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Infochemically mediated tritrophic interaction webs on cabbage plants

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Abstract In response to damage by herbivores, plants are known to emit infochemicals that enhance the effectiveness of insect parasitoids. Studies on plant–parasitoid interactions mediated by such infochemicals have focused on the tritrophic systems in which plants are infested by a single herbivore species. In natural ecosystems, however, plants are often simultaneously infested by several herbivorous species. The present study focuses on two herbivorous species that simultaneously attack crucifer plants and their respective parasitic wasps. We first show the specific responses of the two specialist parasitic wasps [*Cotesia plutellae* and *C. glomerata* (Hymenoptera: Braconidae)] to infochemicals originating from cabbage plants (*Brassica oleracea* cv. Sikidori) infested by each of their respective host larvae [*Plutella xylostella* (Lepidoptera: Yponomeutidae) and *Pieris rapae* (Lepidoptera: Pieridae)]. We then coupled the two tritrophic systems on the same cabbage plants. These experiments demonstrated the presence of indirect interactions between the two species of herbivores. Overall, the results indicate the presence of infochemically mediated tritrophic interaction webs on a single plant.

Key words Parasitic wasps · Infochemicals · Plant–parasitoid interactions · Enemy-free space · Enemy-dense space

Introduction

Volatile and contact infochemicals that originate from infested plants act as important host-location cues for insect parasitoids (Vet and Dicke 1992; Turlings et al. 1990, 1993; Horikoshi et al. 1997; Takabayashi and Dicke 1996; Powell et al. 1998; De Moraes et al. 1998; Dicke 1999). Previous

studies on plant–parasitoid interactions mediated by these infochemicals have been performed in systems in which an individual plant is infested by one host herbivore species. In natural ecosystems, however, plants are simultaneously infested by several species of herbivores. Organisms using the same resources may compete for resources (interference competition and exploitative competition) (Park 1962; Miller 1967; Eriksson 1979; Tilman and Sterner 1984), interact through common natural enemies (apparent competition) (Holt 1977, 1984; Bonsal and Hassell 1997), or protect each other from natural enemies (apparent mutualism) (Matsuda et al. 1993; Abrams and Matsuda 1996; Pallini et al. 1998). In tritrophic interactions involving plants, herbivores, and parasitoids, infestation by both prey and nonprey species on the same plant may affect the production or function of prey-induced infochemicals. If so, the presence of nonprey herbivore species would either positively or negatively affect plant–parasitoid interactions mediated by infochemicals induced by the prey herbivores. Consequently, the presence of the nonprey herbivores may affect the performance of the prey herbivores.

This article presents the specific responses of the two specialist parasitic wasps (*Cotesia plutellae* and *C. glomerata*) to infochemicals originating from cabbage plants infested by their respective host larvae (*Plutella xylostella* and *Pieris rapae*). Two herbivore species tend to coexist on the same cabbage plants (Iga, unpublished data). Thus, the two tritrophic systems were subsequently experimentally coupled on a single cabbage plant and the responses were reexamined. In addition, chemical analysis of headspace volatiles emitted from cabbage plants with different types of injury was performed. Based on the results, we discussed whether the presence of the nonprey herbivores affected the performance of the prey herbivores.

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Host-searching behavior of *Cotesia plutellae* and *Cotesia glomerata*

Cotesia plutellae is a solitary endoparasitoid of the second to third instars of *P. xylostella*. When exposed to a host-

infested plant, the female *C. plutellae* hovers 2–3 cm from the leaf before landing. After landing, it then walks slowly around the leaf, waving its antennae. If it encounters a host-infested site, it starts intensive searching of the site with quick antennal contact. It also raises its wings and bends its abdomen toward the host-infested site (Shiojiri et al. 2000b). Through this behavior, female *C. plutellae* are able to locate their host larvae.

Cotesia glomerata is a gregarious endoparasitoid of the first to third instars of *P. rapae*. This wasp shows similar host-searching behavior to *C. plutellae*. The female *C. glomerata* lands on a leaf of either *Rorippa indica* (wild crucifer) or other crucifers infested by *P. rapae* larvae (Sato 1988; Takabayashi et al. 1998). It then walks around slowly, with its antennal tips touching the leaf surface. When it comes within about 10 mm of a part damaged by larval feeding, it raises its antennae and turns toward the host-infested edge. It then starts intensive searching with antennal contact, raised wings, or bending its abdomen forward (Sato 1979).

