



Semiochemistry of the Bruchidae species

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ARTICLE INFO

Article history:

Received 9 February 2018
Received in revised form
12 April 2018
Accepted 24 April 2018

Keywords:

Sex pheromones
Bruchids
Cuticular compounds
Stored pests
Bean weevils

ABSTRACT

The coleopteran insects of the Bruchidae family are one of the major pests of stored products like beans and leguminous seeds in general. Bruchids have co-evolved with the seeds of leguminous plants dealing with the toxic compounds from the seeds. These insects eat a considerable part of the stored product and also contaminate the grains with their dead bodies, wings, and excreta. Among all the pests, insect damage in stored grains alone could escalate to cause up to 100% loss.

An alternative to managing this pest insect is the use of pheromones. Sex pheromones provide important signals in sexual communication. Generally, volatile sex pheromones are released to attract the opposite sex from a distance, and contact sex pheromones help in partner discrimination and can elicit courtship.

The main focus of this article is to review the results on the chemical identification of pheromones of insect pests of the family Bruchidae in stored products.

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1. Introduction

Grain legumes account for about 27% of the world's primary crop production and contribute 33% of the dietary needs of humans (Vance, 2001). Insects are competing with humans for food. Not only do they damage the field crops, but they also go with the grains even to the storehouses and warehouses causing severe

damage. Insects eat a considerable part of the stored product and also contaminate the grains with their dead bodies, wings, and excreta. In many cases, small improvements in storage methods have led to better protection of stored products resulting in lower loss. Even good storage practices (e.g. following good hygiene practices during handling and storage, adequate drying of stored grains to a safe moisture content, among others) are not always effective in preventing storage loss (Ghosh et al., 2007). Storage pests may still manage to reach the product and cause irreparable damage (Kawuki et al., 2005). Among all the pests, insect damage in

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stored grains alone could escalate to cause up to 100% loss as reported for chickpeas (Guleria and Tikku, 2009).

Coleopteran insects of the family Bruchidae, one of the major seed weevils, have been associated with the seeds of leguminous plants through co-evolutionary processes; the bruchids have adapted to the toxic compounds from the seeds (Sales et al., 2000). Some of the major pulse bruchids are *Callosobruchus maculatus* (Fabricius), *Callosobruchus chinensis* (Linnaeus), *Callosobruchus analis* (Fabricius), *Callosobruchus rhodesianus* (Pic), *Callosobruchus dolichosi* (Gyllenhal), *Callosobruchus subinnotatus* (Pic), *Callosobruchus phaseoli* (Gyllenhal), *Acanthoscelides obtectus* (Say), *Zabrotes subfasciatus* (Boheman), among others. These insects multiply rapidly under suitable environmental conditions, such as high humidity and optimum temperature (Appleby and Credland, 2004).

Pheromones are naturally occurring organic chemicals which are produced and released by an organism in order to transmit information to another individual of the same species. In insects, sex pheromones provide important signals in sexual communication. Generally, volatile sex pheromones are released to attract the opposite sex from a distance and contact sex pheromones help in partner discrimination and can elicit courtship (Blomquist and Howard, 2003; Lepri, 2003). Sex pheromones constitute either single compounds or compositions of several compounds and can either be highly species-specific or shared among several species. The detection of infestation is the most crucial part of stored product management. In the management of stored products, insect pheromones and other semiochemicals can be used to control the pest populations by means of mass trapping, attracticides, repellents, deterrents and mating disruption methods (Cox, 2004; Phillips and Throne, 2010). Usually, sex and aggregation pheromones are impregnated in rubber septa and located into a pheromone trap to detect the infestation. Stored grain insects may be detected with several types of traps either by attractant or aggregation compounds (Vick et al., 1990). As an example of the use of pheromones in stored pest management, it can be mentioned that the pheromone lures of *Rhyzopertha dominica*, *Tribolium castaneum*, and *Trogoderma granarium* are commercially available and used worldwide (Cross et al., 1976; Suzuki and Mori, 1983). With a proper knowledge of bruchid pheromones, pest control measures will certainly gain a new insight and increase attention on developing a new trapping system for insects of this family.

In this article, research on bruchid pheromones is reviewed. Its main focus is on the chemical identification of pheromones of insect pests of the family Bruchidae in stored products.

2. Identification of pheromones by species

2.1. *Acanthoscelides obtectus* S.

