HERBIVORE-INDUCED RICE GRAIN VOLATILES AFFECT ATTRACTION BEHAVIOR OF HERBIVORE ENEMIES

QingFeng Tang, TianSheng Yang and JunQi Jiang

SUMMARY

The responses of female Lariophagus distinguendus *(Hymenoptera: Pteromalidae) to volatile signals derived from herbivore-induced rice grain was investigated in the static four-chamber olfactometer. Results showed that the* L. distinguendus *females, irrespective of experience, were apparently attracted by the odors released from rice grain. The active chemicals in the saliva of the maize weevil,* Sitophilus zeamais*, that elicit the production of rice volatiles was investigated. Results showed that artificially damaged grains do not emit large amounts of volatiles that attract the experienced parasitoid females emitted by the* S. zeamais *larvae damaged grains. Further experiments revealed the experienced* L. distinguendus *females were apparently attracted by the odors released from rice induced by the saliva of the weevil larvae. Moreover, we compared the responses of female parasitoids to odors released from rice induced by protein substances of regurgitant and non-protein substances. The experiments revealed that volatiles attracting parasitoid* L. distinguendus *are possibly induced by the some protein substances from weevil larvae saliva. The effect of experience on the response of the parasitoids to several stimuli was discussed.*

Introduction

In many parts of the world rice is the major component of the diet. Unfortunately, a large proportion of the annual yield is lost during storage, and these losses have been partly attributed to insect pests resulting in the deterioration of the quality and the quantity of stored rice grains (Machado *et al.*, 2008). To protect grains from the insect damages, tons of insecticides have been applied to control the pests, which have resulted in environmental damages, pest resurgence, pest resistance to insecticides, and lethal effects on non-target organisms. Furthermore, because of cost, these pesticides are becoming increasingly inaccessible to farmers, particularly in developing countries. This fact, combined with the consumer's demand for residue-free food, prompted researchers to evaluate other alternative reduced-risk control methods for stored-grain protection (Tang *et al.*, 2009). To resolve the above problems, new environmental friendly methods to control the insect damages have become of interest to researchers; biological control of pests using parasitoids or predators is an example (Scholler *et al.*, 1997). The use of natural enemies such as parasitoids for the control of stored-product pests has been suggested for many years (Hase, 1924; Ryabov, 1926). However, little is known about tritrophic interactions among rice grain, insect herbivores, and natural enemies of the herbivores.

The use of specific attractants might represent an option to increase the presence of the parasitoid wasp in granary or could be coupled with biocontrol programmes to improve biocontrol services. The option is effective in controlling insect pests of stored products and has a positive impact on the quality of stored cereal products. These chemicals that are beneficial for both the carnivores and the plant have been termed 'herbivore induced synomones' (HIS). Since the first description of this interaction between plants, herbivores and carnivores mediated by HIS there have been numerous studies on this phenomenon. There is evidence to suggest that HIS can regulate tritrophic interactions among plants, insect herbivores, and natural enemies of the herbivores (Steinberg *et al.*, 1993; Ockroy *et al.*, 2001; Tinzaara *et al.*, 2005; Dalessandro *et al.*, 2009; Deshpande and Kainoh, 2012; Peñaflor and Bento, 2013; Desurmont *et al.*, 2015; Yoneya and Miki, 2015). To date, HIS have been demonstrated mostly in the somatic tissue of plants, particularly for foliage. It is well documented that carnivorous arthropods often use volatile chemical cues that are released from the food plants of their victims when searching for prey or hosts. By way of comparison, little is known about the release of HIS from reproductive tissue such as rice grain (Tang *et al.*, 2009).

The present paper is devoted to a tritrophic system consisting of the rice grains (*Oryza. sativa* L.), larvae of the maize weevil *Sitophilus zeamais* (Coleoptera: Curculionidae) that are endophytic in rice grains, and the pteromalid wasp *Lariophagus distinguendus* (Hymenoptera: Pteromalidae), an idiobiont ectoparasitoid of beetle larvae, infesting seeds and grains. The maize weevil *S. zeamais* is one of the most common and destructive storage pests of stored cereal grains in the world. The adult beetles can attack whole grains, and eggs are laid

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SUSTANCIAS VOLÁTILES DE GRANOS DE ARROZ INDUCIDAS POR HERVÍBOROS AFECTAN LA ATRACCIÓN DE ENEMIGOS HERBÍVOROS

