



Short-range cues mediate parasitoid searching behavior on maize: The role of oviposition-induced plant synomones

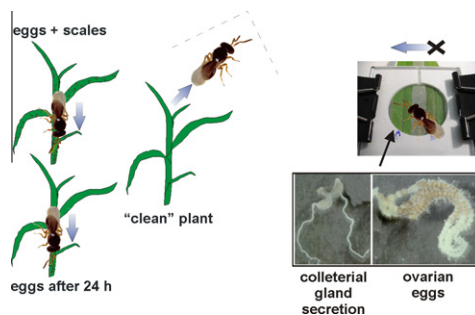
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HIGHLIGHTS

- ▶ Stemborer oviposition on maize induces systemic emission of short-range synomones.
- ▶ Induced synomones elicit arrestment of the egg parasitoid.
- ▶ Synomones plus host kairomones increase host finding efficiency.
- ▶ Sources of synomone elicitor are the colleterial gland secretion and eggs.
- ▶ Induction starts 24 h after oviposition and lasts at least till 72 h.

GRAPHICAL ABSTRACT



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ABSTRACT

Host searching by egg parasitoids faces a main constraint due to low detectability of cues from host eggs. Therefore egg parasitoids have developed distinctive strategies by exploiting cues that originate from non-target instars of the host and/or from plants. The scelionid *Telenomus busseolae* is specialized on concealed eggs of *Sesamia nonagrioides* and other noctuid stemborers. In this paper we show that oviposition by *S. nonagrioides* induces changes in the cues present on maize leaf surface, which arrest naïve females of *T. busseolae*. The induction appears to be systemic as the parasitoid also responds to leaves and leaf portions that are not directly affected by ovipositing females. Such oviposition-induced, short-range, plant synomones, acting in sequence with the kairomonal cues from scales left on the plant by the ovipositing host female, significantly increases parasitoid efficiency during host finding. The elicitor of plant response originates from the host female reproductive system, being contained both in the host's ovarian eggs and in the colleterial gland secretion. Induction starts 24 h after oviposition and lasts at least till 72 h. The ecological role of this oviposition-induced plant synomone in host searching by *T. busseolae* is discussed.

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1. Introduction

Plants react to herbivore attacks activating a multitude of defense responses (Kessler and Baldwin, 2002; Pieterse and Dicke, 2007; Heil, 2008), including the recruitment of natural enemies of arthropod attackers (Rasmann et al., 2005; D'Alessandro and Turlings, 2006; Bruinsma and Dicke, 2008; Dicke et al., 2009). Since the initial discovery of herbivore-induced plant volatiles (HIPVs) that act as synomones attracting parasitoids and predators (Dicke

and Sabelis, 1988; Turlings et al., 1990), a huge number of studies demonstrated that plants of more than 13 families respond to the assault of chewing and piercing-sucking arthropods, both above and below ground (Dicke et al., 1990, 2009; Turlings et al., 1990; Dicke, 1999; Van Tol et al., 2001; Rasmann et al., 2005; Steidle et al., 2005; Arimura et al., 2009; Bruinsma et al., 2010; Wu and Baldwin, 2010).

Maize plants chewed on by caterpillars were among the earliest systems studied (Turlings et al., 1990; Potting et al., 1995). A compound of the caterpillar oral secretion, named volicitin, was shown to elicit the emission of volatile synomones that attracted the caterpillar parasitoid (Turlings et al., 1990; Alborn et al., 1997;

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D'Alessandro et al., 2009). The amount and type of volatiles emitted in maize changed with time (Turlings et al., 1998; Hoballah and Turlings, 2005), genotype (Turlings et al., 1998; Gouinguéné et al., 2001; Degen et al., 2004), type of damage (Turlings et al., 1998), and was affected by abiotic factors (Gouinguéné and Turlings, 2002) and other biotic factors such as fungi (Rostás et al., 2006).

In addition to feeding damage, also oviposition alone (Bruce et al. 2010; Tamiru et al. 2011, 2012) or in combination with feeding (Meiners and Hilker, 1997, 2000; Hilker and Meiners, 2002; Hilker et al., 2002a; Colazza et al., 2004a,b) may induce plant responses with the emission of synomones that act at long distance attracting egg parasitoids. The egg parasitoids exploit such highly detectable and reliable volatiles induced in plants soon after herbivore eggs are laid, receiving an important advantage from this “early alert” (*sensu* Hilker and Meiners, 2006).

The oviposition-induced volatile synomones known so far are emitted both from arboreal (perennial) plants and from herbaceous (annual) plants, as a consequence of egg deposition by phytophagous species belonging to Hymenoptera, Coleoptera, Heteroptera or Lepidoptera. Such volatile synomones are exploited by egg parasitoids belonging to Eulophidae, Platygasteridae (=Scelionidae, see Sharkey, 2007, and Murphy et al., 2007) and Trichogrammatidae (Meiners and Hilker, 2000; Hilker and Meiners, 2002; Hilker et al., 2002a; Colazza et al., 2004a,b; Tamiru et al., 2011, 2012). The mechanisms underlying the emission of these synomones are often associated to the presence of plant damage, either during oviposition and/or as a consequence of feeding on the host plant, in combination with elicitors contained in the reproductive system secretion or in the saliva (Hilker et al., 2002a,b; Colazza et al., 2004a,b). However, when adults are not able to cause feeding damage, such as in Lepidoptera, just egg deposition appears to be responsible for synomone induction (Tamiru et al., 2011, 2012).