One of the most economically important pests of stored dried beans, *Phaseolus vulgaris* L. (Fabaceae), worldwide is the dried bean beetle, *Acanthoscelides obtectus* Say (Coleoptera: Chrysomelidae, Bruchinae) (Abate and Ampofo, 1996; Imura, 1990). This insect can complete its entire life cycle on stored seeds without returning to the field; larvae are well-protected feeding within the seeds, being this the main reason why management strategies target adult beetles (Southgate, 1979). The economic damage caused by larvae developing inside beans is extremely important in some countries where the seeds of Leguminosae represent a fundamental food resource (Abate and Ampofo, 1996). *A. obtectus* has the ability to reproduce without diapause, which enables it to be highly competitive when invading stored products (Alvarez et al., 2005; Labeyrie, 1990).

Fifty years ago, a single sex-specific compound was isolated from surface hexane extracts of males and proposed as a sex

attractant (Hope et al., 1967). Later, the compound was identified as the allenic methyl (*E,R*)-2,4,5-tetradecatrienoate (**1**) (Fig. 1) (Horler, 1970). Bioassays carried out using a synthetic molecule failed to obtain any conclusive results (Pirkle and Boeder, 1978). A few years after this publication, the existence of deterrent pheromones emitted by males and females on beans that stimulated a dispersion behaviour in bean beetles was postulated (Szentesi, 1981). This information suggested that *A. obtectus* releases chemical signals on beans informing conspecific females the presence of eggs and/or larvae to favor a more uniform distribution of eggs and minimize competition among larvae in beans (Parsons and Credland, 2003). This effect was attributed partially to high molecular weight alkanes (C25 to C31) with limited volatility suggesting a short-range action on females (Nazzi et al., 2008).

The cuticular hydrocarbons (CHCs) composition of *A. obtectus* was subject to study (Savković et al., 2012). These chemical compounds, that cover insect integument, has been highlighted as an important determinant of insect metabolism and biology (e.g., Ginzl and Blomquist, 2016; Menzel and Schmitt, 2012; Pavković-Lučić et al., 2012). A total of 21 compounds were identified from hexane cuticular extracts of *A. obtectus*, including n-alkanes, mono- and di-methylalkanes and one trimethylalkane, ranging from C25 to C31; being 9,13-dimethyl-heptacosane and n-heptacosane the most abundant compounds in all the samples assayed (Savković et al., 2012). On the other hand, the 5,9-dimethyl-heptacosane, 11-methyl-nonacosane, and 11,15-dimethyl-nonacosane compositions showed statistically significant differences between genders. The presence of sexual dimorphism suggests that the cuticle's composition acts as a contact pheromone, more precisely, the mixture of CHCs acts as a recognition pheromone (Ferveur, 2005; Savković et al., 2012).

Recently, the cuticular composition of *A. obtectus* males and females was re-analysed (Vuts et al., 2015b). In this work, methyl (*E,R*)-2,4,5-tetradecatrienoate and octadecanal (**2**) were identified as male-specific cuticular compounds (Fig. 1). Total inhibition of mating behaviour was observed when methyl (*E,R*)-2,4,5-tetradecatrienoate was added on females. In this way, a new role was found for the methyl ester, which apart from being a male-produced sex pheromone, acts as a male recognition signal in *A. obtectus*. Males transfer this molecule onto females during mating, resulting in mated females being avoided by courting males (Vuts et al., 2015b). Besides, octadecanal was found to synergize the activity of the ester as a sex attractant for females (Annoscia et al., 2010).

Afterwards, a dynamic headspace collection from unmated males was assayed and six major components were identified (Vuts et al., 2015a). The chemical identity of these molecules was methyl (2*E*,4*Z*,7*Z*)-2,4,7-decatrienoate (**3**), methyl (2*E*,4*Z*)-2,4-decadienoate (**4**), sesquiterpenes (3*Z*,6*E*)- and (3*E*,6*E*)- α -farnesene (**5** and **6**, respectively), **1**, and **2**. A complete blend containing all six male-specific compounds proved to have full activity (Vuts et al., 2015a).

2.2. *Callosobruchus* spp.

One of the most economically important genus of stored seed pests are *Callosobruchus* (Coleoptera: Chrysomelidae: Bruchinae), (1990; Labeyrie, 1981). The females lay their eggs on seeds, and the newly emerged larvae immediately bore into seeds. They spend their entire larval stage inside the seed feeding, and before they pupate, larvae make galleries for adult emergence. Each larvae consumes a considerable amount of the seed content (Rees, 1995).