These observations suggest that both *C. plutellae* and *C. glomerata* initially locate host-infested plants by reacting to volatiles emitted from the plants (Takabayashi et al. 1998; Shiojiri et al. 2000a). After landing, they use contact chemicals from the host-infested edge as searching cues (Sato 1979; Horikoshi et al. 1997; Shiojiri et al. 2000b). In the present study, we focused on the flight responses and the antennal searching behavior of each wasp species.

Factors responsible for flight response of parasitoids to host-infested plant

The flight responses of female *C. plutellae* and *C. glomerata* to two potted cabbage plants were observed in a cage (25 × 35 × 30 cm) with three windows covered with nylon gauze and one door in a climate-controlled room (25° ± 2°C, 50%–70% relative humidity [RH]) (Shiojiri et al. 2000a). Each wasp was released at the midpoint between the two potted plants. Before the bioassay, all herbivores and herbivore-related products were removed from the plants. The damage to the cabbage plants was similar in degree and form, regardless of the type of damage (artificial damage or herbivore damage). Thus, the observed flight responses of the wasps could not be attributed to visual factors.

When given the choice, *C. plutellae* wasps showed a significant preference for *P. xylostella*-infested cabbage plants over either uninfested, artificially damaged, or *P. rapae*-infested cabbage plants (Fig. 1A). As all herbivores and herbivore-related products had been removed from the plants, it was suggested that the wasps located infested plants using volatile infochemicals produced by the host-infested plants.

Cotesia glomerata showed a significant preference for *P. rapae*-infested cabbage plants over uninfested plants in the cage (Fig. 1B), but showed no preference between *P. rapae*-infested or *P. xylostella*-infested cabbage plants (Fig. 1B). The wasp also showed no preference between *P. rapae*-