QingFeng Tang, TianSheng Yang y JunQi Jiang

RESUMEN

En un olfatómetro de cuatro cámaras se estudiaron las respuestas de hembras de Lariophagus distinguendus *(Hymenoptera: Pteromalidae) a señales volátiles provenientes de granos de arroz e inducidas por herbívoros. Los resultados mostraron que las hembras de* L. distinguendus*, independientemente de su experiencia, son atraídas por los olores despedidos por los granos de arroz. Se investigaron las sustancias activas presentes en la saliva del gorgojo del maíz,* Sitophilus zeamais*, que inducen la producción de sustancias volátiles en el arroz. Los resultados mostraron que los granos de arroz artificialmente dañados no emiten cantidades de sustancias volátiles capaces de atraer a parasitoides hembras experimentadas emitidas por las larvas de S. zeamais de granos dañados. Experimentos adicionales revelaron que las hembras experimentadas de* L. distinguendus *eran aparentemente atraídas por los olores desprendidos de los granos de arroz e inducidos por la saliva de las larvas de gorgojos. Adicionalmente se compararon las respuestas de los parasitoides hembra a olores emanados del arroz inducidas por proteínas del vómito y por sustancias no proteicas. Los experimentos mostraron que los productos volátiles que atraen los parasitoides de* L. distinguendus *son inducidos probablemente por algunas sustancias proteicas de la saliva del gorgojo. Se discute el efecto de la experiencia previa en la respuesta de los parasitoides a diversos estímulos.*

SUBSTÂNCIAS VOLÁTEIS DE GRAÕS DE ARROZ INDUZIDAS POR HERVÍBOROS AFETAM A ATRAÇÃO DE INIMIGOS HERBÍVOROS

QingFeng Tang, TianSheng Yang e JunQi Jiang

RESUMO

Em um olfatômetro de quatro câmaras se estudaram as respostas de fêmeas de Lariophagus distinguendus (Hymenoptera: Pteromalidae) a sinais voláteis provenientes de grãos de arroz e induzidas por herbívoros. Os resultados mostraram que as fêmeas de L. distinguendus, independentemente de sua experiência, são atraídas pelos odores desprendidos pelos grãos de arroz. Investigaram-se as substancias ativas, presentes na saliva do gorgulho do milho, Sitophilus zeamais, que induzem à produção de substâncias voláteis no arroz. Os resultados mostraram que os grãos de arroz artificialmente danificados não emitem quantidades de substâncias voláteis capazes de atrair parasitoides fêmeas experimentadas emitidas pelas larvas de S. zeamais de grãos danificados. Experimentos adicionais revelaram que as fêmeas experimentadas de L. distinguendus eram aparentemente atraídas pelos odores desprendidos dos grãos de arroz e induzidos pela saliva das larvas de gorgulhos. Adicionalmente se compararam as respostas dos parasitoides fêmeas a odores emanados do arroz induzidas por proteínas do vômito e por substancias não proteicas. Os experimentos mostraram que os produtos voláteis que atraem os parasitoides de L. distinguendus são induzidos provavelmente por algumas substâncias proteicas da saliva do gorgulho. Discute-se o efeito da experiência prévia na resposta dos parasitoides a diversos estímulos.

inside kernels in which the larvae feed and develop entirely and pupate. The oviposition hole is closed with an egg plug (Hill, 1983; Storey, 1987; Kouninki *et al*., 2007). *L. distinguendus* has been suggested as a biological control agent against the maize weevil in grain stores. The parasitoid egg is laid into the infested grains beside the beetle larva. Females of *L. distinguendus* have been reported to locate its host by volatiles derived from infested grain (Steidle and Scholler, 1997). However, the attractiveness mechanisms of herbivore-induced rice grain volatiles to parasitoid are still unknown.

The present study was initiated to elucidate the effects of herbivore-induced rice grains volatiles on the taxis behavior of *L. distinguendus* and its mechanisms. Such research was of importance to reveal the mechanism of indirect defense of rice grains against larvae of *S. zeamais* and, it was also very important in the understanding of the ecological functions of herbivore-induced rice grains volatiles. The results would provide new information to the biological control efficiency of parasitic wasp on stored-grain pests, which represents a technical support of great demand in green grain storage.

Materials and methods

Insect rearing

All insect rearing was carried out at 26 ±1ºC, 70 ±5% relative humidity (r.h.) and a photoperiod of L14: D10. To rear *L. distinguendus*, 50 newly emerged adult wasps were placed into Petri dishes (9cm diameter, 1cm high) with ~50g of rice grains infested by 3rd-4th instar larvae of *S. zeamais* and kept there until their death. After a developing time of 19-21 days, parasitoids emerged from the next generation were collected daily from each Petri dish. To rear *S. zeamais*, 30 adults were allowed to oviposit into 300ml of rice grains with about 14% moisture content in glass jars (8cm diameter, 10cm high). To obtain unmated males or females of *S. zeamais*; adults were separated by dimorphic rostral characteristics within 12h of emergence (Halstead, 1963).