Callosobruchus species are polyvoltine and can reproduce continuously under optimal conditions; the population increases rapidly with the concomitant economically significant seed damage

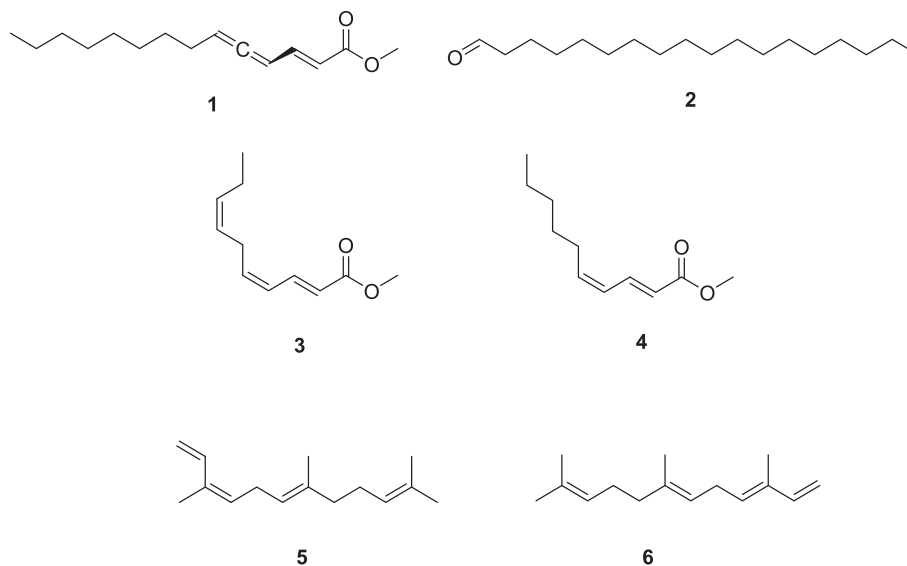


Fig. 1. Pheromone structures of *A. obtectus*.

(Imura, 1990; Rees, 1995; Watanabe, 1990). *Callosobruchus maculatus* F. has been reported only in cultivated and stored legumes, while *Callosobruchus chinensis* L. is capable to also infest a few wild legumes (Shinoda et al., 1992; Tuda et al., 2005).

2.2.1. *Callosobruchus chinensis* L.

Several classes of semiochemicals have been studied in *C. chinensis*, including oviposition stimulants from host seeds (Ignacimuthu et al., 2000; Matsumoto et al., 1994; Tebayashi et al., 1995; Ueno et al., 1990), an oviposition marking pheromone (Honda and Ohsawa, 1990; Oshima et al., 1973; Sakai et al., 1986), and a female sex pheromone (Tanaka et al., 1981).

A kairomone which promotes oviposition composed by a synergistic mixture of D-catechin (**7**), Taxifolin (**8**) and Quercimeritrin (**9**) was isolated from aqueous extracts of azuki bean *Vigna angularis* (Fig. 2) (Matsumoto et al., 1994; Tebayashi et al., 1995; Ueno et al., 1990). When D-catechin was tested individually, it was the most active compound. Moreover, an oviposition-deterrent pheromone was extracted with diethyl-ether from eggs, although its chemical composition remains unknown (Tanaka, 1991, 2000). On the other hand, volatiles from uninfested or egg carrying seeds were reported to act as attractants, while deterrence increases as the development of the eggs progresses into larval stages (Ignacimuthu et al., 2000).

Mate location and mating processes in *C. chinensis* are mediated

by two distinct pheromonal signals: a sex pheromone that attracts males from a distance and a contact sex pheromone that elicits copulation behaviour from males (Tanaka et al., 1981). Erectin was described as the contact sex pheromone that induces *C. chinensis* males to protrude the aedeagus and attempt copulation (Tanaka et al., 1981). This pheromone has been characterized as a mixture of one dicarboxylic acid, (*E*)-3,7-dimethyl-2-octene-1,8-dioic acid (**10**), and C25–C35 straight-chain and methyl-branched hydrocarbons (3-methylpentacosane, 11-methylheptacosane, 3-methylheptacosane, 11-methylnonacosane, 13-methylnonacosane, 11,15-dimethylnonacosane, 13-methylhentriacontane, 9,13-dimethylhentriacontane and 11,15-dimethyltrtriacontane), (Fig. 2) (Tanaka et al., 1981, 1982). Recently, the stereoisomeric composition of the copulation release pheromone of the *C. chinensis* was determined to be a mixture of *R*:*S* = 3.3–3.4:1 (Yajima et al., 2007).