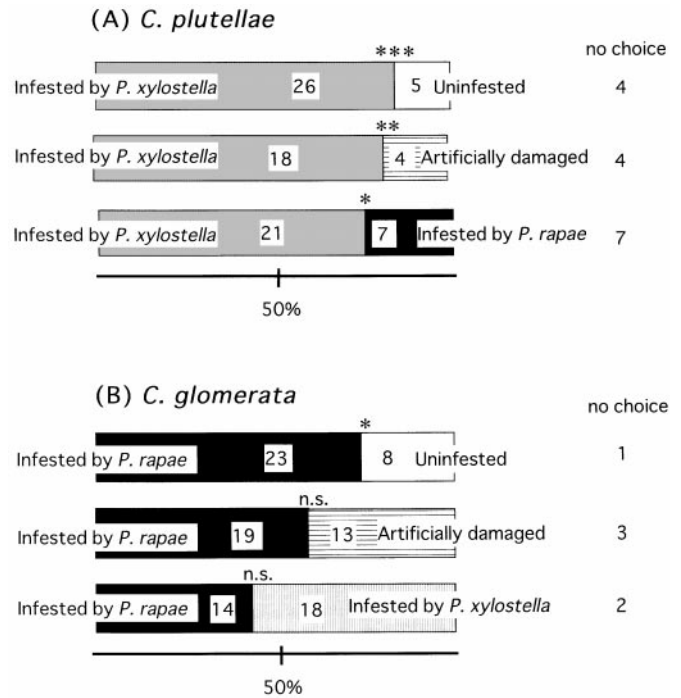
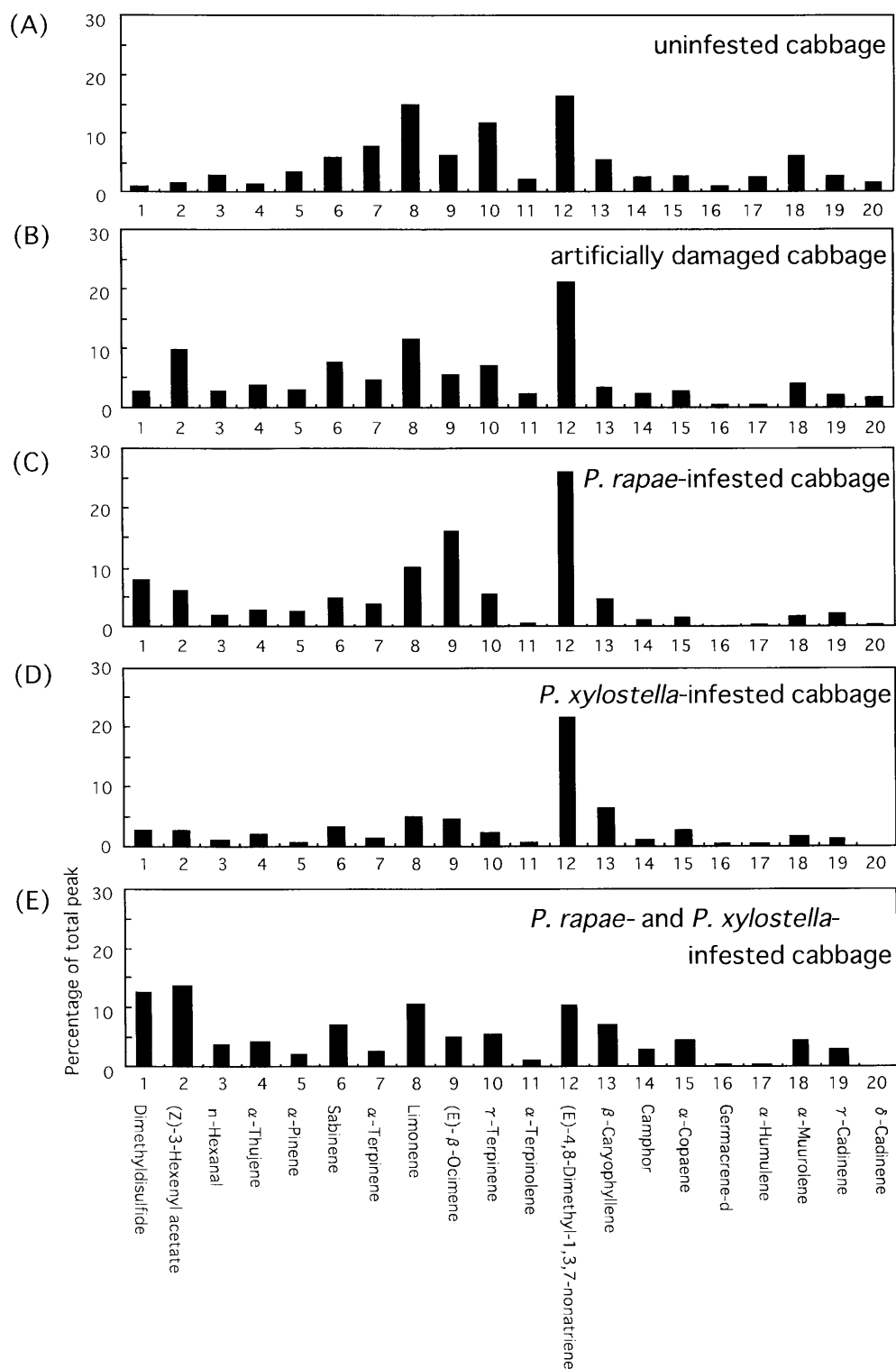


Fig. 1. **A** Flight responses of *Cotesia plutellae* females to a *Plutella xylostella*-infested crucifer plant versus a *P. rapae*-infested or an uninfested cabbage plant. **B** Flight responses of *C. glomerata* females to a *P. rapae*-infested cabbage plant versus a *P. xylostella*-infested or an uninfested cabbage plant (data from Shiojiri et al. 2000a). Asterisks indicate statistically significant preferences within the binomial probability function (*0.01 < *P* < 0.05; **0.001 < *P* < 0.01; ****P* < 0.001; n.s., nonsignificant preference)

infested or artificially damaged cabbage plants (Fig. 1B). These data suggest that *C. glomerata* responds to volatiles emitted by cabbage plants with physical damage to their leaves. Takabayashi et al. (1998) reported that *C. glomerata* could not distinguish between host-infested *R. indica* plants (wild crucifer) and artificially damaged plants. Furthermore, Geervliet et al. (1996) reported that *C. glomerata* preferred Brussels sprouts infested by nonhost species (*P. xylostella* and *Mamestra brassicae*) to uninfested plants.

