oehlschlager et al. 2002). However, area-wide efforts are preferred for maximal effect because it minimizes the risk of re-infestation from nearby crops where trapping was not implemented (Haney et al. 2009; Reddy et al. 2012; Drmić et al. 2017). As many as 1800 acres of surrounding crops were identified to be at risk if one plot remained untreated in an area-wide study of the boll weevil (Haney et al. 2009). Mass-trapping can be improved when kairomones that synergize the response to pheromone are used in conjunction with pheromone traps (Perez et al. 1997; Marques et al. 2011; Vera et al. 2016).

Due to the considerable investment of resources involved in pheromone-based mass trapping this tactic is not used as a preventative tactic. Rather its use is usually triggered by monitoring and in conjunction with other tactics. For example, high weevil population densities indicated by pheromone-baited traps initiated mass-trapping for *R. obscurus* (Reddy et al. 2011, 2012). Similarly, after treatment of *A. grandis* infestations with insecticides, pheromone-based mass trapping has been used to try to remove any remaining females (Haney et al. 2009).

Mating-disruption

Mating-disruption is the most widely used pheromone-based direct control tactic for insects. In the majority of cases, mating disruption is used in conjunction with other tactics as part of an IPM programme (Witzgall et al. 2010). The most successful applications of this tactic typically involve systems where the mechanisms of how mating-disruption occurs (i.e., how mating is disrupted) have been identified and are then exploited (Miller et al. 2006a; Miller and Gut 2015). Multiple mechanisms exist and likely act together to disrupt mating (Cardé and Minks 1995, Cardé 2007). Factors that influence the prevalence of particular mechanisms include pheromone formulation, the method of pheromone release and the biology and behavior of the target pest (Evenden 2016).

Mating-disruption can occur through either competitive (false-trail following) or non-competitive (camouflage or sensory imbalance) mechanisms. Models of mating-disruption make different predictions depending on the mechanisms involved (Evenden 2016). In general, models predict that under competitive attraction (false-trail following), mating-disruption will increase non-linearly with dispenser density and that complete interruption of mate-finding is not possible (Miller et al. 2006b). They also predict that mating disruption by competitive attraction is affected by target pest population density, and that the effect is stronger the less competitive lures are with live insects (Barclay and Judd 1995; Miller et al. 2006b; Byers 2007). Conversely, models of mating-disruption by non-competitive mechanisms predict that mating-disruption is independent of target pest population density. When camouflage is the non-competitive mechanism, mating-disruption is hypothesized to be optimized by pheromone blends that most closely resemble the pheromone blend released by conspecifics (Cardé 1990). When sensory imbalance is the mechanism, models predict that the efficacy of mating-disruption will increase with pheromone release rate from dispensers (Barclay and Judd 1995; Miller et al. 2006a). Miller et al. (2006b) tested model assumptions with available literature and suggested that competitive attraction is the primary mechanism of mating-disruption for moths.

The available literature on mating-disruption in weevils is limited. Rhizome weevil males, *O. longicollis*, displayed confused behaviour (i.e. males exhibited courtship among themselves, not toward females) when they were exposed to high doses of the sex pheromone (Ravi and Palaniswami 2002). This suggests that the sensory imbalance mechanism may contribute to mating-disruption of rhizome weevils. In contrast, host-synergized pheromone traps for *S.*

oryzae (Trematerra and Girgenti 1989) and *A. eugenii* weevils (Eller et al. 1994) showed superior attractive power compared to wild calling conspecifics. We hypothesize that these traps may be able to disrupt mating in a competitive mating-disruption mechanism, but this requires investigation.

Monitoring

The most common application of pheromones in IPM is for survey and detection. These applications include seasonal phenology and population estimation, decision support and early detection and delimitation of invasive species (Suckling 2016). Decision support applications require thresholds for decisions on management interventions and often these are not available. The plum curculio, *C. nenuphar*, has been monitored in apple (Piñero and Prokopy 2003), and peach (Johnson et al. 2002; Leskey and Wright 2004; Akotsen-Mensah et al. 2010) orchards, where the optimal blend of synergistic host- and pheromone volatiles, best trap type as well as economic thresholds were investigated. Optimal sensitivity is essential due to the high risk of large infestations resulting from even a small number of emerged adults. For example, the pepper weevil, *E. eugenii*, can lay up to 300 eggs in their lifetime of up to 3.5 weeks (Capinera 2014), and the citrus root weevil female, *D. abbreviatus*, that can lay up to 29 000 eggs in its lifetime of three to four months (Mannion et al. 2003).

As in mass trapping, lure-and-kill, lure-and-infect and mating disruption (depending on the mechanism), lure efficacy is critical to programme success. Typically, the optimal blend mirrors the ratio of components released by the insect (Tewari et al. 2014). Due to differences in the molecular weight and polarity of pheromone components, the ratio found inside the insect does not always reflect that released. Additionally, some species store compound precursors in the gland which undergo conversion to bioactive compounds as they are released (Teal and Tumlinson 1986). As mentioned previously, trap design can also influence the capture and retention of insects (Allison and Redak 2017) and must also be optimized.