Insects for bioassays

Parasitoids used in experiments were about 3 days old. To obtain naive parasitoids for bioassays, freshly emerged male and female parasitoids were collected from the infested grains within 1h of emergence and kept in Petri dishes on moistened filter paper in a climatic chamber without host odors under the same conditions as described above.

To obtain experienced parasitoid females, recently emerged (<24h) wasps were placed into Petri dishes containing rice grains infested by weevil larvae and imagines of *S. zeamais*. Females were allowed to mate and oviposit for 2 days. Subsequently, they were removed and kept in Petri dishes with moistened filter paper until they were used in the experiments on the following day.

Static four-chamber olfactometer

The response of female parasitoids to different odor samples was examined using a static four-chamber olfactometer, as described by Ruther and Steidle (2000). The olfactometer (Figure 1) was made of acrylic and consisted of a cylinder (4cm high, 19cm diameter) divided by vertical plates into four chambers. On the top of the cylinder, a walking arena (1cm high, 19cm diameter) was placed consisting of plastic gauze (0.5mm mesh) with a rim of acrylic (0.9cm high) and covered with a glass plate to prevent parasitoids from escaping. No airflow was generated. An odor sample was placed in a Petri dish (5.5cm diameter) with brown filter paper (4cm diameter) in one chamber or in two opposite chambers. Volatiles were allowed to diffuse through the gauze, resulting in an odor field in the walking arena above. The remaining chambers contained Petri dishes with brown filter paper as controls.

General methods for bioassays

Evaluations were performed under constant temperature and humidity at 26 ±1ºC and 70±5% r.h., in the darkness under red light to avoid distraction of parasitoids by light

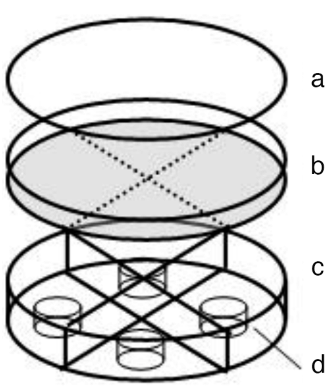

Figure 1. Static four-chamber-olfactometer used for bioassays. a: glass plate, b: arena, c: cylinder, d: Petri dish.

but to enable observations. Behavioral data were visually recorded using a stopwatch. To avoid biased results due to possible side preferences of the parasitoids, the position of the olfactometer was rotated 90º clockwise after every test. Contamination of the walking arena with sample odors or by possible pheromones of the parasitoids was avoided by cleaning the walking arenas and glass plates with ethanol and demineralized water before each insect. For all experiments, odor samples were renewed after five parasitoids had been tested.

Fifty parasitoids were tested for each type of sample. Each individual parasitoid was used only once. At the start of each bioassay, the parasitoids were released individually in the center of the walking arena and their standing times in the four sectors above the arena were registered for 600s. The time the parasitoids spent walking in the areas directly above the Petri dishes with odor samples was compared to the areas with control Petri dishes and used to assess the stopping effect of an odor sample. Parasitoids that walked for less than 50% of the total observation time were not included in the statistical analysis.

Collection of weevil regurgitant

Instars of the maize weevil, *S. zeamais*, were obtained from rearing facilities. They were placed on rice for 12-16h before their regurgitant was collected. The collection procedure was described by Turlings *et al.* (1993). Briefly, well-fed instars were held with a pair of lightweight forceps and gently squeezed in the head region with another pair. This caused the instars to empty their foregut content (regurgitant), which was collected by drawing it via a 100ml capillary tube into a vial under low vacuum. The samples were preserved with 5ml of 0.05M sodium phosphate (pH 8.0) and used for bioassays within 12h.

Responses of L. distinguendus females to S. zeamais larvae induced rice grains volatiles

A series of experiments were conducted to test the attraction of *L. distinguendus* females to herbivore-induced odors emitted from rice grains using the static four-chamber olfactometer descried above. Fifty weevil larvae infested grains from which larvae, faeces, and egg plugs had been removed (infested grain only; LIGO) *vs* 50 healthy grains, which had been artificially damaged (artificially damaged grain; AG). Two empty petri dishes (C) were used as control.

The infested grain tested by weevil larvae was obtained by dissecting grains infested by 3rd-4th instar weevil larvae. The infested grain material was cleaned from faeces using a fine brush. Artificially damaged grains were cut with scissors, knives or needles in order to better mimic damages caused by the gnawing larvae.