Chemical analysis revealed a characteristic blend of volatiles emitted from plants infested by *P. rapae*, those infested by *P. xylostella*, and artificially damaged plants, and this blend differed from that emitted from uninfested plants (Fig. 2). In the headspace of uninfested cabbage plants, limonene, γ -terpinene, and (*E*)-4,8-dimethyl-1,3,7-nonatriene were the major compounds (Fig. 2A). By contrast, in the headspace of *P. rapae*-infested plants, limonene, (*E*)- β -ocimene, and (*E*)-4,8-dimethyl-1,3,7-nonatriene were the major compounds (Fig. 2C). *P. xylostella*-infested plants emitted (*E*)-4,8-dimethyl-1,3,7-nonatriene as the major compound (Fig. 2D). Artificially damaged plant emitted (*Z*)-3-hexenyl acetate, limonene, and (*E*)-4,8-dimethyl-1,3,7-nonatriene as major compounds (Fig. 2B). Each wasp species could make a distinction between the blend from uninfested plants and that from host-infested plants.

Fig. 2. Composition of the blend of volatiles emitted from a cabbage plant (20-cm height, 5–6 leaves) with different treatments. **A** Uninfested cabbage plant. **B** Artificially damaged cabbage plant (~15%–20% of leaf surface was gradually damaged with a hole puncher three times over 24h). **C** Cabbage plant infested by five *P. rapae* larvae (~15%–20% of leaf surface was infested with second to third instars for 24h). **D** Cabbage plant infested by 20 *P. xylostella* larvae (~15%–20% of leaf surface was infested with second to third instars for 24h). **E** Cabbage plant infested by both herbivore species (~15%–20% of leaf surface was infested by each herbivore species for 24h). Volatile compounds were drawn from the headspace of bottles containing infested or uninfested plants into a glass tube packed with Tenax TA adsorbents (100mg, mesh 20/35) for 2h at a flow rate of 100 ml/min. The collected volatile compounds were analyzed by gas chromatography–mass spectrometry (GC-MS) (GC: Hewlett Packard 6890 [Agilent Technologies, Palo Alto, USA] with HP-5MS capillary column; 30 m long, 0.25 mm ID, 0.25- μ m film thickness, injection temperature 250°C; MS: Hewlett Packard 5973 mass selective detector, Agilent Technologies, 70 eV) equipped with a thermal desorption cold trap injector (TCT; Varian Chrompack International B.V., Middelburg, The Netherlands). Oven temperature of GC-MS was programmed to rise from 40°C (5-min hold) to 280°C at 15°C/min. Compounds were identified by comparing their spectra with mass spectra in the database (Wiley 275, version C.00.00, Wiley, New York, USA), in addition to data related to herbivore-induced volatile compounds from lima bean plants. We repeated the chemical analysis for each treated plants five times



The fact that *C. plutellae* preferred *P. xylostella* (host)-infested plant volatiles over *P. rapae* (nonhost)-infested plant volatiles (Fig. 1A) suggests that the wasp distinguishes between the blend of volatiles from host- and nonhost-infested plants. In contrast, *C. glomerata* showed equal preference toward *P. rapae* (host)-infested plants and artificially damaged plants (Fig. 1B). Plants emit so-called green leaf volatiles (GLVs) when they are artificially dam-

aged (Matsui 1998). *C. glomerata* may respond to a certain blend of GLVs. In fact, (Z)-3-hexenyl acetate, a GLV, was observed in the volatiles from artificially damaged plants as one of the major compounds. Mattiacci et al. (1994) reported that *C. glomerata* preferred *P. brassicae* (host)-infested Brussels sprouts over uninfested ones and that GLVs emitted from infested Brussels sprouts were higher than those emitted from uninfested ones.

