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Chemotaxis and Ecology of Oviposition in Major Scarab Beetle Soil Pests of Crops – A review

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Abstract

Anomala corpulenta, *Holotrichia oblita*, and *Holotrichia parallela* are scarab beetles and major soil-dwelling insect pests. Their larvae feed on roots of peanuts, soybean and potato, causing considerable yield loss (15-100%). Adults of *Potosia brevitarsis* are active above ground and feed on a range of fruits and sweet corn while its larvae feed on roots, dung and decaying matter. The pest status and management of these scarab beetles is a challenge to the farming community across the globe due to bans on soil insecticides, pesticide resistance, and limited efficacy of foliar insecticides. Understanding the chemical ecology of oviposition in these beetles is key to the development of alternative control strategies such as attract-and-kill traps. This review recorded 138 Volatile Organic Compounds (VOCs) from oviposition hosts of these beetles. These are green leaf volatiles, sex pheromones and odors from decomposing materials. These compounds are identified as terpenoids, aliphatic alcohols, esters, aldehydes, alkenes, alkanes, ketones, aromatic compounds, carboxylic acids, and heterocyclic compounds. They are also reported to bind on chemosensory receptors, which may justify oviposition behavioral responses in these beetles. Research gaps are highlighted to underpin the designing of further in-depth studies to develop selective and safer control measures for Integrated Pest Management programs.

Key words: *Anomala corpulenta, chemotaxis, oviposition ecology, Holotrichia oblita, Holotrichia parallela, Potosia brevitarsis*

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Introduction

The metallic green beetle, *Anomala corpulenta* (Motschulsky, 1854), the dark black chafer, *Holotrichia parallela* (Motschulsky 1854), the large black chafer, *Holotrichia oblita* (Falderman, 1835), and the white-spotted flower chafer, *Potosia brevitarsis* (Leiwis, 1835), also published as *Protaetia/Postosia/ brevitarsis/brevitaris* all belong to the family Scarabaeidae within the insect order Coleoptera (Figure 1).

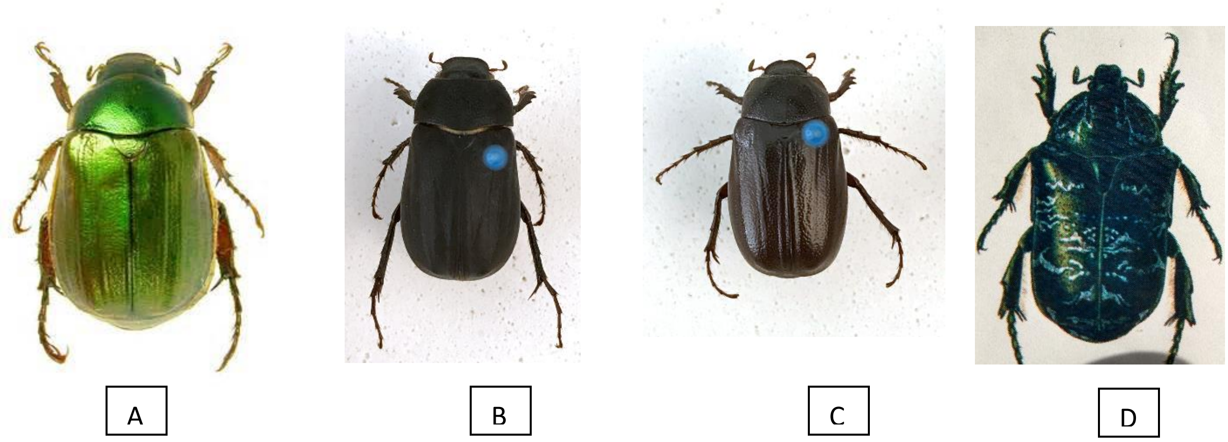

Figure 1. *From left to right, adults of Anomala corpulenta, Holotrichia parallela, Holotrichia oblita and Potosia brevitarsis (Courtesy to Zhang Shuai), the blue spot-on B and C is a pin attaching the insect to the board where they are conserved in the laboratory*

Figure 2. From left to right Branches with leaves of the waxyleaf privet (Ligustrum lucidum Aiton) and the elm tree (Ulmus pumila L.)

Holotrichia parallela and *H. oblita* are recorded under the sub-family Melolonthinae (Li et al., 2010) while *A. corpulenta* and *P. brevitarsis* belong to the sub-family Rotelinae (Li et al., 2015) and Cetoniinae (Wen et al., 2004), respectively. Multiple records reporting the aforementioned four species as crop pests are found in China, Japan, South Korea, North Korea and Russia (Toepfer et al., 2014). From these points on, we will refer to these four scarab beetles as SBs.

Key food crops such as peanuts, soybean, potato and corn are attacked by *A. corpulenta*, *H. oblita* and *H. parallela* (Zhang et al., 2006, Yu et al., 2007 and Li et al., 2015), while *Potosia brevitarsis,* is a pest of sweet corn and fruits (Wen et al., 2004 and Chen & Li, 2011), particularly, in Western China. Yield losses inflicted by the SBs are estimated in the range of 15-100% depending on the type of crop and the agro-ecological zone (Yu et al., 2007 and Luo et al., 2008). The management of these SBs as pests of crops is difficult due to several factors: (1) complexity of their biology, ecology and behavior, (2) lack of proper IPM strategies, (3) ineffectiveness of biological control (Wei et al., 1995), (4) resistance to high toxicity insecticides, and (5) banning of soil insecticides (Chen & Zhao, 2008). Such complex scenario calls for the prompt research and development of Integrated Pest Management (IPM) programs that include alternative and effective control methods.

This review highlights current knowledge on chemical volatiles, behavioral responses and the ecology of oviposition in major scarab beetle pests of crops. Where possible, similar information on insects in the same taxa has been included to steer the way to future related research. For example, it is now known that, the acceptance or rejection of host plants for oviposition occurs mainly as response to stimuli at the leaf surface (Potter & Held, 2002). Subsequently, the female takes the final decision to oviposit or not, based on the balance between opposing positive and negative cues from phytochemicals (Renwick & Chew, 1994).

Field and laboratory experiments established that not only plant volatiles attract SBs for oviposition, but also application of organic fertilizers such as broiler litter, cow manure, hay and milorganite. The presence of these fertilizers resulted in higher densities of grubs by attracting ovipositing females and acting as food attractant for larvae in the green June beetle, *Cotinis nitida* L. (Coleoptera: Cetoniinae) (Brandhorst-Hubbard et al., 2001).