Responses of L. distinguendus females to S. zeamais larvae regurgitant induced rice grains volatiles

A series of experiments was conducted to test the attraction of *L. distinguendus* females to regurgitant-induced odors emitted from rice grains, using the original regurgitant (OR) or boiled regurgitant (BR). The original regurgitant was centrifuged at 1000rpm for 10min; the pH of the supernatant adjusted with citric acid and centrifuged again at 15000pm for 30min. The resulting supernatant (protein substances; RP) was used for bioassays, while the resulting precipitate (non-protein substances; RNP) was washed with 0.05M sodium phosphate (pH 8.0) and re-dissolved in the same volume of the original solution (RNP). Finally, part of the protein-containing supernatant (RP) was boiled in order to denature the proteins (BP).

A 1mm diameter hole, ~2mm deep, was drilled on healthy rice grains. Three different experiments were conducted using the static four-chamber olfactometer to test the attraction of *L. distinguendus* females to regurgitant induced rice grains volatiles: 1) Rice grains (50g) were infused 2µl of the OR extract *vs* 50g of grains infused 2µl of the BR extract, and two empty petri dishes. 2) Grains (50g) infused 2µl of the RP extract *vs* 50g of grains infused 2µl of RNP extract, and two empty petri dishes. 3) Rice grains (50g) infused 2µl of RP extract *vs* 50g infused 2µl BP extract, and two empty petri dishes. The infused rice was placed separately in the Petri dishes and kept in humidifiers containing a saturated sodium chloride solution at 65-70% r.h. for seven days before being used.

Statistical analysis

The Friedman ANOVA was used to test for differences between the four areas. In case that significant differences were found, the Wilcoxon-Wilcox-test for multiple comparisons (Sachs, 1992) was used to determine which sectors are different from each other.

Results

Responses of female parasitoids to S. zeamais induced rice grain volatiles

Naive and experienced *L. distinguendus* females spent significantly ($P<0.05$) more time in treatment odor fields compared to control odor fields, in experiments involving either rice grains infested by *S. zeamais* from which weevil, faeces, and egg plugs had been removed or artificially damaged rice grains (Figures 2 and 3). Naive *L. distinguendus* females showed no statistically significant difference ($P>0.05$) in their choice between rice grains infested by *S. zeamais* and artificially damaged rice grains (Figure 2). However, in contrast to inexperienced parasitoids, experienced *L. distinguendus* females were

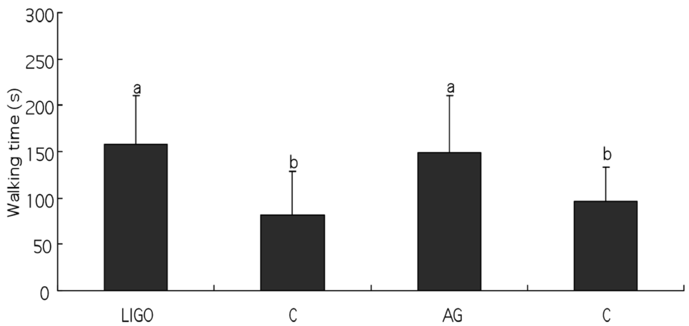

Figure 2. Mean walking time (±SD; n=50) of naive females of *Lariophagus distinguendus* in a four chamber olfactometer. LIGO: areas above Petri dishes with infested grains by weevil larvae from which larvae, feces, and egg plugs had been removed; AG: artificially damaged grains; C: areas above control Petri dishes. Bars with different letters are significantly different at P<0.05.

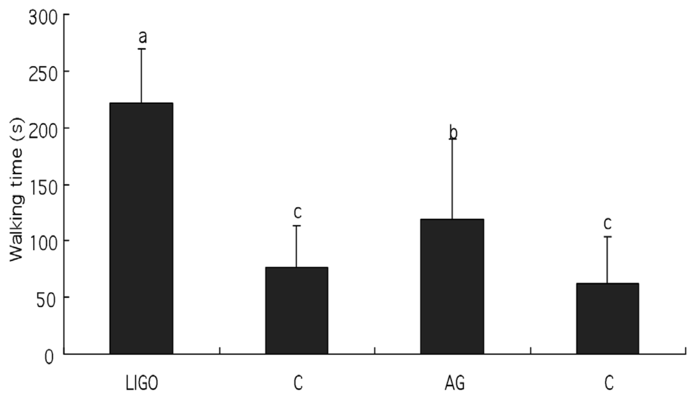

Figure 3. Mean walking time (±SD; n=50) of experienced females of *Lariophagus distinguendus* in a four chamber olfactometer. LIGO, AG and C as in Figure 2. Bars with different letters are significantly different at P<0.05.