In 2008, (2*Z*,6*E*)- and (2*E*,6*E*)-7-ethyl-3,11-dimethyl-2,6,10-dodecatrienals (**11** and **12**, respectively) were reported as female sex pheromones of *C. chinensis*. These compounds are homologs of farnesal, 3,7,11-trimethyl-2,6,10-dodecatrienal, in which a C-7 ethyl group is substituted by a methyl group (Shimomura et al., 2008). Pure compounds and their mixtures were active in behavioural assays under laboratory conditions.

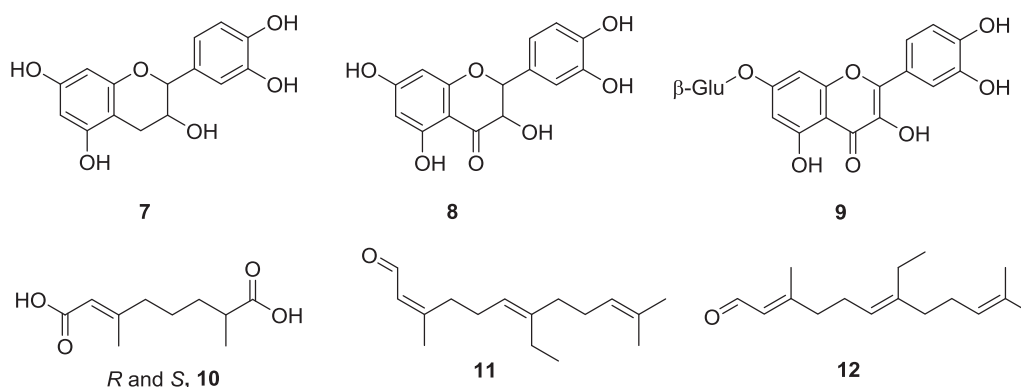


Fig. 2. Semiochemical structures of *C. chinensis*.

2.2.2. *Callosobruchus maculatus* F.

Callosobruchus seed beetles are pests of stored pulses, particularly in tropical and subtropical regions, being *Callosobruchus maculatus* (F.) the major pest of cowpeas and other legumes in those areas (Rees, 2004). A female sex pheromone has been identified in *C. maculatus* (Qj and Burkholder, 1982; Ramaswamy et al., 1995). Five acid compounds were isolated from virgin females: (3Z)-3-methyl-3-heptenoic acid (**13**), (3E)-3-methyl-3-heptenoic acid (**14**), 3-methyleneheptanoic acid (**15**), (2Z)-3-methyl-2-heptenoic acid (**16**), and (2E)-3-methyl-2-heptenoic acid (**17**), (Fig. 3) (Phillips et al., 1996). A comparison of the activities among them found that the 3Z and 3E compounds elicited the highest responses, and these were similar to the response elicited by the combination of all the molecules. Behavioural and electroantennographic (EAG) assays showed that **13** elicited by itself significantly higher male responses than **16** by itself, while a mixture of 25% **16** and 75% **13** elicited significantly higher responses from males than either of the two chemicals alone (Ramaswamy et al., 1995; Shu et al., 1996).

On the other hand, the chemical composition of chickpea bean and mung bean waxes and their influence on beetle behaviour were studied (Parr et al., 1998). Fatty acids presented to beetles like behenic acid (C22), arachidic acid (C20), and lignoceric acid (C24), among others, stimulated oviposition. The oleic acid (C18:1) produced a dual behaviour according to its concentration. In low quantities, oleic acid stimulated oviposition, while higher amounts of it reduced oviposition (Parr et al., 1998).

Moreover, in 2007 contact sex pheromone of *C. maculatus* was characterized as a mixture of dicarboxylic acids and hydrocarbons, 2,6-dimethyloctane-1,8-dioic acid (**18**) and nonanedioic acid (**19**), and a mixture of C27–C35 straight-chain and methyl-branched hydrocarbons (Fig. 3) (Nojima et al., 2007). *C. maculatus* has a similar contact sex pheromone system to that of *C. chinensis*. In fact, high proportions of males, of both *C. chinensis* and *C. maculatus*, exhibited copulation behaviour to females of other species in laboratory bioassays (Nojima et al., 2007).

2.2.3. *Callosobruchus analis* F.