Conclusions

Pheromones have significant potential for use in IPM of weevil pests. When pheromone-based lures are used correctly, superior pest management can be achieved, even if adult weevils are only exposed to the environment during brief intervals in their life cycles. The process of pheromone development is, however, difficult and requires in-depth knowledge of the chemical ecology of a target pest. This paper considered the available literature and identified several factors that can influence the identification and implementation of

pheromones in weevil IPM programmes; including the unique factors that influence production and responsiveness toward correctly identified pheromone constituents, presented in the correct ratio to individual weevil species. The outlined procedures in this review could guide future investigations to facilitate faster identification and development of pheromone based pest management practices.

References

- Akotsen-Mensah C, Boozer R, Fadamiro HY. 2010. Field evaluation of traps and lures for monitoring Plum Curculio (Coleoptera: Curculionidae) in Alabama peaches. *Journal of Economic Entomology* 103: 744-753.
- Akotsen-Mensah C, Boozer RT, Fadamiro HY. 2012. Influence of orchard weed management practices on soil dwelling stages of Plum Curculio, *Conotrachelus nenuphar* (Coleoptera: Curculionidae). *Florida Entomologist* 95: 882-889.
- Allison JD, Cardé RT. 2016. Variation in moth pheromones: causes and consequences. In: Allison JD, Cardé RT (eds). *Pheromone communication in moths: evolution, behavior and application*. California: University of California Press. pp 365-394.
- Allison JD, Redak RA. 2017. The impact of trap type and design features on survey and detection of bark and woodboring beetles and their associates: A review and meta-analysis. *Annual Review of Entomology* 62: 127-146.
- Alpizar D, Fallas M, Oehlschlager AC, Gonzalez LM, Chinchilla CM, Bulgarelli J. 2002. Pheromone mass trapping of the West Indian sugarcane weevil and the American palm weevil (Coleoptera: Curculionidae) in Palmito palm. *Florida Entomologist* 85: 426-430.
- Ambrogi BG, Cortés AM, Zarbin PH. 2012. Identification of male-produced aggregation pheromone of the Curculionid beetle *Sternechus subsignatus*. *Journal of Chemical Ecology* 38: 272-277.
- Ambrogi BG, Vidal DM, Zarbin PHG, Rosado-Neto GH. 2009. Aggregation pheromone in Curculionidae (Insecta: Coleoptera) and their taxonomic implication. *Química Nova* 32: 2151-2158.
- Azuara-Domínguez A, Cibrián-Tovar J, Terán-Vargas AP, Segura-León OL, Cibrián-Jaramillo Al. 2013. Factors in the response of agave weevil, *Scyphophorus acupunctatus* (Coleoptera: Curculionidae), to the major compound in its aggregation pheromone. *Southwestern Entomologist* 38: 209-220.
- Barclay HJ, Judd GJR. 1995. Models for mating disruption by means of pheromone for insect pest control. *Population Ecology* 37: 239-247.
- Barnes BN, Capatos D. 1989. Evidence for an aggregation pheromone in adult frass of banded fruit weevil, *Phlyctinus callosus* (Schoenherr) (Coleoptera: Curculionidae) *Journal of Applied Entomology* 108: 512-518.
- Blight MM, Wadhams LJ. 1987. Male-produced aggregation pheromone in pea and bean weevil, *Sitona lineatus* (L.). *Journal of Chemical Ecology* 13: 733-739.

- Booth DC, Phillips TW, Claesson A, Silverstein RM, Lanier GN, West JR. 1983. Aggregation pheromone components of two species of *Pissodes* weevils (Coleoptera: Curculionidae) isolation, identification, and field activity. *Journal of Chemical Ecology* 9: 1-12.
- Borden JH, Nair KK, Slater CE. 1969. Synthetic juvenile hormone: induction of sex pheromone production in *Ips confusus*. *Science* 166: 1626-1627.
- Branco S, Mateus EP, Gomes da Silva MDR, Mendes D, Pereira MMA, Schütz S, Paiva MR. 2019. Identification of pheromone candidates for the Eucalyptus weevil, *Gonipterus platensis* (Coleoptera, Curculionidae). *Journal of Applied Entomology* 144: 1-13.
- Bredenhand E, Van Hoorn A, May F, Ferreira T, Johnson S. (2010) Evaluation of techniques for monitoring banded fruit weevil, *Phlyctinus callosus* (Schöenherr) (Coleoptera: Curculionidae), infestation in blueberry orchards *African Entomology* 18: 205-209.
- Budenberg WJ, Ndiege IO, Karago FW. 1993. Evidence for volatile male-produced pheromone in banana weevil *Cosmopolites sordidus*. *Journal of Chemical Ecology* 19: 1905-1916.
- Byers JA. 1981. Pheromone biosynthesis in the bark beetle, *Ips paraconfusus*, during feeding or exposure to vapours of host plant precursors. *Insect Biochemistry* 11: 563-569.
- Byers JA. 2007. Simulation of mating disruption and mass trapping with competitive attraction and camouflage. *Environmental Entomology* 36: 1328-1338.
- CABI 2019. Citrus weevil: *Diaprepes abbreviatus*. Retrieved from <https://www.plantwise.org/knowledgebank/datasheet/19691#ImpactSection>.
- Capinera JL (Producer). 2014. Pepper weevil: *Anthonomus eugenii* Cano. *Featured Creatures*. [Pepper weevil life cycle parameters] Available at http://entnemdept.ufl.edu/creatures/veg/beetle/pepper_weevil.htm
- Cardé RT. 1990. Principles of mating disruption. In: Ridgway RL, Silverstein RM, Inscoc MN (eds). *Behavior-modifying chemicals for insect management: applications of pheromones and other attractants*. New York: Marcel Dekker. pp 47-71.
- Cardé RT. 2007. Using pheromones to disrupt mating of moth pests. In: Kogan M, Jepson P (eds). *Perspectives in ecological theory and Integrated Pest Management*. Cambridge: Cambridge University Press. pp 122-169.
- Cardé RT, Minks AK. 1995. Control of moth pests by mating disruption: successes and constraints. *Annual Review of Entomology* 40: 559-585.
- Chambers J, Van Wyk CB, White PR, Gerrard CM, Mori K. 1996. Grain weevil, *Sitophilus granarius* (L.): antennal and behavioral responses to male-produced volatiles. *Journal of Chemical Ecology* 22: 1639-1654.
- Collins JK. 1996. *Studies on sex pheromones and biology of the pecan weevil, Curculio caryae (Coleoptera: Curculionidae), and the sex pheromone of the hickory shuckworm, Cydia caryana, (Lepidoptera: Tortricidae)*. (PhD thesis), Oklahoma Panhandle State University, Stillwater, OK.
- Cork A. 2016. Pheromones as management tools: mass trapping and lure-and-kill. In: Allison JD, Cardé RT (eds). *Pheromone communication in moths: evolution, behavior and application*. California: University of California Press. pp 349-364.
- Cork A, Lobos EA. 2003. Female sex pheromone components of *Helicoverpa gelotopoeon*: first heliothine pheromone without (Z)-11-hexadecenal. *Entomologia Experimentalis et Applicata* 107: 201-206.