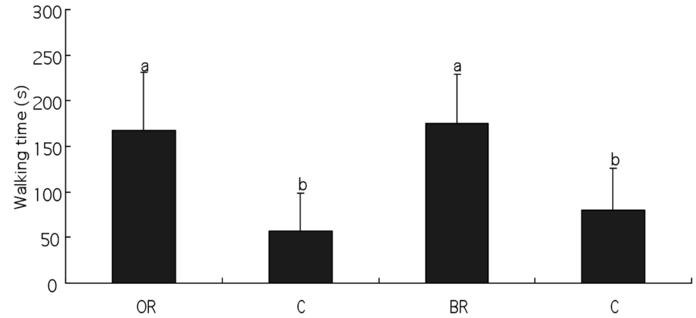

Figure 4. Mean walking time (± SD; n=50) of naive females of *L. distinguendus* in a four chamber olfactometer. OR: areas above Petri dishes with grains which had been infused 2μl oforiginal regurgitant, BR: areas above Petri dishes with grains which had been infused 2μl of boiled regurgitant, C: areas above control Petri dishes. Bars with different letters are significantly different at P<0.05.

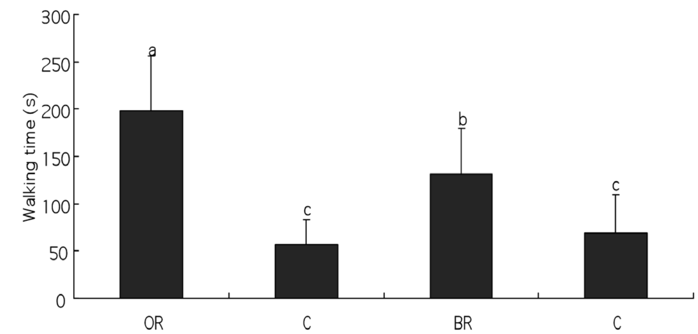

Figure 5. Mean walking time (±SD; n=50) of experienced females of *L. distinguendus* in a four chamber olfactometer. OR, BR and C as in Figure 4. Bars with different letters are significantly different at P<0.05.

strongly (P<0.05) attracted to the rice grains infested by weevil larvae from which weevil, faeces, and egg plugs had been removed over the artificially damaged rice grains (Figure 3). The results strongly suggested that the experienced *L. distinguendus* females were attracted by the specific defensive chemicals released from infested grains.

Responses of female parasitoids to original regurgitant induced rice grain volatiles

Naive and experienced *L. distinguendus* females spent significantly (P<0.05) more time in treatment odor fields compared to control odor fields (Figures 4 and 5). Naive *L. distinguendus* females showed no statistically significant difference (P>0.05) in choice between rice grains which had been infused 2μl OR and rice grains which had been infused 2μl BR (Figure 4). However, in contrast to inexperienced parasitoids, experienced *L. distinguendus* females were strongly (P<0.05) attracted to the rice grains which had been infused 2μl OR over the rice grains which had been infused 2μl BR (Figure 5).

Responses of female parasitoids to protein substances from regurgitant induced rice grain volatiles

Naive and experienced *L. distinguendus* females spent significantly more (P<0.05) time in treatment odor fields compared to control fields of the olfactometer in all experiments (Figures 6 and 7 and, 8 and 9). Naive *L. distinguendus* females showed no statistically significant difference (P>0.05) in choice between between rice grains which had been infused 2μl protein substances and rice grains which had been infused 2μl non-protein substances (Figure 6). However, in contrast to inexperienced parasitoids, experienced *L. distinguendus* females were strongly (P<0.05) attracted to rice grains which had been infused 2μl protein substances over 10 rice grains which had been infused 2μl non-protein substances (Figure 7).

Naive *L. distinguendus* females showed no statistically significant difference (P>0.05) in choice between grains infused 2μl protein substances and boiled protein substances (Figure 8). However, in contrast to inexperienced parasitoids, experienced *L. distinguendus* females showed statistically significant difference (P<0.05) in choice between grains which had been infused 2μl protein substances and grains infused 2μl boiled protein substances (Figure 9). The results strongly suggested that the experienced *L. distinguendus* females were attracted by the grains which had been infused protein substances.