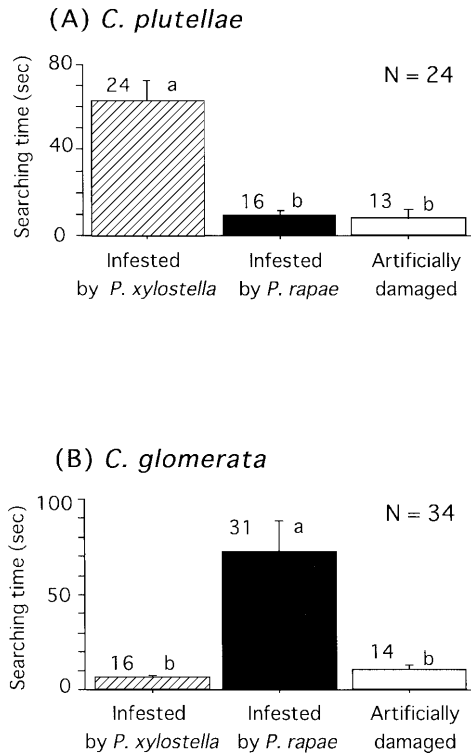


Fig. 3. Searching time (mean \pm SE) of *C. plutellae* (A) and *C. glomerata* (B) on a piece of leaf infested by *P. xylostella*, a piece of leaf infested by *P. rapae*, and an artificially damaged piece. Means followed by different *small letters* for each plant are significantly different according to Tukey–Kramer post hoc multiple mean comparisons ($P < 0.05$). *Numbers on bars* indicate the number of wasps that responded (data from Shiojiri et al. 2000b)

Factors responsible for the host-searching behavior of the parasitoid on the plant

The host-searching behavior of the wasps was observed in a glass tube (20mm diameter, 130mm length). Leaf pieces (10 \times 10mm) infested by either *P. xylostella* or *P. rapae* and a leaf piece with artificial damage were tested. When a wasp showed the same antennation behavior toward a sample as it did to an infested leaf, it was interpreted as an exhibition of host-searching behavior. The duration of the searching behavior was recorded (hereafter called searching time).

The time *C. plutellae* spent searching a piece of cabbage leaf infested by host (*P. xylostella*) larvae was significantly longer than the time spent searching a piece infested by nonhost (*P. rapae*) larvae or artificially damaged pieces (Fig. 3A). Similarly, the searching time of *C. glomerata* was significantly longer on a host (*P. rapae*)-infested piece of cabbage than on a piece infested by nonhost (*P. xylostella*) larvae or on an artificially damaged piece (Fig. 3B). Similar response characteristics were previously reported for *C. glomerata* (Sato et al. 1999b). Based on these results, the antennal responses of the two wasp species appear to be host specific.

The searching time of *C. plutellae* on an artificially damaged piece of leaf with regurgitant applied was significantly

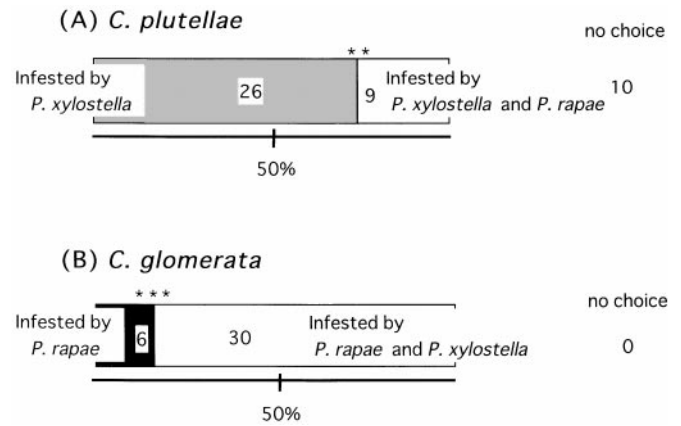


Fig. 4. Flight responses of *C. plutellae* (A) and *C. glomerata* (B) females to a cabbage plant infested by their host (*P. xylostella* and *P. rapae*, respectively) versus a plant infested by both species (data from Shiojiri et al. 2000a). *Asterisks* indicate statistically significant preferences within binomial probability function (**0.001 $< P < 0.01$; *** $P < 0.001$)