- Dickens JC, Wiygul G. 1987. Conspecific effects on pheromone production by the boll weevil, *Anthonomus grandis* Boh. (Coleoptera: Curculionidae). *Journal of Applied Entomology* 104: 318-326.
- Dosunmu OG, Herrick NJ, Haseeb M, Hix RL, Mankin RW. 2014. Acoustic detectability of *Rhynchophorus cruentatus* (Coleoptera: Dryophthoridae). *The Florida Entomologist* 97: 431-438.
- Drmic Z, Tóth M, Lemić D, Grubišić D, Pospíšil M, Bažok R. 2017. Area-wide mass trapping by pheromone-based attractants for the control of sugar beet weevil (*Bothynoderes punctiventris* Germar, Coleoptera: Curculionidae). *Pest Management Science* 73: 2174-2183.
- Ehounou G, Ouali-N'goran S-WM. 2018. Biological studies on palm tree weevil *Rhynchophorus phoenicis* Fabricius (Coleoptera; Curculionidae): an interest food bug in Côte d'Ivoire (West Africa). *International Journal of Biosciences* 13: 137-147.
- El-Shafie HAF, Faleiro JR. 2017. Optimizing components of pheromone-baited trap for the management of red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in date palm agro-ecosystem. *Journal of Plant Diseases and Protection* 124: 279-287.
- Eller FJ, Bartelt RJ. 1996. Grandisoic acid, a male-produced aggregation pheromone from the Plum Curculio *Conotrachelus nenuphar*. *Journal of Natural Products* 59: 451-453.
- Eller FJ, Bartelt RJ, Shasha BS, Schuster DJ, Riley DG, Stansly PA, Mueller TF, Shuler KD, Johnson B, Davis JH, Sutherland CA. 1994. Aggregation pheromone for the pepper weevil, *Anthonomus eugenii* Cano (Coleoptera: Curculionidae): identification and field activity. *Journal of Chemical Ecology* 20: 1537-1555.
- Evenden M. 2016. Mating disruption of moth pests in integrated pest management: A mechanistic approach. In: Allison JD, Cardé RT (eds). *Pheromone communication in moths: evolution, behavior and application*. California: University of California Press. pp 365-394.
- Faustini DL, Giese WL, Phillips JK, Burkholder WE. 1982. Aggregation pheromone of the male granary weevil, *Sitophilus granarius* (L.). *Journal of Chemical Ecology* 8: 679-687.
- Garnas JR, Hurley BP, Slippers B, Wingfield MJ, Roux J. 2016. Insects and diseases of mediterranean forests: a South African perspective. In: Paine TD, Lieutier F (eds). *Insects and diseases of Mediterranean forest systems*. Switzerland: Springer. pp 397-430.
- Gebeyehu S, Wingfield MJ. 2003. Pine weevil *Pissodes nemorensis*: threat to South African pine plantations and options for control. *South African Journal of Science* 99: 531-536.
- Giblin-Davis RM, Gries R, Crespi B, Robertson LN, Hara AH, Gries G, O'Brien CW, Pierce HD. 2000. Aggregation pheromones of two geographical isolates of the New Guinea sugarcane weevil, *Rhabdoscelus obscurus*. *Journal of Chemical Ecology* 26: 2763-2780.
- Giblin-Davis RM, Gries R, Gries G, Peña-Rojas E, Pinzón I, Peña JE, Perez AL, Pierce HD, Oehlschlager AC. 1997. Aggregation pheromone of palm weevil, *Dynamis borassi*. *Journal of Chemical Ecology* 23: 2287-2297.
- Giblin-Davis RM, Oehlschlager AC, Perez A, Gries G, Gries R, Weissling TJ, Chinchilla CM, Peña JE, Hallett RH, Pierce HD, Gonzalez LM. 1996. Chemical and behavioral ecology of palm weevils (Curculionidae: Rhynchophorinae). *The Florida Entomologist* 79: 153-167.
- Gitau CW, Bashford R, Carnegie AJ, Gurr GM. 2013. A review of semiochemicals associated with bark beetle (Coleoptera: Curculionidae: Scolytinae) pests of coniferous trees: a focus