The bruchid, *Callosobruchus analis* L., is a common storage insect pest of leguminous pulses (Bawa et al., 2017). Cork et al., 1991 identified **16**, as a single pheromone produced by female *C. analis* (Cork et al., 1991). The same compound was reported as part of the sex pheromone of *C. maculatus*.

Contact sex pheromones have been characterized by *C. chinensis* and *C. maculatus* as a mixture of monoterpene dicarboxylic acids and some hydrocarbons as it was described before (sections 2.2.1 and 2.2.2). However, comparisons of cross-copulatory activity (i.e., interspecific copulatory activity) among four congeneric species revealed that both beetles lacked the ability to discriminate their conspecific and/or heterospecific partners (Shimomura et al.,

2010d). On the other hand, male *C. analis* exhibited copulatory behaviour only in response to conspecific females among the four species, thus concluding the existence of a contact sex pheromone in this species (Shimomura et al., 2010d). Nevertheless, **18**, previously reported as a contact sex pheromone of *C. maculatus* (Nojima et al., 2007), and **10**, which was reported as a contact sex pheromone of *C. chinensis* (Tanaka et al., 1981, 1982) were found as contact sex pheromones of female *C. analis* (Shimomura et al., 2010a). Furthermore, the chirality of these compounds was determined as (2S, 6R)-dimethyloctane-1,8-dioic acid (*R*-**18**) and (3E, 7S)-dimethyl-2-octene-1,8-dioic acid (*S*-**10**), which means that both compounds were stereochemically pure, unlike the case of *C. maculatus* and *C. chinensis* (Fig. 4) (Shimomura et al., 2010a).

2.2.4. *Callosobruchus subinnotatus* P.

Bambara groundnut (*Vigna subterranea* L.) is the major source of dietary proteins for people in some parts of western Africa. The stored product insect, *C. subinnotatus*, is a major pest producing high loss to stored Bambara groundnut (Bawa et al., 2017; Lale and Vidal, 2001).

The production of sex pheromone by the *C. subinnotatus* female has been demonstrated studying male responses to virgin female extracts in EAG experiments and behavioural assays (Shu et al., 1998). The sex pheromone produced by *C. subinnotatus* females was identified as **16** and **17** (Shu et al., 1998, 1999). Both compounds were reported by *C. maculatus* and **16** was reported by *C. analis*.

C. subinnotatus is a tropical insect with distinct adult polymorphism. Two morphs of each sex, differing in their morphology, physiology, and behaviour, was reported (Appleby and Credland, 2001). Behavioural studies demonstrated that both males morph their response to the blends of **16** and **17** in several proportions (Fig. 4), (Mbata et al., 1999). Moreover, static-flow (with no air flow) olfactometric assays were conducted using *Callosobruchus subinnotatus* males finding that males were able to follow odour trails to the source. When the insects were tested in a Y-tube olfactometer, that provided directional wind cues, the latency period was longer than in static bioassays (Mbata et al., 2000). The same experiments were carried out with *C. maculatus* responding to sex pheromone of *C. subinnotatus*, but males of *C. subinnotatus* did not respond to that of *C. maculatus* (Mbata et al., 2000). These results allowed to postulate that **16** must have acted as an antagonist

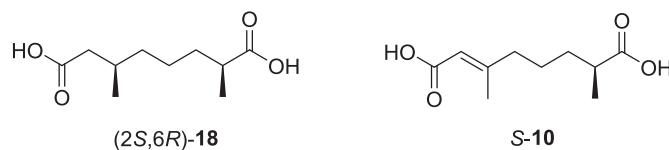


Fig. 4. Pheromone structures of *C. analis*.

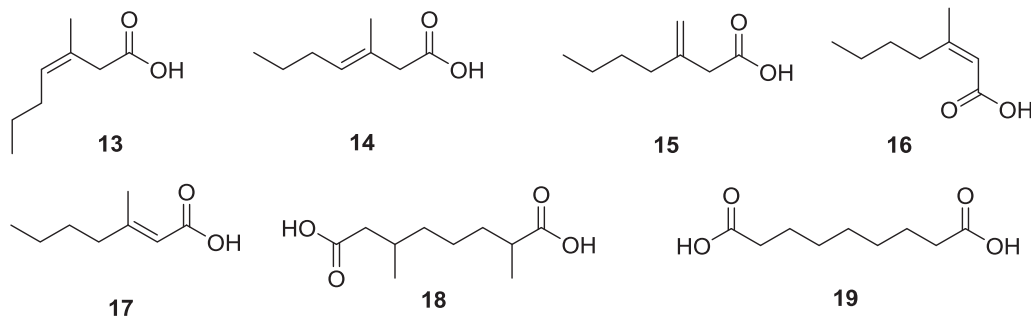


Fig. 3. Pheromone structures of *C. maculatus*.

inhibiting the response of *C. subinnotatus* to the sex pheromone of *C. maculatus* (Mbata et al., 2000).