Recent papers revealed that in addition to mid- and long-range volatile synomones, also short-range synomones, perceived after the parasitoids have alighted on the plant, can be induced by herbivore oviposition (Fatouros et al., 2005, 2007, 2009; Conti et al., 2010; Blenn et al., 2012; reviewed by Fatouros et al., 2008; Colazza et al., 2010, and Hilker and Meiners, 2011). Oviposition by *Pieris brassicae* L. (Lepidoptera: Pieridae) on Brussels sprouts, *Brassica oleracea* var. *gemmifera*, induces changes on the chemistry of leaf surface, both locally and systemically, that arrest the egg parasitoids *Trichogramma brassicae* Bezdenko and *T. evanescens* Westwood (Hymenoptera: Trichogrammatidae) (Fatouros et al., 2005, 2007). Egg deposition by *Pieris rapae* L. (Lepidoptera: Pieridae) on the same plants also results in the arrestment of *T. brassicae* wasps (Fatouros et al., 2009). Recently, similar effects were shown on *T. brassicae* after oviposition of *P. brassicae* on *Arabidopsis thaliana* leaves (Blenn et al., 2012).

In a different system involving plants of *B. oleracea* var. *sabauda* and the harlequin bug *Murgantia histrionica* Hahn (Heteroptera: Pentatomidae), the combination of egg deposition, feeding punctures and chemical footprints of the herbivore on the lower leaf surface resulted in the induction of short-range synomones which are active for the egg parasitoid *Trissolcus brochymenae* Ashmead (Hymenoptera: Platygasteridae). Induced chemicals are perceived from a very short range and after the parasitoid contact with the upper (adaxial) leaf surface, opposite the treated (abaxial) surface. The response to the induced synomone was shown on the treated leaf portion, on the same leaf but at a close distance from the treated portion, and on the leaf above the treated leaf, thus demonstrating a systemic effect. Induction time was less than 24 h, whereas signal duration was related to the suitability of the host eggs, as the parasitoids did not respond to plants carrying old or hatched eggs (Conti et al., 2010).

The tritrophic system studied in this paper is composed of corn, *Zea mays* L., the stemborer *Sesamia nonagrioides* Lefebvre (Lepidop-

tera: Noctuidae) and the egg parasitoid *Telenomus busseolae* Gahan (Hymenoptera: Platygasteridae). This system is characterized by the presence of concealed egg masses glued below the leaf sheath of maize plants, obviously prior of any damage or wounding from the herbivore, and no apparent damage is caused during oviposition. Egg parasitoids, after having alighted on the plant, are faced with the challenging task of locating the host eggs using reliable cues. However, the kairomones present on *S. nonagrioides* eggs (Conti et al., 2003) appear hardly detectable and probably can be exploited only at a very short range. An important role in host location by the parasitoid could be exerted by the scales from the Lepidoptera female abdomen, which are left on the plant during oviposition. These scales induce an arrestment response in species of *Telenomus* and *Trichogramma* (Gross et al., 1984; Noldus, 1989; Colazza and Rosi, 2001; Salerno et al., 2002; Conti et al., 2003). Preliminary results of *T. busseolae* response to plant volatiles in the olfactometer do not show significant preference for maize plants carrying host eggs compared to clean plants (G. Salerno, E. Conti unpublished data).

In this paper we explore the possible roles of cues from the plant-host complex (*Z. mays* – *S. nonagrioides*) in host location by *T. busseolae* after it has alighted on the plant. In particular we initially consider the role of deposited egg masses in the induction of a short-range synomone, and the parasitoid behavioral responses. We also evaluate the role of host scales in host finding. In a second step we consider the role of egg age in synomone induction in *Z. mays*, and try to elucidate the source of the elicitor by testing plants with artificially applied ovarian eggs and colleterial gland secretion.

2. Materials and methods

2.1. Insect and plant cultures

A *S. nonagrioides* culture was established from pupae collected in central Italy and reared using a meridic diet (Giacometti, 1995). Larvae, sexed pupae and adults were kept inside screened plastic containers in a controlled condition chamber (27 ± 1 °C, 60–80% relative humidity, 16L:8D photoperiod) according to the method described by Giacometti (1995).

The parasitoid *T. busseolae* was obtained from parasitized egg masses of *S. nonagrioides* collected on maize in Turkey and reared in a climatic cabinet (24 ± 2 °C, 70 ± 5% relative humidity, 16L:8D photoperiod) on eggs of the same host. Egg masses were exposed to two or more freshly emerged and mated adult females of *T. busseolae* and the eggs were left to incubate for 18 days. After emergence, males and females were kept together to allow mating. Adult wasps were fed with a solution of sugar (10%), honey (10%), benzoic acid (10%), yeast and water (Safavi, 1968). To reduce variability of parasitoid behavior, about 24 h before the bioassays, 2- to 4-days-old mated females were isolated in small glass vials (10 mm diam. × 25 mm long), provided with a drop of the Safavi diet, and kept in the same climatic cabinet.

Zea mays (line 65B, D.S.A.A., sez. Agronomia, University of Perugia) was sown in pots (8 cm × 8 cm × 9 cm) containing a mix of agriperlite and soil (1:3). Plants were kept in a greenhouse at 25 ± 2 °C, 12L:12D and 50–60% RH, and after emergence were watered daily. For behavioral assays only plants that were approximately 3–4 weeks-old, with 3–4 fully expanded true leaves, were employed.

2.2. Plant treatments

The behavioral bioassays were conducted using whole plants or leaf portions. The treatment set up prior to observations is summarized in Table 1.

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