- on beetle interactions with other pests and their associates. *Forest Ecology and Management* 297: 1-14.
- Graham JH, McCoy CW, Rogers JS. 1996. Insect-plant pathogen interactions: preliminary studies of *Diaprepes* root weevils injuries and *Phytophthora* infections. *Florida Agricultural Experiment Station Journal Series* 109: 57–62.
- Hall M. 2018. Pecan weevil. Retrieved from <https://www.coffey.k-state.edu/lawn-garden/gardening/Pecan%20Weevil%20Control.pdf>
- Hallett R, Oehlschlager C, Gries G, Angerilli NPD, Schareqi RK, Gassouma MS, Borden JH. 1993. Field testing of aggregation pheromones of two Asian palm weevils. In "Proceedings of the PORIM International Palm Oil Congress: Update and Vision, 20-25 September, Kuala Lumpur, Malaysia.
- Haney PB, Lewis WJ, Lambert WR. 2009. *Cotton production and the boll weevil in Georgia: history, cost of control, and benefits of eradication*. College of Agricultural and Environmental Sciences, the University of Georgia, Athens, GA, USA.
- Hardee DD, Graves TM, McKibben GH, Johnson WL, Gueldner RC, Olsen CM. 1974. A slow-release formulation of grandlure, the synthetic pheromone of the boll weevil. *Journal of Economic Entomology* 67: 43-46.
- Hardie J, Minks AK. 1999. *Pheromones of non-lepidopteran insects associated with agricultural plants*. Wallingford, Oxon, UK: CABI Pub.
- Hazzouri KM, Sudalaimuthuasari N, Kundu B Nelson, D, Al-Deeb MA, Le Mansour A, Spencer JJ, Desplan C, Amiri KMA. 2020. The genome of pest *Rhynchophorus ferrugineus* reveals gene families important at the plant-beetle interface. *Communications Biology* 3: 323-337.
- Heath RR, Coffelt JA, Sonnet PE, Proshold FI, Dueben B, Tumlinson JH. 1986. Identification of sex pheromone produced by female sweetpotato weevil, *Cylas formicarius elegantulus* (Summers). *Journal of Chemical Ecology* 12: 1489-1503.
- Hedin PA, Dollar DA, Collins JK, Dubois JG, Mulder PG, Hedger GH, Smith MW, Eikenbary RD. 1997. Identification of male pecan weevil pheromone. *Journal of Chemical Ecology* 23: 965-977.
- Hedin PA, Lindig O, Wiygul G. 1982. Enhancement of boll weevil *Anthonomus grandis* Boh. (Coleoptera: Curculionidae) pheromone biosynthesis with JH III. *Experientia* 38: 375-376.
- Hedin PA, McKibben GH, Mitchell EB, Johnson WL. 1979. Identification and field evaluation of the compounds comprising the sex pheromone of the female boll weevil. *Journal of Chemical Ecology* 5: 617-627.
- Heuskin S, Verheggen FG, Haubruge E, Wathélet JP, Lognay G. 2011. The use of semiochemical slow-release devices in integrated pest management strategies. *Biotechnologie, Agronomie, Société et Environnement*, 15, 459-470.
- Hibbard BE, Webster FX. 1993. Enantiomeric composition of grandisol and grandisol produced by *Pissodes strobi* and *P. nemorensis* and their electroantennogram response to pure enantiomers. *Journal of Chemical Ecology* 19: 2129-2141.
- Hughes PR. 1974. Myrcene: a precursor of pheromones in *Ips* beetles. *Journal of Insect Physiology* 20: 1271-1275.
- Illescas-Riquelme CP, Llanderal-Cázares C, Ruiz-Montiel Cs, González-Hernández Hc, Alatorre-Rosas R, Cruz-López L, Rojas JC. 2016. Evidence for male-produced aggregation