It is also known that adults of scarab beetles exhibit oviposition preference for more suitable hosts that could enhance their offspring survival (Szendrei et al., 2005). This is the case of *Phyllophaga cuyabana* Moser (Coleoptera: Melolonthinae) which lays a larger number of eggs under soybean (*Glycine max* L.) and sunflower (*Helianthus annus* L.) compared to cotton (*Gossypium hirsutum* L.) (Oliveira et al., 2007). This can be partially explained by the greater amount of residues provided by leguminous crops which serve as food source for first and second instar larvae (Silva & Salvadori, 2004). However, adult feeding preference and offspringperformance cannot always be correlated. This is the case of polyphagous scarab beetles such as *Popillia japonica* Newman (Coleoptera: Scarabeidae), which is attracted by a wide array of plants regardless their suitability as host to larval stages (Oliveira et al., 2007). It is noteworthy to point out that, compared to food-searching behaviors, few cues are known to be involved in the selection of oviposition sites (Potter & Held, 2002). Particular strategies, such as "habitat manipulation" highlight the importance of better understanding oviposition ecological dynamics in successful control strategies (Gurr et al., 2004). For example, changing the composition of host plants has been reported to influence insect reproduction behavior (Hartwig & Ammon, 2002), and natural predator's density.

Ecological and Biological Conditions of Oviposition

For the oviposition to happen, some ecological factors such as climatic conditions must be conducive for the adults. Usually, the first adult flights of these SBs are observed during slightly different months of the year but, the adults are generally recorded more active in summer (May-August), when the temperature and soil moisture content are favorable for the survival of their life stages (eggs, larvae, pupae and adults) (Table 1). Field observations using light traps revealed that adult of *Holotrichia oblita* is the first to emerge as it is observed in April with peaks in May-June, and that the adult activity sensibly declines in July towards August when they are no longer seen (Hui et al., 1987). The adults of *Anomala corpulenta* emerge in May and are more active in June (Kuoh & Chang 1959). Similarly, *Potosia brevitarsis*, appears in May but it is more active in July (Hui et al., 1987). The last scarab beetle to emerge is *Holotrichia parallela* observed in June with adult flight peaks in July and adult activity declining in September (Kuoh & Chang, 1959 and Chuno et al., 1960).

The above-mentioned patterns of the SBs are consistent with the cropping season, optimum temperature and relative humidity. An ambient temperature of 25^0C and a relative humidity in the range 50-70%, have been reported adequate throughout the development of the four growth stages of the SBs (Hui et al., 1987). In addition, eggs have been recorded in soil depths ranging from 5 to 10 cm (Kuoh & Chang, 1959) and when they emerge they mobilize deeper to 10-20 cm depths. The latter depth matches nicely with the crop root zone, which is one of the main food sources for scarab larvae (Table 1). Soil moisture content is estimated optimal in the range of 10-30% for all the growth stages, otherwise desiccation or decay of eggs will occur (Dang et al., 2009). For example (Liu et al., 2008) reported that a soil moisture content in the range of 18-20% is the most suitable for egg hatching and early survival of larvae for *H. oblita* but when hibernation conditions occur larvae will go deeper into the soil to 30-40 cm (larval hibernation) and to 10.2 -22.5 cm (pupal hibernation) (Kuoh & Chang (1959).

For successful oviposition to occur, sexual maturity, mating and feeding time must be optimally synchronized in the SBs. Their sexual maturity is attained within 15 or 30 days after the first flight, while the first oviposition is expected 2-3 days after mating (Kuoh & Chang, 1959). Because they are nocturnal insects, light intensity influences their biological activity according to Kuoh & Chang (1959), who reported that the optimum light intensity should be below 60 lux. Further research shows that light intensity out of the range 15-20 lux would interfere with the behavior of the SBs (Professor Yazhong Cao personal communication). In line with this, mating of these beetles occurs early in the night, immediately after emergence from soil (19:30-20:30) and feeding starts soon after until mid-night or in the morning when they go back into soil for oviposition (Chen et al., 2015). *P. brevitarsis* makes the exception as it is active day and night (Hui et al., 1987) and oviposits throughout the year while the maximum oviposition period for the three other beetles, varies from 30-120 days (Table 1).

Table 1. *Summary of biological and ecological conditions for the development stages of the four SBs. The shaded cells indicate that the information does not apply while the dashed cells mean the data could not be retrieved through this review. The superscript numbers stand in for citations or special notes as captured at the end of this table.*

Ecology & Biology	*Anomala corpulenta*				*Holotrichia oblita*			
	Egg	Larva	Pupa	Adult	Egg	Larva	Pupa	Adult
Observation Period (months)	June	June	May-Aug.[4]	May-June[4,5]	May	May-Aug.	Aug.	April-Aug.[9]
Adult Daily Emergence from Soil (hour: minutes)	▨	▨	▨	19:30[5]	▨	▨	▨	19:30-20:00
Sexual Maturity (days following first flight from soil)	▨	▨	▨	15-30	▨	▨	▨	15-30
Mating time	▨	▨	▨	19:30-20:00 [5]	▨	▨	▨	20:00-20:30
Adult Feeding time	▨	▨	▨	20:00-24h[5]	▨	▨	▨	-
Adult Back to soil (Time of day)	▨	▨	▨	24 h -Dawn[5]	▨	▨	▨	23-24 h
First oviposition (days after mating)	▨	▨	▨	2-3 [5]	▨	▨	▨	-
Maximum Oviposition Period (Length in days)	▨	▨	▨	30	▨	▨	▨	90-120[8]
Average Number of eggs produced*	▨	▨	▨	22-82 [5]	▨	▨	▨	84-145[6, 7]
Larval instars	-	3 instars	▨	▨	▨	3 instars	▨	▨
Larvae feeding period	▨	till Nov.[5]	▨	▨	▨	till Nov.[5]	▨	▨
Found in soil (cm beneath the soil surface)	6 [5]	7[5]	10-20	-	5-10	10-20	10-20	10-20 [9]
Soil depth for hibernation of larvae (cm beneath the soil surface)	-	30-40	10.2-22.5 [5]	-	-	30-40	-	-
Larvae emergence after hibernation	▨	end March[5]	▨	▨	▨	March-April [5]	▨	▨
Optimum Soil Moisture Content for Survival (%)	10-30[NB]	10-15[1]	15-20[1]	15[1]	10-20[1]	10-15[1]	15-20[1]	15 [1]
Temperature (^{0}C)	25^{0}C	25^{0}C	25^{0}C	25^{0}C	25^{0}C	25^{0}C	25^{0}C	25^{0}C [9]
Relative Humidity (%)	▨	▨	▨	50-70	▨	▨	▨	50-70
Light (lux)	▨	▨	▨	< 60 [5]	▨	▨	▨	15-20
Stage duration (days)	9 [5]-10.7[2]	180[3]-333[5,9]	7-10[5,9]	30♂-37♀ [5]	10	310	20	109.8♂-155.5♀[8]
Life cycle (Generations per year)	≤1 [5]				1-2 [9,11]			