Discussion and Conclusion

Many parasitoids are able to learn to locate their hosts using cues associated with the hosts or host's environment (Tumlinson *et al*., 1992; Godfray, 1994; Canale *et al*., 2014). They appear to associate them with the presence of a host (associate learning) or generally increase their response to stimuli by a certain experience, as shown for parasitoids of many families (Vet and Dicke, 1992). They direct host location by using innate cues from different, taxonomically non-related hosts and host plants (seeds). Like numerous other insects, *L.*

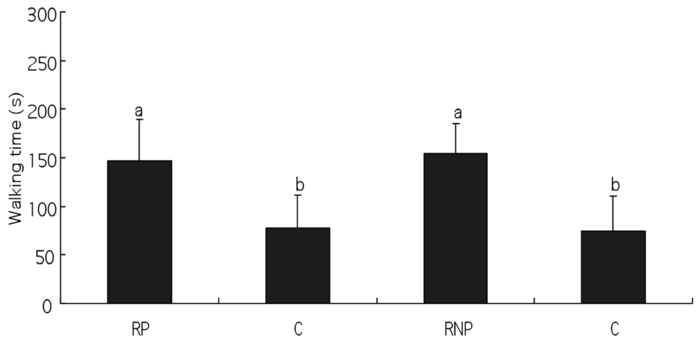

Figure 6. Mean walking time (±SD; n=50) of naive females of *L. distinguendus* in a four chamber olfactometer. RP: areas above Petri dishes with grains which had been infused 2µl of protein substances, RNP: areas above Petri dishes with grains which had been infused 2µl of non-protein substances, C: areas above control Petri dishes. Bars with different letters are significantly different at P<0.05.

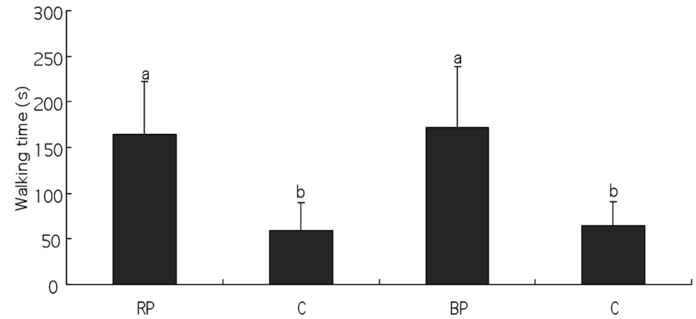

Figure 8. Mean walking time (±SD; n=50) of naive females of *L. distinguendus* in a four chamber olfactometer. RP: areas above Petri dishes with grains which had been infused 2µl of protein substances, BP: areas above Petri dishes with grains which had been infused 2µl of boiled protein substances, C: areas above control Petri dishes. Bars with different letters are significantly different at P<0.05.

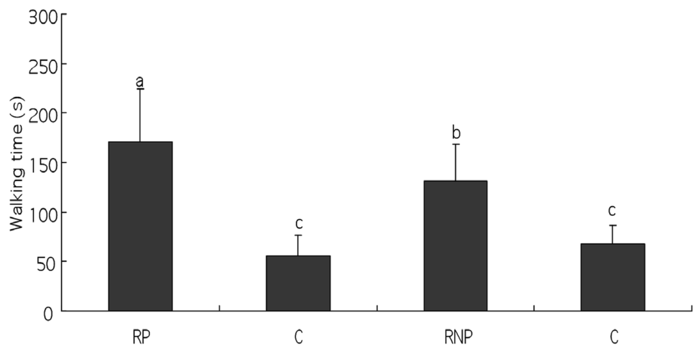

Figure 7. Mean walking time (±SD; n=50) of experienced females of *L. distinguendus* in a four chamber olfactometer. RP, RNP and C as in Figure 6. Bars with different letters are significantly different at P<0.05.

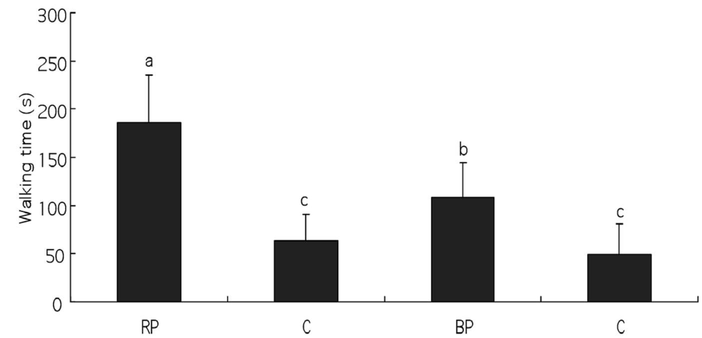

Figure 9. Mean walking time (±SD; n=50) of experienced females of *L. distinguendus* in a four chamber olfactometer. RP, BP and C as in Figure 8. Bars with different letters are significantly different at P<0.05.

distinguendus has been shown to learn from experience (Steidle, 2000). The results obtained are consistent with previous studies, in which *L. distinguendus* showed learning ability in an olfactometer. It will be able to locate further hosts more easily by using these additional stimuli.