2.2.5. *Callosobruchus rhodesianus* (Pic)

The seed beetle, *Callosobruchus rhodesianus* P., is an economic pest of stored legumes, especially cowpeas, in Africa. It is distributed in the Afrotropical region, mainly in southern Africa (Giga and Smith, 1983). The presence of a female-produced sex attractant pheromone component was identified as (3S,6E)-7-ethyl-3,11-dimethyl-6,10-dodecadienal (**20**) (Shimomura et al., 2010b). Besides, an additional electroantennographic active compound was detected without any characterization of its chemical properties. In the same year, the same authors described (E)-6-ethyl-2,10-dimethyl-5,9-undecadienal (**21**) as the other compound (Fig. 5) (Shimomura et al., 2010c).

Similarly to the other *Callosobruchus* species, the cuticular compounds of virgin females were studied to identify the contact sex pheromone (Shimomura et al., 2016). The chromatographic analysis of the active fraction revealed that the main active compounds were 6,10,14-trimethyl-2-pentadecanone (**22**) and 2-nonadecanone (**23**) (Fig. 5), and the synergists were C27–C33 hydrocarbons, n-alkanes, and an homologous series of mono- and dimethyl branched alkanes (Shimomura et al., 2016). The described molecules were different from the contact sex pheromones, monoterpene dicarboxylic acids, identified from congeneric species which justify the mate discrimination specificity in *C. rhodesianus*. Males of *C. maculatus* exhibited copulatory behaviour with females of both *C. maculatus* and *C. rhodesianus*, but males of *C. rhodesianus* attempted to mate with females of *C. rhodesianus* only (Shimomura et al., 2016). In order to establish the cause of this asymmetric cross-copulatory behaviour in *C. maculatus*, the compounds in the cuticles of female *C. rhodesianus* were studied again (Shimomura et al., 2017). Three compounds were identified: 2-methyloctanedioic acid (**24**), 3-methyloctanedioic acid (**25**), and **19**. However, the first two acid compounds in combination with hydrocarbons elicited significant copulatory induction activity (Shimomura et al., 2017). The structures of these molecules partially resemble **18**, *C. maculatus* contact sex pheromone (Nojima et al., 2007).

3. Pheromones with no chemical identification

Caryedon serratus O. is a pest of groundnuts (*Arachis hypogaea*)

as well as tamarinds (*Tamarindus indica*) (Sharma and Bhargava, 2015). Infestations cause reductions in food value, in the quality of the oil and reduce seed germination. Such damage is particularly significant when the peanuts are destined for confectionery purposes. In 1993 a female sex pheromone was proposed for this species based on behavioural assays (Chaïbou et al., 1993). Up to this point, this pheromone has not been identified. In a similar way, a female sex pheromone was proposed for *Bruchidius atrolineatus*, a pest of cowpea, without structural elucidation (Nammour et al., 1988; Pouzat and Ibeas, 1989).

Zabrotes subfasciatus B. is one of the main pests of stored beans, causing qualitative and quantitative loss in grains and seeds of legumes, mainly in the warmest regions of the world (Dendy and Credland, 1991). Behavioural experiments showed that females of *Zabrotes subfasciatus* produce a sex pheromone which triggers off male locomotor activity (Pimbert, 1987). These observations were confirmed by EAG experiments (Pimbert and Pouzat, 1988).