[1]Dang et al. (2007&2009),[2]Wang et al., 2011, [3]Li et al., 2010, [4]Chuno et al., 1960, [5]Kuoh and Chang, 1959, [6]Liu et al. (2008) [7]Zhou et al. (2009) and [8]Chen et al. (2015), [9] Hui et al., (1987), [10]Song et al., (2008), [11]Wang et al., 1989. *Average cumulative amount of eggs per female, +Cow and sheep dung also in pig dung rich in humus, [NB]Soil moisture content lower than 10% or higher than 30%, eggs will decay or desiccate (Kuoh and Chang, 1959)

Ecology & Biology	*Holotrichia parallela*				*Potosia brevitarsis*			
	Egg	Larva	Pupa	Adult	Egg	Larva	Pupa	Adult
Observation Period (months)	July [9]	July [9]	-	June-July-September[4,5]	-	-	-	May- August [9]
Adult Daily Emergence from Soil (hour: minutes)				19:30-20:30				Day time [9]
Sexual Maturity (days following first flight from soil)				15-30				15-30
Mating time				20:00-22:00[9]				Day and night [9,11]
Adult Feeding time				21-24h				Day and night [9,11]
Adult Back to soil (Time of day)				23-24 h or Dawn				-
First oviposition (days after mating) [5]				2-3				-
Maximum Oviposition Period (Length in days)				40				Throughout life time [11]
Average Number of eggs produced*				23-316 [9]				18-72 [9,2]
Larval instars		3 instars				2-3 [3]		
Larvae/adult feeding period		till Nov.[5]						1st 10 days Sept.[11]
Found in soil (cm beneath the soil surface)	5-10	10-20	10-20		5-10[9]	10-20		-
Soil depth-hibernation (cm)		30-40	10.2-22.5 [5]			+Organic manure	-	
Larvae emergency after hibernation		end March[5]				-	-	
Optimum Soil Moisture Content for Survival (%)	10-30[NB]	10-15[1]	15-20[1]	15[1]	10-20[1]	-	-	-
Temperature (^{0}C)	25^0C			25^0C	-	-	-	25^0C
Relative Humidity (%)				50-70%				50-70%
Light (lux)				15-20 lux [9]				15-20
Stage duration (days)	10[12]	17.2-16.6-90[NB]	16-21 [9]	60-90[12]	7[2]-11 [9]	9-13-80[9]	30[10]	45 [9]
Life cycle (Generations per year)	1 year [5]				1 year [9]			

[1]Dang et al. (2009),[2]Wang et al., 2011, [3]Li et al., 2010, [4]Chuno et al., 1960, [5]Kuoh and Chang, 1959, [6]Liu et al. (2008) [7]Zhou et al. (2009) and [8]Chen et al. (2015), [9] Hui et al., (1987), [10]Xu et al., 2009, [11]Chen et al., 2006, [12]Luo, 1981, *Average cumulative amount of eggs per female, +Cow and sheep dung also in pig dung rich in humus, [NB]Soil moisture content lower than 10% or higher than 30%, eggs will decay or desiccate (Kuoh and Chang, 1959), ** For adult emergence from soil for mating and feeding, H. parallela makes exception as it emerges once every 2 days (Hui et al., 1987)

average cumulative amount of eggs per female is 22-82 eggs for *A. corpulenta* (Kuoh & Chang 1959), 84-145 eggs for *H. obilta* (Liu et al., 2008 and Zhou et al., 2009), 23-316 for *H. parallela* (Hui et al., 1987) and 18-72 for *P. brevitarsis* (Hui et al., 1987 and Wang et al., 2011).

Oviposition Preference and Larval Feeding hosts

Larval stages of these insects are spent in the soil where they feed on roots of a range of crops (Wei et al., 1989) with the exception of *P. brevitarsis* that feeds on decomposing manure rich in organic materials (Wen et al., 2004). Female choice for oviposition host in the SBs is linked with the availability of conditions that will sustain the development of their offspring. This is particularly important for larval feeding, which is mediated by chemical stimuli from the hosts (Meng et al., 1999). Choice-feeding bioassays and knowledge on oviposition hosts (Table 2), reveals that the oviposition hosts generally correlate with the larval feeding hosts. However, for *H. parallela* the larval feeding host is 2.5 fold as many as the adult feeding hosts as opposed to adults of *P. brevitarsis*, which feed on nine different plants and their larvae only feed on one type of plant.

Table 2. ***Feeding and oviposition host plants for the scarab beetle Anomala corpulenta, Holotrichia parallela, Holotrichia oblita and Potosia brevitarsis***