- pheromone in *Sphenophorus incurrens* (Coleoptera: Curculionidae). *The Florida Entomologist* 99: 522-527.
- Imrei Z, Lohonyai Z, Szarukán I, Smart L, Vuts J, Kárpáti Z, Woodcock C, Chamberlain K, Koczor S, Abaev V, Fail J, Birkett M, Pickett J, Tóth M. 2017. *A review and recent developments in research of chemical communication in Sitona spp. (Coleoptera: Curculionidae): pheromones and plant volatiles*. ISCE/APACE 2017 Annual Meeting. Poster. Kyoto, Japan.
- Innocenzi PJ, Hall DR, Cross JV. 2001. Components of male aggregation pheromone of strawberry blossom weevil, *Anthonomus rubi* Herbst. (Coleoptera: Curculionidae). *Journal of Chemical Ecology* 27: 1203-1218.
- Johnson DT, Mulder PG, McCraw BD, Lewis BA, Jervis B, Carroll B, McLeod PJ. 2002. Trapping Plum Curculio *Conotrachelus nenuphar* (Herbst) (Coleoptera: Curculionidae) in the southern United States. *Environmental Entomology* 31: 1259-1267.
- Jones IF, Schroeder WJ. 1983. Study of first-instar *Diaprepes abbreviatus* (Coleoptera: Curculionidae) activity for control purposes. *Journal of Economic Entomology* 76: 567-569.
- Jurenka R. 2004. Insect pheromone biosynthesis. *Topics in Current Chemistry* 239: 97-132.
- Kamiya AC, Silva WD, Leite MOG, Tironi P, Wadt L, Bento JMS. 2015. Mating behavior and evidence for male-produced aggregation pheromone in *Cyrtomon luridus* (Boheman) (Coleoptera: Curculionidae: Entiminae). *Journal of Insect Behavior* 28: 55-66.
- Köhler R, Irias-Mata A, Ramandey E, Purwestri R, Biesalski HK. 2020. Nutrient composition of the Indonesian sago grub (*Rhynchophorus bilineatus*). *International Journal of Tropical Insect Science* 40: 677-686.
- Langstrom B. 1982. Abundance and seasonal activity of adult *Hylobius* weevils in reforestation areas during first years following final felling. *Communicationes Instituti Forestalis Fenniae* 106: 4-22.
- Lapointe SL, Alessandro RT, Robbins PS, Khrimian A, Svatos A, Dickens JC, Otálora-Luna F, Kaplan F, Alborn HT, Teal PEA. 2012. Identification and synthesis of a male-produced pheromone for the neotropical root weevil *Diaprepes abbreviatus*. *Journal of Chemical Ecology* 38: 408-417.
- Larsson MC. 2016. Pheromones and other semiochemicals for monitoring rare and endangered species. *Journal of Chemical Ecology* 42: 853-868.
- Laurent P, Frérot B. 2007. Monitoring of European corn borer with pheromone-baited traps: review of trapping system basics and remaining problems. *Journal of Economic Entomology* 100: 1797-1807.
- Leskey TC. 2006. Visual cues and capture mechanisms associated with traps for Plum Curculio (Coleoptera: Curculionidae). *Journal of Entomological Science* 41: 97-106.
- Leskey TC, Wright SE. 2004. Monitoring Plum Curculio, *Conotrachelus nenuphar* (Coleoptera: Curculionidae), populations in apple and peach orchards in the mid-Atlantic. *Journal of Economic Entomology* 97: 79-88.
- Malo EA, Gutiérrez-Escobar V, Castrejón-Ayala F, Rojas JC. 2020. The aggregation pheromone of *Metamasius spinolae* (Coleoptera: Dryophthoridae) revisited: less is more. *Environmental Entomology* 49: 803-809.

- Mannion C, Hunsberger A, Peña JE, Osborne L. 2003. Oviposition and larval survival of *Diaprepes abbreviatus* (Coleoptera: Curculionidae) on select host plants. *Florida Entomologist* 86: 165-173.
- Marques FA, Zaleski SRM, Lazzari SMN, Frensch G, Senhorini GA, Maia BHLNS, Tröger A, Francke W, Ieded ET, Mori K. 2011. Identification of (1R, 2S)-grandisal and (1R, 2S)-grandisol in *Pissodes castaneus* male-produced volatiles: evidence of a sex pheromone. *Journal of the Brazilian Chemical Society* 22: 1050-1055.
- Miller JR, Gut LJ. 2015. Mating disruption for the 21st century: matching technology with mechanism. *Environmental Entomology* 44: 427-453.
- Miller JR, Gut LJ, de Lame FM, Stelinski LL. 2006a. Differentiation of competitive vs. non-competitive mechanisms mediating disruption of moth sexual communication by point sources of sex pheromone (part I): Theory. *Journal of Chemical Ecology* 32: 2089-2114
- Miller JR, Gut LJ, de Lame FM, Stelinski LL. 2006b. Differentiation of competitive vs. non-competitive mechanisms mediating disruption of moth sexual communication by point sources of sex pheromone (part 2): Case studies. *Journal of Chemical Ecology* 32: 2115-2143.
- Mitchell EB, Hardee DD. 1974. Seasonal determination of sex ratios and condition of diapause of boll weevils in traps and in the field. *Environmental Entomology* 3: 386-388.
- Mody NV, Hedin PA, Neel WW, Miles DH. 1975. Hydrocarbons from males, females, and larvae of pecan weevil: *Curculio caryae* (Horn). *Lipids* 10: 117-119.
- Mutis A, Parra L, Palma R, Pardo F, Perich F, Quiroz A. 2009. Evidence of contact pheromone use in mating behavior of the raspberry weevil (Coleoptera: Curculionidae). *Environmental Entomology* 38: 192-197.
- Nadel RL, Wingfield MJ, Scholes MC, Lawson SA, Slippers B. 2012. The potential for monitoring and control of insect pests in southern hemisphere forestry plantations using semiochemicals. *Annals of Forest Science: Official journal of the Institut National de la Recherche Agronomique (INRA)* 69: 757-767.
- Oehlschlager AC, Chinchilla C, Castillo G, Gonzalez LM. 2002. Control of red ring disease by mass trapping of *Rhynchophorus Palmarum* (Coleoptera: Curculionidae). *The Florida Entomologist* 85: 507.
- Oehlschlager AC, Prior RNB, Perez AL, Gries R, Gries G, Pierce HD, Laup S. 1995. Structure, chirality, and field testing of a male-produced aggregation pheromone of Asian palm weevil *Rhynchophorus bilineatus* (Montr.) (Coleoptera: Curculionidae). *Journal of Chemical Ecology* 21: 1619-1629.
- Padilla-Cubas A, Carnero Hernandez A, Garcia-del-Pino F. 2010. Laboratory efficacy against neonate larvae of the banana weevil *Cosmopolites sordidus* of two indigenous entomopathogenic nematode species from the Canary Islands (Spain). *International Journal of Pest Management* 56: 211-216.
- Palacio-Cortés AM, Valente F, Saad EB, Tröger A, Francke W, Zarbin PHG. 2015. (1R,2S,6R)-Papayanol, aggregation pheromone of the guava weevil, *Conotrachelus psidii*. *Journal of the Brazilian Chemical Society* 26: 784-789.
- Palanichamy S, Padmanaban B, Mohamed MIF, Mustaffa MM. 2011. A simple and low cost semiochemical based trapping method for the management of banana pseudostem weevil,