4. Conclusions

Bruchids are serious pests of dried, stored, durable agricultural commodities and of many value-added food products and nonfood derivatives of agricultural products worldwide. The detection of infestation is a most crucial part of stored product management. In the early stages of attack the only symptoms are the presence of eggs cemented to the surface of the seeds or grains. To minimize the use of insecticides and to maximize the application of an eco-friendly and sustainable approach should be the aims for managing stored grain insects below the economic threshold level. The importance of semiochemicals in a pest management program under field conditions is the topic of several studies, but this is not so in storage conditions (Agelopoulos et al., 1999; Jones, 1998; Phillips, 1997; Phillips et al., 2000). Many types of traps are used for monitoring populations of stored product insect populations such as moth and beetles in warehouses and mills (Burkholder, 1990; Cogan et al., 1990; Mullen, 1992; Phillips, 1997; Plarre, 1998). Moreover, the reports of semiochemicals used for management or monitoring of the Bruchids species are scarce. This is due to the fact that the pheromones produced by stored-product beetles are generally more complex when compared with the pheromones produced by stored-product moths. The synthesis of these molecules requires a more complicated chemistry, apart from the fact that the pheromone lures generally involve a mix of a large number

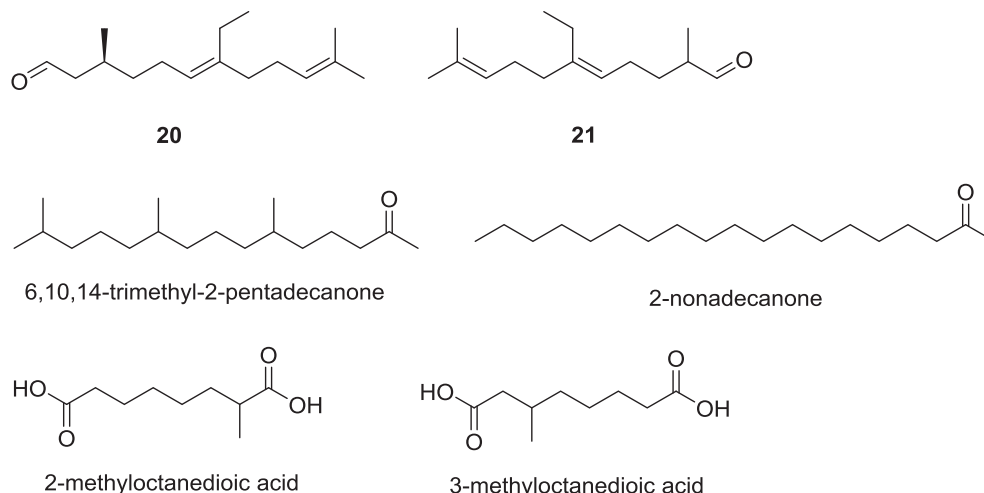


Fig. 5. Pheromone structures of *C. rhodesianus*.

Table 1
Bruchidae pheromones summary.