longer than on an artificially damaged control piece (Shiojiri et al. 2000b). The wasp did not show any antennal searching behavior on filter paper impregnated with regurgitant (Shiojiri et al. 2000b). These data indicate that both the cabbage leaf and the regurgitant of *P. xylostella* larvae are involved in the production of infochemicals and thus both promote host-searching behavior in the wasps. Previous reports have similarly indicated that in the *C. glomerata*, *P. rapae*, and *R. indica* systems both plant juice and host regurgitant enhance host-searching behavior through the production of infochemicals (Sato 1979; Horikoshi et al. 1997). These findings provide evidence that host specificity is the result of chemical differences in the oral secretions of each herbivore species.

Presence of nonhost larvae and host larvae on the same plant affects searching behavior of parasitic wasps

The two tritrophic systems were coupled under laboratory conditions to determine the effects of simultaneous attack by two species of herbivores on the host-searching behavior of the wasps. The flight and antennal searching responses of the two parasitic wasps were observed. When comparing the attractiveness of cabbage plants infested by both herbivore species versus that of plants infested by their respective host species, *C. plutellae* showed a significant preference toward the latter (Fig. 4A) whereas *C. glomerata* showed a significant preference toward the former (Fig. 4B).

Plants infested by both herbivore species emitted a different blend of volatiles compared to those infested by either of the two herbivore species (Fig. 2E). In the headspace of plants infested by both herbivore species, dimethyldisulfide, (*Z*)-3-hexenyl acetate, and limonene

were found to be major compounds. The amount of (*E*)-4,8-dimethyl-1,3,7-nonatriene from the plants infested by both herbivore species was not as high as that emitted from the plants infested by either of the two herbivore species. This change may explain in part the observation that *C. plutellae* preferred host-infested plants to plants infested by both herbivore species and *C. glomerata* preferred plants infested by both herbivore species to host-infested plants.

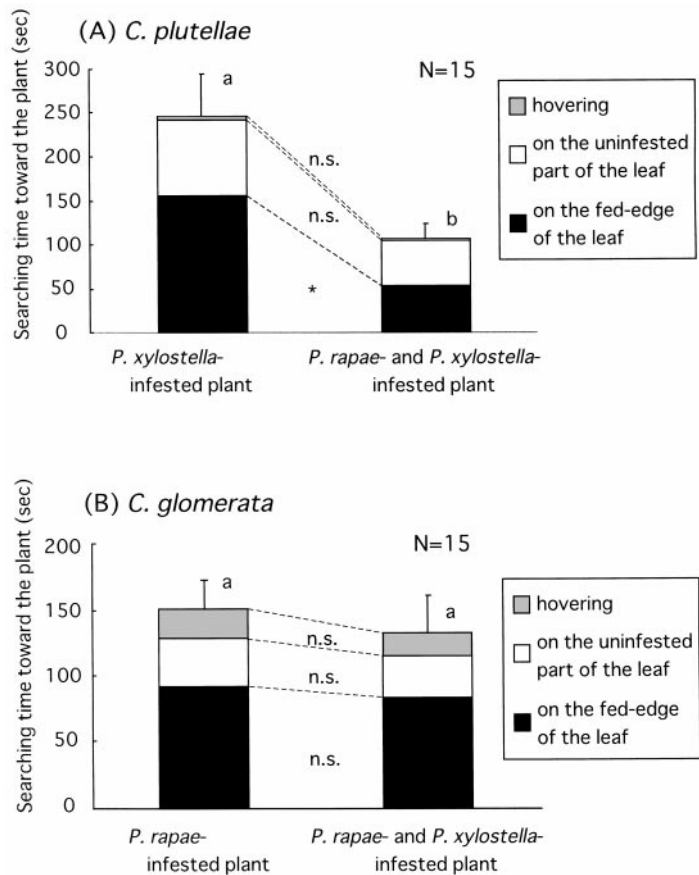
We observed the host-searching behavior of *C. plutellae* and *C. glomerata* toward a cabbage plant that was infested by host herbivores or one that was infested by both herbivore species in a clear plastic cage ($25 \times 35 \times 30$ cm) in a climate-controlled room ($25^\circ \pm 2^\circ\text{C}$; 50%–70% RH and 16L:8D). For preparation of host-infested plants, 20 second- or third-instar *P. xylostella* or 5 second-instar *P. rapae* were randomly placed on a plant and kept there for 24 h. For preparation of plants infested by both herbivore species, 20 second- or third-instar *P. xylostella* and 5 second-instar *P. rapae* were randomly placed on the plant and kept there for 24 h. After 24 h, ~15% of the leaf surface was consumed by each herbivore species. We placed the cabbage plant at the center of the floor in the cage. In one corner of the cage, we then released a single wasp from its glass tube. After the wasp landed on the plant, we recorded the host-searching behavior until the wasp flew away from the plant to land on the inner wall of the cage. This observa-