Herbivore-induced plant odors have been reported to be used as chemical cues in the foraging behavior of natural enemies. When plants are invaded by larvae of insects or other arthropods, they usually produce and release defensive chemicals that can be recognized by predators and parasitoids to locate their victims. These plant chemicals may also serve as 'alarm signals' that are exploited by predators and parasitoids to locate their victims. There is considerable evidence that the volatile 'alarm signals' are induced by interactions of substances from the herbivore with the damaged plant tissue (Steowe *et al.*, 1995). However, so far few experimental evidences have been reported to support this, and the release of herbivore-induced synomones (HIS) has almost exclusively been demonstrated in somatic plant tissues. In 2005, Steidle *et al.* concluded that the grains have the ability to 'whisper for help' of the parasitoid *L. distinguendus*. However, it was not demonstrated whether potential HIS were actively produced by infested grains or are a by-product of grain metabolism.

Experienced *L. distinguendus* females were strongly attracted to the grains to which protein substances from original regurgitant had been applied. As demonstrated by Turlings *et al.* (1991) for the parasitoid *Cotesia marginiventris* (Cresson) and its host *Spodoptera exigua* (Hfibner) and, by Mattiacci *et al.* (1995) for *Cotesia glomerata* (L.) and its host *Pieris brassicae* (L.), plant volatiles can be induced by the regurgitate of caterpillars. Thus, it seems likely that parasitoid attracting volatiles are also induced by the saliva of the weevil larvae or females. Although theoretically less likely, some generalist predators appear to make some use of plant volatiles to locate prey. Yellow jacket wasps in the *Vespula vulgaris* species group are attracted to mixtures of (E)-2-hexenal with either a-terpineol or linalool-all ubiquitous components of volatiles from plants under attack by herbivores (Steowe *et al.*, 1995).

Herbivore-induced plant odors play major roles in the foraging behavior of natural enemies. When the larval stages of insects or other arthropods are the targets, a foraging strategy is employed. Under the condition that some specific chemical cues are used in the communication between insect pests and their natural enemies (Cox, 2004), the strategy of applying semiochemicals into the biological controls has been considered to attract parasitoids or predators into a crop or increase the amount of time they spend in a field. Therefore, increased understanding of the chemically mediated interactions between arthropod hunters and their victims will be useful for the biological controls of pests on a crop. Our ultimate goal is to be able to develop an environmentally friendly method to control the pest resurgence on a crop and reduce the currently heavy dependence on pesticides.

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REFERENCES

Canale A, Geri S, Benelli G (2014) Associative learning for host-induced fruit volatiles in *Psyttalia concolor* (Hymenoptera: Braconidae), a koinobiont parasitoid of tephritid flies. *Bull. Entomol. Res. 104*: 774-780.

Cox PD (2004) Potential for using semiochemicals to protect stored products from insect infestation. *J. Stored Prod. Res. 40*: 1-25.

Dalessandro M, Brunner V, Vonmerey G, Turlings TCJ (2009) Strong attraction of the parasitoid *Cotesia marginiventris* towards minor volatile compounds of maize. *J. Chem. Ecol. 35*: 999-1008.

Deshpande SA, Kainoh Y (2012) Herbivore egg deposition induces tea leaves to arrest the egg-larval parasitoid *Ascogaster reticulate*. *Entomol. Exp. Appl. 144*: 172-180.

Desurmont GA, Laplanche D, Schiestl FP, Turlings TCJ (2015) Floral volatiles interfere with plant attraction of parasitoids: ontogeny-dependent infochemical dynamics in *Brassica rapa*. *BMC Ecol. 15*: 1-11.

Godfray HCJ (1994) *Parasitoids*. Princeton University Press, Princeton, NJ, USA. 59 pp.

Halstead DGH (1963) The separation of *Sitophilus oryzae* (L.) and *S. zeamais* Motschulsky (Col., Curculionidae), with a summary of their distribution. *Ent. Mon. Mag. 99*: 72-74.

Hase A (1924) Zur Kenntnis wirtschaftlich wichtiger Tierformen. I. Über den Stech- und Legeakt, sowie über den Wirtswechsel von *Lariophagus distinguendus*. Chalcididae. Pteromalini. *Naturwissenschaften 20*: 377-384.

Hill DS (1983) *Agricultural Insect Pests of the Tropics and their Control*. 2nd ed. Cambridge University Press. Cambridge, UK. 122 pp.

Kouninki H, Hancel T, Noudjou FA (2007) Toxicity of some terpenoids of essential oils of *Xylopia aethiopica* from Cameroon against *Sitophilus zeamais* Motschulsky. *J. Appl. Entomol. 131*: 269-274.