	Host Plants	***A. corpulenta***		***H. oblita***		***H. parallela***		***P. brevitarsis***	
		Adult	**Larva**	**Adult**	**Larva**	**Adult**	**Larva**	**Adult**	**Larva**
1.	Apple fruit *(Malus pumila* Miller*)*[3]	-	-	-	-	-	-	+	-
2.	Beet *(Beta vulgaris)* [2]	-	-	-	+	-	-	-	-
3.	Carrot (*Daucus carota* L.) [3]	-	-	-	-	-	-	+	-
4.	Chestnut (*Castanea mollissima)*[1]	-	-	+	-	-	-	-	-
5.	Chinese lacquer tree *(Toxicodendron vernicifluum* Stokes) F. Barkley [1]	-	-	+	-	-	-	-	-
6.	Chinese white poplar *(Populus tomentosa)*[1]	-	-	+	-	-	-	-	-
7.	Common wheat (*Triticum aestivum L.*)[2]	*	+	*	+	*	+	-	-
8.	Corn *(Zea mays* L.) [3]	*	+	*	+	*	+	+	-
9.	Cotton (*Gossypium hirsutum* L.) [2]	-	-	-	+	-	-	-	-
10.	Cow and pig dung[4]	-	-	-	-	-	-	*	+
11.	Elm tree *(Ulmus pumila* L.*)* [1,6]	-	-	+	-	+	-	-	-
12.	Grape *(Vitis spp.)* [3]	-	-	-	-	-	-	+	-
13.	Hemp *(Cannabis sativa)*[2]	-	-	-	+	-	-	-	-
14.	Irish potato *(Solanum tuberosum L.)* [1]	*	+	*	+	*	+	-	-
15.	Lesser yam (*Dioscorea esculenta* Lour.) [2]	-	-	-	+	-	-	-	-
16.	Melon (*Benincasa hispida* Thunb. (Cogn.)[3]	-	-	-	-	-	-	+	-
17.	Mulberry (*Morus australis* Poir) Morus *australis)*[1]	-	-	+	-	-	-	-	-
18.	Oak (*Quercus palustris* Münchh) *Quercus palustris*[1]	-	-	+	-	-	-	-	-
19.	Peaches (*Prunus persica* L.) [3]	-	-	-	-	-	-	+	-
20.	Peanut *(Arachis hypogaea L)*[1,6]	+*	+	+*	+	*	+	-	-
21.	Plums (*Prunus salicina* Lindl) [3]	-	-	-	-	-	-	+	-
22.	Sorghum *(Sorghum bicolor L.)* [2]	-	-	-	+	-	-	-	-
23.	*Soybean (Glycine max* L.*)* [1,6]	+*	+	+*	+	*	+	-	-
24.	Sunflower *(Helianthus annuus L.)* [3]	-	-	-	-	-	-	+	-
25.	Tomato **(***Solanum lycopersicum* L.) [3]	-	-	-	-	-	-	+	-
26.	Velvetweed (*Abutilon theophrasti* Medik)	-	-	-	-	+	-	-	-
27.	Walnut *(Juglans regia* L.)[1]	-	-	+	-	-	-	-	-
28.	Waxleaf privet *(Ligustrum quihoui* Carrière)	+	-	-	-	-	-	-	-

[1]Luo and Cui, 1995, [2]Wei et al., 1989, [3]Wen et al., 2004, [4]Li et al., 2010, [5]Li W-Z et al., 2010, [6]Li et al., 2009
*‘+’ indicates feeding host ’ * ’ host for oviposition and ‘-‘ not documented*

Adults of *A. corpulenta* and *H. oblita* are particular as they both feed and oviposit in peanuts and soybeans, albeit these crops are not their first feeding choice (Table 2). These observations are consistent with the theory of ‘Adult Oviposition Preference and Offspring Performance’, (Thompson, 1987). The ‘*Oviposition Preference*’ is described as the hierarchical ordering of plant species by ovipositing females, and it is expressed as the proportion of eggs laid on each of the plant species (Thompson, 1983). On the other hand (Scriber & Slanky, 1981) reported that ‘*offspring performance*’ can be used as a composite term to indicate survival at all immature stages (egg, larva, pupa), larval nutritional indices, growth rate, pupal mass, resultant adult fecundity and longevity.

Observations from a more than three years monitoring of the pest status of the SBs in China and Rwanda (Zhang Shuai personal communication), show high occurrence of larvae in peanuts, soybean and corn, which suggests these crops are the favorable host for *A. copulenta*, *H. oblita* and *H. parallela*.

This is consistent with findings from other insect taxa that clearly show the correlation between adult oviposition preference and larval performance. For example, Rausher (1984), recorded a correlation between the oviposition preference of the female beetles, *Deloyata guttata* (Coleoptera: Chrysomelidae) with the performance of their offspring, which later was linked to the evolution of host specificity (Bush & Diehl, 1982 and Futuyma & Peterson, 1985).

Feeding choice also influences fecundity on the SBs. When *H. oblita* adults are feed with elm tree leaves they have longer pre-oviposition period and survival time but when they are feed on oilseed rape, survival time is short and oviposition is impaired; furthermore, feeding *H. oblita* with Cattail (*Humulus spp.*) leads to higher fecundity per adult female (156.7 eggs) compared to elm leaves (145.4 eggs); egg hatching rate is higher when *H. oblita* is fed with peanut leaves (91.7%) and elm leaves (90.2%), while lower (46.7%) when fed with ryegrass (Liu et al., 2008). As for *P. brevitarsis,* egglaying is higher (18.4 eggs) when reared on corn compared to apple and peach (Hui et al., 1987).

Mechanisms Underlying Chemotaxis to Volatile Organic Compounds

Several cues are usually involved in eliciting behavioral responses in insects. These consist mainly of thermal, visual, tactile, and chemical cues. Many insect behaviors are initiated by chemical volatiles (i.e. molecules or assemblages of molecules) emitted by plants or insects. These molecules travel through the air and usually make contact with specialized structures in sensory organs (e.g. sensillae on the antennae). Sensory organs are porous and facilitate access of the molecules to olfactory receptors (part of receptor neurons) under the cuticle; once the molecules bind to the receptors, the signal transduction to the nervous system is effective (Laughlin *et al.*, 2008). After signal transduction, molecules are degraded by odorant-degrading enzymes (Leal, 1998 & Leal, 2013). A number of binding sites have been identified in this process, these include odorant-binding proteins (OBPs), chemosensory proteins (CSPs), sensory neuron membrane proteins, gustatory receptors, and ionotropic receptors.

Odorant-binding proteins and CSPs are the most abundant in the antenna sensilla of insects (Sanchez-Gracia et al., 2009). The OBPs are soluble proteins secreted in the sensilla lymph and are sophisticated chemical sensors and key drivers in chemical communication in insects (Pelosi & Maida, 1995). OBPs have been characterized from a range of insects (Vogt et al., 1991, 1999) including SBs such as *A. corpulenta*, *H. oblita* and *H. parallela.* To date, 15 OBPs have been identified in *A. corpulenta* Li et al. (2015), 2 OBPs (*Hpar*OBP-1 and *Hpar*OBP- 2) in *H. parallela* (Ju et al., 2012), and four OBPs (*Hobl*OPB1, 2, 3 &4) in *H. oblita* (Deng et al., 2011 and Wang et al., 2013).

Chemosensory Proteins also called Olfactory Specific D like (OS-D like) proteins, are recorded among the most important chemoreceptors (Robertson et al., 1995). They are not only found in antennae but also in proboscises, maxillary palps, labial palps, tarsus, abdomen, truncus, cuticle, legs, wings and pheromone glands (Jacquin-Joly et al., 2001). Two CSPs have so far been characterized in *H. oblita* (*HoblCSP1* and *HoblCSP 2*), which are specific for the transportation of sex pheromones (Lartigue et al., 2002) but are also involved in the binding of other ligands such as plant volatiles α-ionone, β-ionone and cinnamaldehyde (Wang et al. 2013 and Sun et al., 2014) (see Table 3).