tion was repeated ten times. A Macintosh computer running Observer software was used to record these behavioral activities.

The time spent searching by *C. plutellae* on a plant previously infested by both herbivore species (106.7 ± 17.6 s) was significantly shorter than that on plants infested by only the host species (246.5 ± 47.0 s) according to Student's *t* test ($t = 2.784$, $P = 0.0095$) (Fig. 5A). This decrease can be attributed to the reduced searching time on the fed-edge of the leaf (*t* test; $t = 2.306$, $P = 0.0287$) (Fig. 5A). Thus, the presence of *P. rapae* (nonhost) -infested edge decreased the host-searching time of *C. plutellae* on the plant. Each wasp showed antennation only to the host-infested edge (Fig. 3). On the plants infested by both herbivore species, we observed that *C. plutellae* suddenly stopped the searching behavior and flew away when encountering the *P. rapae* (nonhost) -infested edge (Shiojiri, personal observation). The presence of *P. rapae* (nonhost) -infested edge might have hampered host-searching behavior on the leaf.

The searching time of *C. glomerata* on plants previously infested by both species (135.1 ± 29.5 s), on the other hand, did not differ significantly from that on the host-infested plant (146.4 ± 20.8 s) according to Student's *t* test ($t = -0.318$, $P = 0.753$) (Fig. 5B). The presence of the host-infested edge and nonhost-infested edge did not affect the host-searching time of *C. glomerata* on the plant.

Fig. 5. Resident time (mean \pm SE) of (A) *C. plutellae* and (B) *C. glomerata* on a cabbage plant infested by the host larvae and those infested by both host and nonhost larvae. The total searching time, time spent hovering, searching on the uninfested part of the leaf, and searching on the fed-edge of the leaf were compared by Student's *t* test. Total searching time followed by different letters for each wasp differed significantly ($*0.01 < P < 0.05$; *n.s.*, not significantly different)



Discussion and conclusion

In the present study, we observed infochemically mediated tritrophic interaction webs on a cabbage plant (Fig. 6). In