- Odoiporus longicollis* Olivier (Coleoptera:Curculionidae) *Advances in Applied Science Research* 2: 69-73.
- Patrock RJ. 1986. *Observations on the behavior and host relations of the pepper weevil Anthonomus eugenii Cano (Coleoptera: Curculionidae) in Florida.* (MSc thesis), University of Florida, Gainesville.
- Perez AL, Campos Y, Chinchilla CM, Oehlschlager AC, Gries G, Gries R, Giblin-Davis RM, Castrillo G, Peña JE, Duncan RE, Gonzalez LM, Pierce HD, McDonald R, Andrade R. 1997. Aggregation pheromones and host kairomones of West Indian sugarcane weevil, *Metamasius hemipterus sericeus*. *Journal of Chemical Ecology* 23: 869-888.
- Phillips JK, Chong JM, Andersen JF, Burkholder WE. 1989. Determination of the enantiomeric composition of (*R**, *S**)-1-ethylpropyl 2-methyl-3-hydroxypentanoate, the male-produced aggregation pheromone of *Sitophilus granarius*. *Entomologia Experimentalis et Applicata* 51: 149-153.
- Phillips TW, West JR, Foltz JL, Silverstein RM, Lanier GN. 1984. Aggregation pheromone of the deodar weevil, *Pissodes nemorensis* (Coleoptera: Curculionidae): isolation and activity of grandisol and grandisal. *Journal of Chemical Ecology* 10: 1417-1423.
- Pickett JA, Wadhams LJ, Woodcock CM. 1997. Developing sustainable pest control from chemical ecology. *Agriculture, Ecosystems & Environment* 64: 149-156.
- Piñero JC, Agnello AM, Tuttle A, Leskey TC, Faubert H, Koehler G, Los L, Morin G, Leahy K, Cooley DR, Prokopy RJ. 2011. Effectiveness of odor-baited trap trees for Plum Curculio (Coleoptera: Curculionidae) monitoring in commercial apple orchards in the northeast. *Journal of Economic Entomology* 104: 1613-1621.
- Piñero JC, Prokopy RJ. 2003. Field evaluation of plant odor and pheromonal combinations for attracting Plum Curculios. *Journal of Chemical Ecology* 29: 2735-2748.
- Piñero JC, Wright SE, Prokopy RJ. 2001. Response of Plum Curculio (Coleoptera: Curculionidae) to odor-baited traps near woods. *Journal of Economic Entomology* 94: 1386-1397.
- Prinsloo GL, Uys VM. 2015. African palm weevil *Rhynchophorus phoenicis*. In: *Insects of cultivated plants and natural pastures in southern Africa*. South Africa: Entomological Society of South Africa, pp 546-547.
- Ramirez-Lucas P, Rochat D, Zagatti P. 1996. Field trapping of *Metamasius hemipterus* with synthetic aggregation pheromone. *Entomologia Experimentalis et Applicata* 80.
- Rannestad OT, Sæthre M-G, Maerere AP. 2011. Migration potential of the banana weevil. *Agricultural and Forest Entomology* 13: 405-412.
- Ravi G, Palaniswami NS. 2002. Evidence for a female-produced sex pheromone in the banana pseudostem weevil, *Odoiporus longicollis* Olivier. *Current Science* 83: 893-898.
- Reddy GVP, Balakrishnan S, Remolona JE, Kikuchi R, Bamba JP. 2011. Influence of trap type, size, color, and trapping location on capture of *Rhabdoscelus obscurus* (Coleoptera: Curculionidae). *Annals of the Entomological Society of America* 104: 594-603.
- Reddy GVP, Shi P, Mann CR, Mantanona DMH, Dong Z. 2012. Can a semiochemical-based trapping method diminish damage levels caused by *Rhabdoscelus obscurus* (Coleoptera: Curculionidae)? *Annals of the Entomological Society of America* 105: 693-700.
- Reis AC, Neta PLS, Jordão JsP, Moura JIcL, Vidal DM, Zarbin PHG, Fávoro CF. 2018. Aggregation pheromone of the bearded weevil, *Rhinostomus barbirostris* (Coleoptera:

- Curculionidae): identification, synthesis, absolute configuration and bioactivity. *Journal of Chemical Ecology* 44: 463-470.
- Ribeiro TP, Arraes FBM, Lourenço-Tessutti IT, Silva MS, Lisei-de-Sá ME, Lucena WA, Macedo LLP, Lima JN, Santos Amorim RM, Artico S, Alves-Ferreira M, Mattar Silva MC, Grossi-de-Sa MF. 2017. Transgenic cotton expressing Cry10Aa toxin confers high resistance to the cotton boll weevil. *Plant Biotechnology Journal* 15: 997-1009.
- Rivera MJ, Martini X, Khimian A, Stelinski L. 2017. A weevil sex pheromone serves as an attractant for its entomopathogenic nematode predators. *Chemoecology* 27: 199-206.
- Roseland CR, Bates MB, Oseto CY. 1990. Role of a male-produced pheromone of the red sunflower seed weevil (Coleoptera: Curculionidae) in host finding. *Environmental Entomology* 19: 1675-1680.
- Ruiz-Montiel C, García-Coapio G, Rojas JC, Malo EA, Cruz-López L, Del Real I, González-Hernández H. 2008. Aggregation pheromone of the agave weevil, *Scyphophorus acupunctatus*. *Entomologia Experimentalis et Applicata* 127: 207-217.
- Ruiz-Montiel C, González-Hernández H, Leyva J, Llanderal-Cazares C, Cruz-López L, Rojas JC. 2003. Evidence for a male-produced aggregation pheromone in *Scyphophorus acupunctatus* Gyllenhal (Coleoptera: Curculionidae). *Journal of Economic Entomology* 96: 1126-1131.
- Ruiz-Montiel C, Rojas JC, Cruz-López L, González-Hernández H. 2009. Factors affecting pheromone release by *Scyphophorus acupunctatus* (Coleoptera: Curculionidae). *Environmental Entomology* 38: 1423-1428.
- Schröder ML, Slippers B, Wingfield MJ, Hurley BP. 2019. Invasion history and management of Eucalyptus snout beetles in the *Gonipterus scutellatus* species complex. *Journal of Pest Science* 93: 11-25.
- Silva D, Salamanca J, Kyryczenko-Roth V, Alborn HT, Rodriguez-Saona C. 2018. Comparison of trap types, placement, and colors for monitoring *Anthonomus musculus* (Coleoptera: Curculionidae) adults in highbush blueberries. *Journal of Insect Science* 18: 1-9.
- Simpson SE, Nigg HN, Coile NC, Adair RA. 1996. *Diaprepes abbreviatus* (Coleoptera: Curculionidae): host plant associations. *Environmental Entomology* 25: 333-349.
- Slone DH, Sullivan BT. 2007. An automated approach to detecting signals in electroantennogram data. *Journal of Chemical Ecology* 33: 1748.
- Suckling DM. 2016. Monitoring for surveillance and management. In: Allison JD, Cardé RT (eds). *Pheromone communication in moths: evolution, behavior and application*. California: University of California Press. pp 337-347.
- Szendrei Z, Averill A, Alborn H, Rodriguez-Saona C. 2011. Identification and field evaluation of attractants for the cranberry weevil, *Anthonomus musculus* Say. *Journal of Chemical Ecology* 37: 387-397.
- Szmedra PI, McClendon RW, Wetzstein ME. 1991. Economic risk efficiency of boll weevil eradication. *Southern Journal of Agricultural Economics* 23: 237-245.
- Tafoya F, Lopez-Collado J, Stanley D, Rojas JC, Cibrian-Tovar J. 2003. Evidence of an aggregation pheromone in males of *Metamasius spinolae* (Coleoptera: Curculionidae). *Environmental Entomology* 32: 484-487.