Machado EHL, Alves LC, Faustino MAD, Machado EDL (2008) Occurrence of weevils (Insecta: Coleoptera) in pet food traded in the metropolitan region of Recife, Pernambuco State, Brazil. *Neotrop. Entomol. 37*: 602-605.

Mattiacci L, Dicke M, Posthumus MA (1995) β-Glucosidase: An elicitor of herbivoreinduced plant odor that attracts host-searching parasitic wasps. *Proc. Nat. Acad. Sci. 92*: 2036-2040.

Ockroy MLB, Turlings TCJ, Edwards PJ, Fritzschehoballah ME, Ambrosetti L, Bassetti P, Dorn S (2001) Response of natural populations of predators and parasitoids to artificially induced volatile emissions in maize plants (*Zea mays* L.). *Agr. Forest Entomol. 3*: 201-209.

Peñaflor MFGV, Bento JMS (2013) Herbivore-induced plant volatiles to enhance biological control in agriculture. *Neotrop. Entomol. 42*: 331-343.

Ruther J, Steidle JLM (2000) Mites as matchmakers: semiochemicals from host-associated mites attract both sexes of the parasitoid *Lariophagus distinguendus*. *J. Chem. Ecol. 26*: 1205-1217.

Ryabov MA (1926) The possibilities of applying the parasitic method of control in the case of the granary pests. *Rev. Appl. Entomol. 14*: 26.

Sachs L (1992) *Angewandte Statistik*. Springer. Berlin, Germany. p. 12.

Scholler M, Prozell S, Al-Kirshi AG, Reichmuth C (1997) Towards biological control as a major component of integrated pest management in stored product protection. *J. Stored Prod. Res. 33*: 81-97.

Steidle JLM (2000) Host recognition cues of the granary weevil parasitoid *Lariophagus distinguendus*. *Entomol. Exp. Appl. 95*: 185-192.

Steidle JLM, Fischer A, Gantert C (2005) Do grains whisper for help? Evidence for herbivore-induced synomones in wheat grains. *Entomol. Exp. Appl. 115*: 239-245.

Steidle JLM, Scholler M (1997) Olfactory host location and learning in the granary weevil parasitoid *Lariophagus distinguendus* (Hymenoptera: Pteromalidae). *J. Insect Behav. 10*: 331-342.

Steinberg S, Dicke M, Vet LE (1993) Relative importance of infochemicals from first and second trophic level in long-range host location by the larval parasitoid *Cotesia glomerata*. *J. Chem. Ecol. 19*: 47-59.

Steowe MK, Turlings TCJ, Lounghrin JH, Lewis WJ, Tumlinson JH (1995) The chemistry of eavesdropping, alarm, and deceit. *Proc. Nat. Acad. Sci. 92*: 23-28.

Storey CL (1987) Effect and control of insects affecting corn quality. In Watson SA, Ramstad PE (Eds.) *Corn Chemistry and Technology*. American Association of Cereal Chemists, St. Paul, MN, USA. pp. 185-199.

Tang QF, Wu YJ, Liu BM, Yu ZL (2009) Olfactory responses of *Lariophagus distinguendus* (Hymenoptera: Pteromalidae) to volatile signals derived from host habitats. *Philipp. Agric. Sci. 92*: 133-142.

Tinzaara W, Gold CS, Dicke M, Vanhuis A (2005) Olfactory responses of banana weevil predators to volatiles from banana pseudostem tissue and synthetic pheromone. *J. Chem. Ecol. 31*: 1537-1553.

Tumlinson JH, Turlings TCJ, Lewis WJ (1992) The semiochemical complexes that mediate insect parasitoid foraging. *Agric. Zool. Rev. 5*: 221-252.

Turlings TCJ, Mccall PJ, Alborn H, Tumlinson JH (1993) An elicitor in caterpillar oral secretions that induces corn seedlings to emit chemical signals attractive to parastic wasps. *J. Chem. Ecol. 19*: 411-425.

Turlings TCJ, Tumlinson JH, Heath RR, Proveaux AT, Doolittle RE (1991) Isolation and identification of the allelochemicals that attract the larval parasitoid, *Cotesia marginiventris* (Cresson), to the microhabitat of one of its hosts. *J. Chem. Ecol. 17*: 2235-2251.

Vet LEM, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol. 37*: 141-172.

Yoneya K, Miki T (2015) Co-evolution of foraging behaviour in herbivores and their natural enemies predicts multifunctionality of herbivore-induced plant volatiles. *Funct. Ecol. 29*: 451-461.