| Compound | Species | Action | References | Activity has been confirmed by other groups ^d |
|--|---------------------------------------|-----------------------------------|---|--|
| | <i>Acanthoscelides obtectus</i> S. | | | |
| methyl (<i>E,R</i>)-2,4,5-tetradecatrienoate (1) | | male sex pheromone ^a | Horler, 1970. | Yes |
| octadecanal (2) | | deterrent pheromone ^b | Vuts et al., 2015a,b. | Yes |
| methyl (2 <i>E</i> ,4 <i>Z</i> ,7 <i>Z</i>)-2,4,7-decatrienoate (3) | | male sex pheromone | Annoscia et al., 2010. | Yes |
| methyl (2 <i>E</i> ,4 <i>Z</i>)-2,4-decadienoate (4) | | male sex pheromone | Vuts et al., 2015a,b. | Not |
| (3 <i>Z</i> ,6 <i>E</i>)- α -farnesene (5) | | male sex pheromone | Vuts et al., 2015a,b. | Not |
| (3 <i>E</i> ,6 <i>E</i>)- α -farnesene (6) | | male sex pheromone | Vuts et al., 2015a,b. | Not |
| C25 to C31 <i>n</i> -alkanes and branched alkanes | | deterrent pheromone | Savković et al., 2012. | Yes |
| | <i>Callosobruchus chinensis</i> L. | | | |
| D-catechin (7) | | oviposition stimulant | Ueno et al., 1990. | Yes |
| Taxifolin (8) | | oviposition stimulant | Matsumoto et al., 1994. | Yes |
| Quercimeritrin (9) | | oviposition stimulant | Tebayashi et al., 1995. | Yes |
| (<i>E</i>)-3,7-dimethyl-2-octene-1,8-dioic acid (10) (R,S mixture) | | contact sex pheromone | Tanaka et al., 1981; Yajima et al., 2007. | Yes |
| C25–C35 <i>n</i> -alkanes and branched alkanes | | contact sex pheromone | Tanaka et al., 1981; Yajima et al., 2007. | Yes |
| (2 <i>Z</i> ,6 <i>E</i>)-7-ethyl-3,11-dimethyl-2,6,10-dodecatrienal (11) | | female sex pheromone ^c | Shimomura et al., 2008. | Not |
| (2 <i>E</i> ,6 <i>E</i>)-7-ethyl-3,11-dimethyl-2,6,10-dodecatrienal (12) | | female sex pheromone | Shimomura et al., 2008. | Not |
| | <i>Callosobruchus maculatus</i> (F.) | | | |
| (3 <i>Z</i>)-3-methyl-3-heptenoic acid (13) | | female sex pheromone | Phillips et al., 1996. | Yes |
| (3 <i>E</i>)-3-methyl-3-heptenoic acid (14) | | female sex pheromone | Phillips et al., 1996. | Yes |
| 3-methyleneheptanoic acid (15) | | female sex pheromone | Phillips et al., 1996. | Yes |
| (2 <i>Z</i>)-3-methyl-2-heptenoic acid (16) | | female sex pheromone | Phillips et al., 1996. | Yes |
| (2 <i>E</i>)-3-methyl-2-heptenoic acid (17) | | female sex pheromone | Phillips et al., 1996. | Yes |
| behenic acid, arachidic acid, lignoceric acid | | oviposition stimulant | Parr et al., 1998. | Yes |
| oleic acid in a low quantity | | oviposition stimulant | Parr et al., 1998. | Yes |
| oleic acid in a high quantity | | oviposition inhibitor | Parr et al., 1998. | Yes |
| 2,6-dimethyloctane-1,8-dioic acid (18) | | contact sex pheromone | Nojima et al., 2007. | Not |
| nonanedioic acid (19) | | contact sex pheromone | Nojima et al., 2007. | Not |
| C25 to C35 <i>n</i> -alkanes and branched alkanes | | contact sex pheromone | Nojima et al., 2007. | Not |
| | <i>Callosobruchus analis</i> F. | | | |
| 16 | | female sex pheromone | Cork et al., 1991. | Not |
| S-10 | | contact sex pheromone | Shimomura et al., 2010a,b,c,d. | Not |
| (2 <i>S</i> ,6 <i>R</i>)- 18 | | contact sex pheromone | Shimomura et al., 2010a,b,c,d. | Not |
| | <i>Callosobruchus subinnotatus</i> P. | | | |
| 16 | | female sex pheromone | Shu et al., 1998; Shu et al., 1999. | Yes |
| 17 | | female sex pheromone | Shu et al., 1998; Shu et al., 1999. | Yes |
| | <i>Callosobruchus rhodesianus</i> P. | | | |
| (3 <i>S</i> ,6 <i>E</i>)-7-ethyl-3,11-dimethyl-6,10-dodecadienal (20) | | female sex pheromone | Shimomura et al., 2010a,b,c,d. | Not |
| (<i>E</i>)-6-ethyl-2,10-dimethyl-5,9-undecadienal (21) | | female sex pheromone | Shimomura et al., 2010a,b,c,d. | Not |
| 6,10,14-trimethyl-2-pentadecanone (22) | | contact sex pheromone | Shimomura et al., 2016. | Not |
| 2-nonadecanone (23) | | contact sex pheromone | Shimomura et al., 2016. | Not |
| C27–C33 hydrocarbons | | contact sex pheromone | Shimomura et al., 2016. | Not |
| 2-methyloctanedioic acid (24) | | contact sex pheromone | Shimomura et al., 2017. | Not |
| 3-methyloctanedioic acid (25) | | contact sex pheromone | Shimomura et al., 2017. | Not |
| 19 | | contact sex pheromone | Shimomura et al., 2017. | Not |

^a Male sex pheromone: pheromone produced by males.

^b Deterrent pheromone: pheromone that produce repellency in conspecifics.

^c Female sex pheromone: pheromone produced by females.

^d This column shows if the compound activity was determined by independent research groups.

of compounds. On the other hand, the uses of kairomones that enhance the attraction to pheromone traps in order to manage the Bruchidae species are understudied. Research should provide new tools to aid in the monitoring of some stored-product insects not just in storage conditions but even in field conditions prior to crop harvest.

In this article, research related to bruchid pheromones has been reviewed. The studies are motivated by the prospect of gaining a better understanding of ecological relationships with the intention to develop environmentally benign methods of stored pest control. In summary, more than twenty-five compounds were characterized as semiochemicals for the Bruchidae family (Table 1).

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