Volatile Compounds and Behavioral Responses of Oviposition

Previous studies revealed a number of VOCs and chemoreceptors associated with signals for host recognition in some of the SBs (Table 3). In some cases, host plants emit identical VOCs that are also released by insect females as sex pheromones; this may create ideal conditions for numerous mating encounters and oviposition events on crop host plants. For example, the terpenoid linalool is a sex pheromone in female *H. parallela*; it specifically binds to *Hpar*OBP-2 (Ju et al., 2012). Linalool is also emitted by leafs of *H. parallela* host plants, corn and peanuts (Oluwafemi et al., 2011 and Cardoza et al., 2002), and it also effectively attracts males when combined with L-isoleucine methyl ester (Li-Mei et al., 2009).

Similarly, 53 kinds of compounds are able to bind on OBP *Acor*OBP1 from *A. corpulenta*; in particular, methyl salicylate and decyl alcohol that are emitted by its most common host plant the waxyleaf privet (*Ligustrum quihoui* Carr.) (Fig. 2). Through this literature search, it was realized that different scarab beetle species can respond to the same VOCs released by a host crop which is thought to explain the co-occurrence of larvae in the same field as it is the case of *H. parallela, H. oblita* and *A. corpulenta* that are commonly recorded in peanut fields in China (Zhang Shuai, personal communication). A terpenoid α –ionone, found in potato (*Solanum tubersum*) and trans-2-Hexanal, an aliphatic aldehyde found in soybean, bind to *Hpar*OBP- 1 (Ju et al., 2012) and *Hobl*OBP 3&4 (Deng et al., 2011 and Wang et al., 2013), which are OBPs from *H. parallela* and *H. oblita*, respectively (Table 3). This interaction between VOCs and OBPs in these beetles might be the reason to support their congregation and oviposition in fields planted with the host crops indicated in this paragraph.

Table 3. *Plant volatile attractants to A. corpulenta, H. parallela, H. oblita and P. Brevitarsis. 'N' indicates 'Not binding' while 'NR' means that the information could not retrieved*

#	Ligands	Type	Origin	Scarab beetle	Binding Site	Reference
1	(E)-2-decen-1-ol	Aliphatic alcohol	Corn- var. deprim (attracts)	NR	NR	Oluwafemi *et al.*, 2011
2		Aliphatic Alkene	Peanut	NR	NR	Cardoza *et al.*, 2002
	(E)-4,8-dimethyl-1,3,7-nonatriene (DMNT)		Corn- var. deprim (repellent)	NR	NR	Oluwafemi *et al.*, 2011
4	(E)-caryophyllene	Terpenoid	Corn- var. deprim (repellent)	NR	NR	Oluwafemi *et al.*, 2011
5	(E)-β-farnesene	Sesquiterpene	Corn- var. deprim (repellent)	NR	NR	Oluwafemi *et al.*, 2011
6	(E, E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT)	Sesquiterpene	Corn- var. deprim (repellent)	NR	NR	Oluwafemi *et al.*, 2011
7	(z) -3-hexen-1-ol/(Z)-3-hexenyl acetate/3-Hexen-1-ol, acetate/ Cis-3-Hexen-1-ol	Aliphatic alcohol	Elm tree	*H. parallela*	*HparOBP-1&2*	Ju *et al.*, 2012
			Corn (var. stylepark)	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013, Buttery & Ling (1984)
			Elm tree	*H. oblita*	*HoblCSP2*	Sun *et al.*, 2014
8	(z) -3-hexenol/trans-2-Hexenol	Aliphatic alcohol	Corn (var. stylepark)	*H.oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
9	(Z)-4-hepten-2-one	Aliphatic ketones	Corn (var. stylepark)	NR	NR	Buttery & Ling (1984)
10	1-Decanal	Aliphatic aldehydes		*H.oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
11	1-dodecene	Aliphatic Alkene	Soybean var. 'PI 227687'	NR	NR	Liu *et al.*, (1988)
12	1-Heptaldehyde	Aldehyde compounds	NR	NR	Not binding HoblCSP	Sun *et al.*, 2014
13	1-Heptanal	Aliphatic aldehydes	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
16	1-Heptanol	Aliphatic alcohol	NR	*H.oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
17	1-Hexanal	Aliphatic aldehydes	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
18	1-Hexanol	Aliphatic alcohol	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
19	1-methyl-naphtalene	Aromatic Alkene	Cow dung	NR	NR	Huang *et al.*, 2007
20	1-Nonanol	Aliphatic alcohol	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
21	1-octanol	Aliphatic alcohol	NR	*H. oblita*	*HoblCSP1&2*	Sun *et al.*, 2014
22	1-Octen-3-ol	Aliphatic alcohol	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
			NR	*H. oblita*	*HoblCSP 1*	Sun *et al.*, 2014
23	1-Pentanal	Aliphatic aldehydes	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
24	1-Propanol	Aliphatic alcohol	NR	*P. brevitarsis*		Chen & Li, 2011
25	2,2- dimethyl hexanal	Aliphatic aldehydes	Soybean (var. 'Davis')	NR	NR	Liu *et al.*, (1988)
26	2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3-(4H)-one (DIMBOA)	Aliphatic ketones	Corn	NR	NR	Konstantopoulou *et al.*, 2004
27	2-butanol	Aliphatic alcohol	Chicken	NR	NR	Yasuhara *et al.* (1989)
28	2-butyl acetate	Aliphatic ester	Chicken	NR	NR	Yasuhara *et al.* (1989)
29	2-Cyclohexen-1-one	Aliphatic ketones	NR	*H.oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
30	2-Ethy1-1- Hexanol	Aliphatic alcohol	Elm tree	*H. oblita*	*HparOBP-1&2*	Ju *et al.*, 2012
31	2-heptanone	Aliphatic ketones	Corn (var. stylepark)	NR	NR	Buttery & Ling (1984)
32	2-hexanone	Aliphatic ketones	Chicken	NR	NR	Yasuhara *et al.* (1989)
33	2-hexenal	Aliphatic aldehydes	Soybean (var. 'Davis')	NR	NR	Liu *et al.*, (1988)
34	2-methylpropionic acid	Carboxylic acid	Chicken	NR	NR	Yasuhara *et al.* (1989)
35	2-pentanol	Aliphatic alcohol	Chicken	NR	NR	Yasuhara *et al.* (1989)
36	2-Phenethyl propionate	Aliphatic ester	NR	*P. brevitarsis*		Chen & Li, 2011
37	2-propanol	Aliphatic alcohol	Chicken	NR	NR	Yasuhara *et al.* (1989)
38	3,7,11,15-tetramethyl-2-hexadecen-1-ol (phytol)	Aliphatic alcohol	Corn	NR	NR	Konstantopoulou *et al.*, 2004
39	3-methyl-1 H-indole	Volatile Organic Compounds	Cow dung	NR	NR	Huang *et al.*, 2007
40	3-methylbutyric acid	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)
41	3-tetradecene	Aliphatic Alkene	Soybean var. 'PI 227687'	NR	NR	Liu *et al.*, (1988)
42	4-ethyl-phenol	Volatile Organic Compounds	Chicken	NR	NR	Huang *et al*, 2007
43	4-hexen-1-ol acetate	Aliphatic alcohol	Soybean (var. 'Davis')	NR	NR	Liu *et al.*, (1988)
44	4-methylpentanoic acid	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)