- Tafoya F, Zuñiga-Delgadillo M, Alatorre R, Cibrian-Tovar J, Stanley D. 2004. Pathogenicity of *Beauveria Bassiana* (Deuteromycota: Hyphomycetes) against the cactus weevil, *Metamasius spinolae* (Coleoptera: Curculionidae) under laboratory conditions. *Florida Entomologist* 87: 533-536.
- Teal PEA, Tumlinson JH. 1986. Terminal steps in pheromone biosynthesis by *Heliothis virescens* and *H. zea*. *Journal of Chemical Ecology* 12: 353-366.
- Tedders WL, Wood BW. 1994. A new technique for monitoring pecan weevil emergence (Coleoptera: Curculionidae). *Journal of Entomological Science* 29: 18-30.
- Tewari S, Leskey TC, Nielsen AL, Piñero JC, Rodriguez-Saona CR. 2014. Use of pheromones in insect pest management, with special attention to weevil pheromones. In: Abrol DP (ed.), *Integrated pest management: current concepts and ecological perspective*. Amsterdam: Elsevier. pp 141-168.
- Tinzaara W, Gold CS, Dicke M, Van Huis A, Nankinga CM, Kagezi GH, Ragama PE. 2007. The use of aggregation pheromone to enhance dissemination of *Beauveria bassiana* for the control of the banana weevil in Uganda. *Biocontrol Science and Technology* 17: 111-124.
- Tinzaara W, Gold CS, Dicke M, Van Huis A, Ragama P. 2005. Factors influencing pheromone trap effectiveness in attracting the banana weevil, *Cosmopolites sordidus*. *International Journal of Pest Management* 51: 281-288.
- Tooke FGC. 1953. *The Eucalyptus snout beetle, Gonipterus scutellatus Gyll. A Study of its ecology and control by biological means*. Pretoria: University of Pretoria.
- Trematerra P, Girgenti P. 1989. Influence of pheromone and food attractants on trapping of *Sitophilus oryzae* (L.) (Col., Curculionidae): a new trap. *Journal of Applied Entomology* 108: 12-20.
- Tumlinson JH, Hardee DD, Gueldner RC, Thompson AC, Hedin PA, Minyard JP. 1969. Sex pheromones produced by male boll weevil: isolation, identification, and synthesis. *Science* 166: 1010-1012.
- Unelius CR, Park KC, McNeill M, Wee SL, Bohman B, Suckling DM. 2013. Identification and electrophysiological studies of (4S,5S)-5-hydroxy-4-methyl-3-heptanone and 4-methyl-3,5-heptanedione in male lucerne weevils. *Naturwissenschaften* 100: 135-143.
- Van Tol RWHM, Bruck DJ, Griepink FC, De Kogel WJ. 2012. Field attraction of the vine weevil *Otiorhynchus sulcatus* to kairomones. *Journal of Economic Entomology* 105: 169-175.
- Van Tol RWHM, Visser JH. 2002. Olfactory antennal responses of the vine weevil *Otiorhynchus sulcatus* to plant volatiles. *Entomologia Experimentalis et Applicata* 102: 49-64.
- Vanderwel D. 1994. Factors affecting pheromone production in beetles. *Archives of Insect Biochemistry and Physiology* 25: 347-362.
- Vera W, Parra L, Quiroz A, Bergmann J. 2016. Attraction to host plant volatiles and feeding performance of *Naupactus xanthographus* (Coleoptera: Curculionidae) is affected by starvation. *Journal of Insect Behavior* 29: 48-56.
- Walgenbach CA, Burkholder WE. 1986. Factors affecting the response of the maize weevil, *Sitophilus zeamais* (Coleoptera: Curculionidae), to its aggregation pheromone. *Environmental Entomology* 15: 733-738.

- Walgenbach CA, Phillips JK, Faustini DL, Burkholder WE. 1983. Male-produced aggregation pheromone of the maize weevil, *Sitophilus zeamais*, and interspecific attraction between three *Sitophilus* species. *Journal of Chemical Ecology* 9: 831-841.
- Weissling TJ, Giblin-Davis RM, Gries G, Gries R, Perez AL, Pierce HD, Oehlschlager AC. 1994. Aggregation pheromone of palmetto weevil, *Rhynchophorus cruentatus* (F.) (Coleoptera: Curculionidae). *Journal of Chemical Ecology* 20: 505-515.
- Wingfield MJ, Slippers B, Hurley BP, Coutinho TA, Wingfield BD, Roux J. 2008. Eucalypt pests and diseases: growing threats to plantation productivity. *Southern Forests: a Journal of Forest Science* 70: 139-144.
- Witzgall P, Kirsch P, Cork A. 2010. Sex pheromones and their impact on pest management. *Journal of Chemical Ecology* 36: 80-100.
- Wolcott GN. 1936. The life history of "*Diaprepes abbreviatus*" L., at Rio Piedras, Puerto Rico. *J. Agric. Univ. Puerto Rico* 20: 883-914.
- Wondafrash M, Slippers B, Garnas J, Hurley BP. 2018. Parasitoid assemblage associated with a North American pine weevil in South Africa. *Agricultural and Forest Entomology* 20: 208-216.
- Wood DL. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Review of Entomology* 27: 411-446.
- Yasuda K. 1995. Mass trapping of the sweet potato weevil *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae) with a synthetic sex pheromone. *Applied Entomology and Zoology* 30: 31-36.
- Yasuda K. 1999. Auto-infection system for the sweet potato weevil, *Cylas formicarius* (Fabricius) (Coleoptera: Curculionidae) with entomopathogenic fungi, *Beauveria bassiana* using a modified sex pheromone trap in the field. *Applied Entomology and Zoology* 34: 501-505.
- Zarbin PHG, Arrigoni EDB, Reckziegel A, Moreira JA, Baraldi PT, Vieira PC. 2003. Identification of male-specific chiral compound from the sugarcane weevil *Sphenophorus levis*. *Journal of Chemical Ecology* 29: 377-386.
- Zarbin PHG, Moreira MAB, Haftmann J, Francke W, Oliveira A. 2007. Male-specific volatiles released by the Brazilian papaya weevil, *Pseudopiazurus obesus*: partial identification and evidence of an aggregation pheromone. *Journal of the Brazilian Chemical Society* 18: 1048-1053.

Supplementary Table captions (all in excel format)

- **Supplementary Table 1:** Affected hosts and industries damaged by species of non-Scolytinae Curculionidae for which pheromones have been investigated as of 2019.
- **Supplementary Table 2:** Differences in life cycles of various species of non-Scolytinae Curculionidae that have been shown to rely on conspecific chemical communication.
- **Supplementary Table 3:** Sampling methods and procedures followed for the identification of pheromone components of non-Scolytinae Curculionidae.
- **Supplementary Table 4:** The range of sampling, screening and identification methods from non-Scolytinae Curculionidae for which pheromones have been identified.