#	Ligands	Type	Origin	Scarab beetle	Binding Site	Reference
45	4-methyl-phenol	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)
46	4-tert-Butyl cyclohexanol	Aliphatic alcohol	NR	NR	*HoblOBP3&4*	Wang *et al.*, 2013
					HparOBP-1&2	Ju *et al.*, 2012
					HoblCSP1&2	Sun *et al.*, 2014
47	6-Methyl-5-hepten-2-one	Aliphatic ketones	Elm tree	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
				H. oblita	*HoblCSP2*	Sun *et al.*, 2014
48	Acetamide	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)
49	Acetic acid	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara et *al.* (1989)
50	Acetoin	Synthetic compounds	NR	*P. brevitarsis*	NR	Chen & Li, 2011
51	Acetone	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)
52	Anisole	Aromatic compound	NR	NR	NR	Sun *et al.*, 2014
53	Anetole	Aromatic compound	NR	*P. brevitarsis*	NR	Chen & Li, 2011
54	Benzaldehyde	Aromatic compound	Elm tree	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
				H. parallela	*HparOBP-2,*	Ju *et al., 2012*
				H. oblita	*HoblCSP1&2*	Sun *et al.*, 2014
55	Benzene	Aromatic compound	Chicken	NR	NR	Yasuhara *et al.* (1989)
56	Benzeneacetaldehyde	Aromatic compound	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
				P. brevitarsis	NR	Chen & Li, 2011
57	Benzyl acetate	Aliphatic Ester	Corn- var. deprim (repellent)	NR	NR	Oluwafemi *et al.*, 2011
58	Benzyl alcohol	Aromatic compound	NR	NR	NR	Sun *et al.*, 2014
				P. brevitarsis	NR	Chen & Li, 2011
59	Butanamide	Amide	Chicken	NR	NR	Yasuhara *et al.* (1989)
60	Butanol	Aliphatic Alcohol	NR	*P. brevitarsis*	NR	Chen & Li, 2011
61	Butyl benzoate	Aliphatic ester	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
62	Butyric acid	Carboxylic acid	Chicken	NR	NR	Yasuhara *et al.* (1989)
63	Camphene	Terpenoid	Elem tree	*H. oblita*	*HoblCSP1*	Sun *et al.*, 2014
64	Caryophyllene	Terpenoid	Corn (var. stylepark)	NR	NR	Buttery & Ling (1984)
65	Cinnamaldehyde	Aromatic compound	R. communis	*H.oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
				H. oblita	*HoblCSP1&2*	Sun *et al.*, 2014
66	Cinnamyl alcohol	Aliphatic alcohol	NR	*P. brevitarsis*	NR	Chen & Li, 2011
67	Cis-2-Hexen-1-ol	Aliphatic alcohol	NR	*H.oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
68	Citronellol	Acyclic mono-terpenoid	NR	*P. brevitarsis*	NR	Chen & Li, 2011
69	Cyclosativene	Aliphatic Alkane	Corn (var. stylepark)	NR	NR	Buttery & Ling (1984)
			Corn (var. NR)	NR	NR	Konstantopoulou *et al.*, 2004
70	Decanal	Aldehyde compound	Elm tree	NR	Not binding HoblCSP	Sun *et al.*, 2014
			Corn- var. deprim (attracts)	NR	NR	Oluwafemi *et al.*, 2011
71	Decane	Aliphatic alkane	NR	*H.oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
72	Dimererhyl phthalate	Aromatic compound	NR	*H. oblita*	*HoblCSP1*	Sun *et al.*, 2014
73	Dimethyl trisulphide	Volatile Organic Compound	Chicken	NR	NR	Yasuhara *et al.* (1989)
74	Diphenyl ketone	Aliphatic ketones	NR	*P. brevitarsis*	NR	Chen & Li, 2011
75	E-2-Hexen-1-ol	Aliphatic alcohol	Elm tree	*H. parallela*	*HparOBP-1*	Ju *et al.*, 2012
76	Ethanol	Aliphatic alcohol	Chicken	NR	NR	Yasuhara *et al.* (1989)
				P. brevitarsis	NR	Chen & Li, 2011
77	Ethyl acetate	Volatile Organic Compound	Chicken	NR	NR	Yasuhara *et al.* (1989)
78	Ethyl butyrate	Volatile Organic Compound	Chicken	NR	NR	Yasuhara *et al.* (1989)
79	Ethyl formate	Volatile Organic Compound	Chicken	NR	NR	Yasuhara *et al.* (1989)
80	Eugenol	Aromatic compound	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
				H. oblita	*HoblCSP1*	Sun *et al.*, 2014
81	Farnesol	Plant volatiles	Elm tree	*H. parallela*	*HparOBP-1*	Ju *et al.*, 2012

#	Ligands	Type	Origin	Scarab beetle	Binding Site	Reference
82	Ferulic acids	Volatile Organic Compounds	Wheat Straw	NR	NR	Bowen & Harper, 1990
83	Geraniol	Terpenoid	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
					Not binding HoblCSP	Sun *et al.*, 2014
				P. brevitarsis	NR	Chen & Li, 2011
84	Geranyl acetate	Aliphatic ester	Corn- var. deprim (repellent)	NR	NR	Oluwafemi *et al.*, 2011
85	Glycine ethyl ester	Aliphatic ester	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
			H. oblita	*H. oblita*	*HoblCSP1&2*	Sun *et al.*, 2014
86	Heptane	Aliphatic alkanes	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
87	Hexane	Aliphatic alkanes	NR	*H. oblita*	Not binding HoblCSP	Sun *et al.*, 2014
88	Hexanoic acid	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)
89	Hexanol	Aliphatic alcohol	NR	*H. oblita*	*HparOBP-1&2*	Sun *et al.*, 2014
				P. brevitarsis	NR	Chen & Li, 2011
90	Hexyl benzoate	Aliphatic ester	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
91	Indole	Heterocyclic compound	Elm tree	*H. oblita*	*HoblCSP1&2*	Sun *et al.*, 2014
			Chicken	NR	NR	Huang *et al.*, 2007
			Corn- var. deprim (repellent)	NR	NR	Oluwafemi *et al.*, 2011
92	L-(2)-linalool	Terpenoid	NR	NR	HoblCSP1&2	Sun *et al.*, 2014
93	Lauric acid	Plant volatiles	Elm tree	*H. parallela*	HparOBP-1	Ju *et al.*, 2012
94	Limonene	Terpenoid	Elm tree	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
95	Linalool	Terpenoids	*H. parallela*	*H. parallela*	HparOBP-2	Ju *et al.*, 2012
			Corn- var. deprim (attracts)	NR	NR	Oluwafemi *et al.*, 2011
			Peanut	NR	NR	Cardoza *et al.*, 2002
96	Linalool oxide	Terpenoid	NR	*H. oblita*	*HoblCSP1&2*	Sun *et al.*, 2014
97	L-Isoleucine methyl ester	Aliphatic ester	*H. parallela*	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
				H. parallela	*HparOBP-1*	Sun *et al.*, 2014

#	Ligands	Type	Origin	Scarab beetle	Binding Site	Reference
98	L-Proline ethyl ester	Aliphatic ester/Sex pheromone	NR	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
99	L-Proline methyl ester	Aliphatic ester/Sex pheromone	*H. oblita*	*H. oblita*	*HoblCSP1*	Sun *et al.*, 2014
100	Methanol	Aliphatic alcohol	NR	*P. brevitarsis*	NR	Chen & Li, 2011
101	Methyl benzoate	Aliphatic ester	NR	*P. brevitarsis*	NR	Chen & Li, 2011
102	Methyl salicylate	Aromatic compound	Waxyleaf privet	*A. corpulenta*	*Acor*OBP1	Wang *et al.*, 2017
			Corn- var. deprim	*H. oblita*	*HoblOBP3&4*	Wang *et al.*, 2013
			Corn- var. deprim	*H. oblita*	*HoblCSP1*	Sun *et al.*, 2014
			NR	*P. brevitarsis*	NR	Chen & Li, 2011
103	Methyl palmitate	Alkane compound	NR	NR	NR	Chen & Li, 2011
104	Myrcene	Terpenoid	NR	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
			Peanut	NR	NR	Cardoza *et al.*, 2002
			Corn- var. deprim (attracts)	NR	NR	Oluwafemi *et al.*, 2011
105	Neophytadiene	Leaf volatiles	Corn	NR	NR	Konstantopoulou *et al.*, 2004
106	Nonanal	Aldehyde compounds	Elm tree	*H. oblita*	Not binding HoblCSP	Sun *et al.*, 2014
			Corn	NR	NR	Konstantopoulou *et al.*, 2004
107	Nonane	Aliphatic alkanes	NR	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
108	Ocimene	Plant volatiles	Elm tree	*H. parallela*	Not binding to *HparOBPs*	Ju *et al.*, 2012
109	Octane	Aliphatic alkanes	NR	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
110	Octylaldehyde	Aldehyde compounds	Elm tree	*H. oblita*	Not binding *HoblCSP*	Sun *et al.*, 2014
111	P-cresol	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)
112	P-cumeric	Volatile Organic Compounds	Wheat Straw	NR	NR	Bowen & Harper, 1990
113	Pentadecanal	Leaf volatiles	Corn	NR	NR	Konstantopoulou *et al.*, 2004
114	Pentanoic acid	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)

#	Ligands	Type	Origin	Scarab beetle	Binding Site	Reference
115	Pentanol	Aliphatic alcohol	NR	*P. brevitarsis*	NR	Chen & Li, 2011
116	P-ethylphenol	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)
117	Phenethyl alcohol	Aliphatic alcohol	NR	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
118	Phenol	Aliphatic alcohol	Chicken	NR	NR	Yasuhara *et al.* (1989)
119	Propanamide	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)
120	Propenol	Aliphatic alcohol	NR	*P. brevitarsis*	NR	Chen & Li, 2011
121	Propionic acid	Volatile Organic Compounds	Chicken	NR	NR	Yasuhara *et al.* (1989)
122	Propyl benzoate	Aliphatic ester	NR	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
123	R-(-)-linalool	Terpenoid	NR	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
124	Retinol	Aliphatic alcohol	NR	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
125	Skatole	Volatile Organic Compounds	Chicken	*H. oblita*	HoblCSP1&2	Wang *et al.*, 2013
126	Terpinen-4-ol	Terpenoid	NR	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
127	Trans-2-hexenal	Aliphatic aldehydes/Green leaf volatile	soybean	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
128	Trans-2-hexenal	Aliphatic aldehydes/Green leaf volatile	soybean	*H. parallela*	HparOBP-1&2	Sun *et al.*, 2014
129	α –ionone	Terpenoid	NR	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
			Potato	*H. parallela*	HparOBP-1	Ju *et al.*, 2012
130	α –pinene	Terpenoid	Elm tree	*H. oblita*	HoblCSP1&2	Sun *et al.*, 2014
131	α-bergamotene	Leaf volatiles	Corn- var. deprim (repellent)	NR	NR	Oluwafemi et al., 2011
132	α-Terpineol	Terpenoid	NR	*H. oblita*	HoblOBP3&4	Wang et al., 2013
133	α-ylangene	Leaf volatiles	Corn (var. stylepark)	NR	NR	Buttery & Ling (1984)
134	β –caryophyllene	Terpenoid	Hemp: *Cannabis spp*)	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
			Castor oil (*R. communis*)	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
135	β –pinene	Terpenoid	Elm tree	*H. oblita*	HoblCSP1&2	Sun *et al.*, 2014
136	β-ionone	Terpenoid	Potato	*H. oblita*	HoblOBP3&4	Wang *et al.*, 2013
137	β-ocimene	Leaf volatiles	Peanut	NR	NR	Cardoza *et al.*, 2002
138	β-sesquiphellandrene	Leaf volatiles	Corn- var. deprim (repellent)	NR	NR	Oluwafemi *et al.*, 2011

Sun et al. (2014) reported that ‘Indole’ (heterocyclic compound) successfully bound to Chemosensory Proteins 1 and 2 found in *H. oblita*. This compound is reported as a green leaf volatile in elm tree (Sun et al., 2008 and Ju et al., 2012) and in a corn variety ‘deprim’ (Oluwafemi et al., 2011). Indole and its isomer 3-methyl-1 H-indole, have also been recorded from odors emitted by decomposing chicken and cow manure, respectively, (Huang et al., 2007). The complexity of the origin of ‘Indole and its isomer would be an entry point for further research on the synergy of the three types of hosts on oviposition preference for this scarab beetle, and pest density in corn fields where cow/chicken manure are applied and elm trees used as hedge.

It is worthy to note that, VOCs from the same crop variety can either be attractants or repellents depending on whether they are induced or naturally emitted. This is the case of the corn variety ‘deprim’, whereby, *Cicadulina storeyi* China (Homoptera: Cicadellidae) was reported repelled by induced VOCs including ‘Indole’ as well as other compounds presented in Table 3 such as methyl salicylate (aromatic compound) and (E)-caryophyllene (terpenoid) (Oluwafemi et al., 2011). On the other hand, *C. storeyi* was attracted by non-induced VOCs such as decanal (aliphatic aldehyde), (E)-2-decen-1-ol (aliphatic alcohol) and linalool (terpenoid) also from un-infested corn variety ‘deprim’ (Oluwafemi et al., 2011). This attraction and repellency of some VOCs provide insights to investigate the behavioral responses of the SBs to volatiles from their hosts.

A number of VOCs from key oviposition hosts of the SBs are presented in Table 3, but related behavioral responses in terms of attractiveness or repellency seems poorly understood as this review only came out with findings by Hao et al. (2005) and Wang & Zhang (2008) who reported that methyl benzoate, ethyl benzoate, phenol, anethole, and diphenyl ketone, are involved in *Potosia brevitarsis* sex attraction. Similarly, Volatile Organic Compounds such as ethyl acetate, phenol, hexylenic aldehyde and butyl acetate were also recorded attractive to *Potosia brevitarsis* in preliminary field tests (Wang & Zhang, 2005).

Knowledge on Chemotaxis in the Management of Scarab Beetle Pests

Innovative technologies that involve volatiles to manage SBs are scarce. An attract-and-kill method was developed and proved effective for the control of *P. brevitarsis* in sweet corn in China. It consisted of placing a specially designed olfactometer with rubber dispensers that contained eight volatile compounds (mainly phenolic compounds, fruit esters, acetoin and aliphatic alcohols) on the sweet corn ears which were sprayed with Malathion one day after. Results from three years of close monitoring revealed that the mean damage value and the percentage of damaged corn ears were significantly lower compared to the control fields in which no treatment was applied (Chen & Li, 2011).

Besides the aforementioned technology, there are not any other management strategies that involve chemical volatiles to control SBs. However, there are success stories on the use of plant volatiles (kairomones) in the monitoring of other scarab beetle pests of crops and directly used for their control (Ladd & Klein 1982). Ladd et al. (1975) reported a three-component lure, phenethylproprionate-eugenol-geraniol (3:7:3) which is currently the most widely used standard food-type lure for surveys of the Japanese beetle, *Popilia japonica* Newman (Coleoptera: Scarabaeidae). The success of the Japanese beetle program motivated worldwide tests for other scarab beetles. Traps baited with methyl antranilate (plant lure) helped to catch five times as many *Anomala rufocuprea* (Coleoptera: Rutelidae) than synthetic sex pheromones (Imai et al., 1997). Most of the kairomones identified so far are flower scents, but also leaf volatiles have been associated with scarab attractions as lures (WS Leal, unpublished data).

Conclusion, Knowledge Gap and Future Research Prospects

This review has been elaborated with the aim of compiling maximum of the available knowledge on chemotaxis and ecology of oviposition in the SBs, with emphasis on VOCs emitted by host plants and odors from decomposing organic materials such as farm yard manure. Efforts were made to relate current knowledge on VOCs to behavioral responses leading to oviposition decisions. Previous research studies came out with a relevant number of VOCs (Table 3) from the key oviposition hosts including peanuts, soybean and corn, which are the most susceptible crops to the damage by the larvae of *A. corpulenta, H. oblita and H. parallela*. Some VOCs from the oviposition hosts for *P. brevitarsis* such as plant volatiles and odors from wheat straw, cow and chicken manure, have also been reported.

The recognition mechanism of VOCs by these three beetles has been determined and it is now known that Odorant Binding Proteins and Chemosensory Proteins, play a pivotal role in the reception and recognition of VOCs from their oviposition hosts. The application of the knowledge on chemotaxis and ecology for the control of *P. brevitarsis* has been done through trials established to assess the effectiveness of VOCs in an attract-and-kill method which was successful for the control of this pest in sweetcorn fields. In the same perspective, further studies are needed to identify specific volatile chemicals from plants that influence the oviposition behavior of females for the other scarab species selected in this review.

Although some VOCs from oviposition hosts of the SBs have been determined, there are still some knowledge gaps that need further in-depth studies to clearly understand the effect of these compounds on oviposition decisions as highlighted below.

1. The reported VOCs have not been specifically assessed as oviposition cues, therefore, their effect on oviposition decisions is not yet clearly understood. This thus leads to recommending more studies to screen current susceptible host crop varieties for the presence of VOCs and investigate their effect on behavioral responses of oviposition for all the SBs. Attention should be made to avoid reporting VOC synonyms as different compounds which was the case in some of the literatures reviewed.
2. This review did not come across with information on chemoreceptors involved in the recognition and transport of VOCs from the hosts of *P. brevitarsis*. In addition, Chemosensory Proteins (CSPs) might also have not yet been identified in *A. corpulenta* and *H. parallela*.

   The following studies should also be thought about for management purposes:
3. **Plant host:** localize the gene regulating or encoding for the production of a specific odorant (attractant/repellent) and modify it (silence/promote) as it has been successful in various plant breeding programs. Test the possibility to use the VOCs as traps/lures in the attract-and-kill strategy or in the formulation of repellents.
4. **SBs**: Modify or alter the receptor functional characteristics following

the Sterile Insect Technique (SIT) model used in other insect taxa such as dipterans and lepidopterans.

5. **Ecology-based Field Management**: Alley cropping whereby fields planted with less susceptible crops being established closer to the alternative feeding source. Furthermore, the identification of host attractants for oviposition of the SBs, can play a key role in biological control, for example guiding the application of lures to attract (at the right time) specialized egg parasitoids.

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