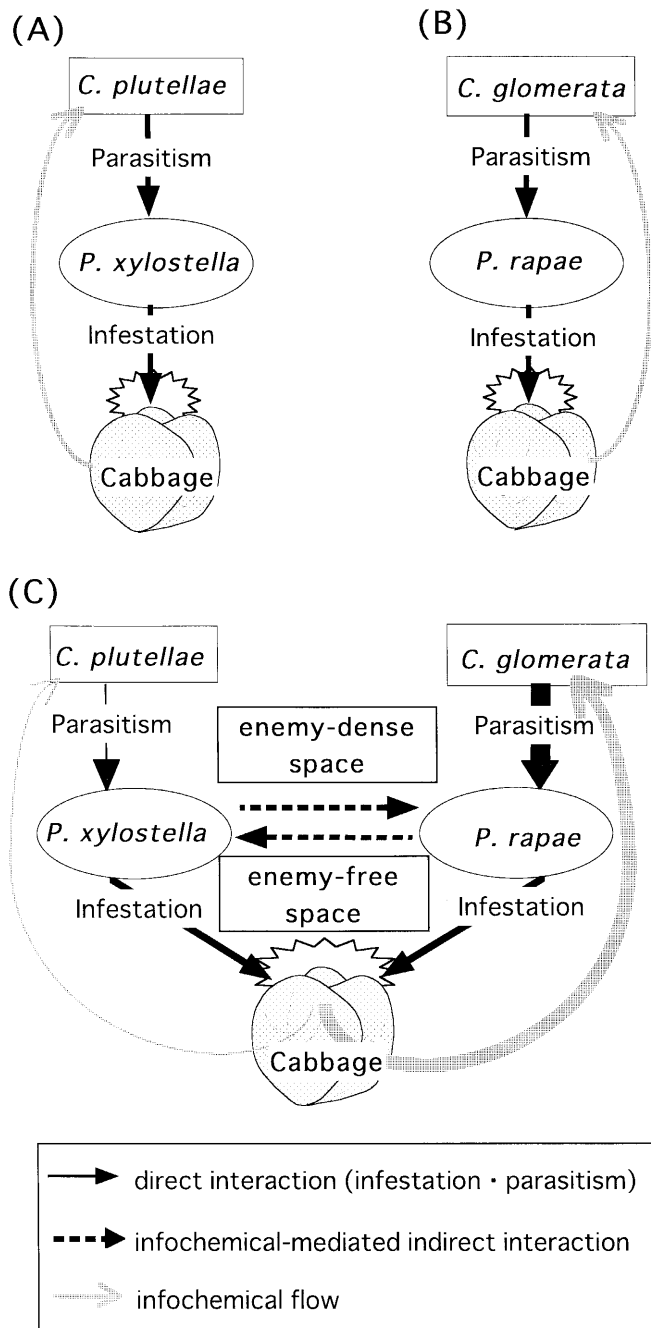


Fig. 6. Infochemically mediated tritrophic interaction webs on cabbage plants. **(A)** Tritrophic interaction consisting of cabbage plants, *P. xylostella*, and *C. plutellae* in which the infested plants recruited the wasp using host-specific volatile infochemicals. **(B)** Tritrophic interaction consisting of cabbage plants, *P. rapae*, and *C. glomerata* in which the infested plants recruited the wasp using host-nonspecific volatile infochemicals. **(C)** Two tritrophic interactions coexisting on the same cabbage plants. The thickness of the arrow of infochemical flow and that of direct interaction indicate the intensity of information available for the wasp and the intensity of interaction between two organisms, respectively

the webs, one tritrophic system (cabbage plant, *P. xylostella* larvae and *C. plutellae*; Fig. 6A) was affected by the presence of the other tritrophic system (cabbage plant, *P. rapae* larvae, and *C. glomerata*; Fig. 6B), and vice versa. When a cabbage plant was simultaneously infested by both *P. xylostella* larvae and *P. rapae* larvae (Fig. 6C), the blend of volatiles emitted from the infested plants was modified from that emitted from a cabbage plant infested by their respective host larvae (see Fig. 2). This information modification increased the attractiveness of the infested plants to *C. glomerata* (infochemical flow of Fig. 6B and 6C), but decreased the attractiveness of the infested plants to *C. plutellae* (infochemical flow of Fig. 6A and 6C).

The greater attractiveness of cabbage plants infested by both herbivore species compared to *P. rapae*-infested cabbage plants in turn would lead to a greater number of *C. glomerata* on the former plants. Thus, the simultaneous presence of the two herbivore species on the same plant intensifies the prey-predator interaction between *P. rapae* larvae and *C. glomerata*, and such plants are considered to be "enemy-dense space" (Sato et al. 1999a) for *P. rapae* larvae (Fig. 6). The indirect interaction between *P. xylostella* larvae and *P. rapae* larvae caused by the negative effect of the former larvae on the parasitism of the latter larvae by *C. glomerata* through chemical information is referred to as "negative infochemical-mediated indirect interaction."

In contrast, the lesser attractiveness of cabbage plants infested by both herbivore species compared to *P. xylostella*-infested cabbage plants in turn would lead to fewer *C. plutellae* on the former plants. Furthermore, the duration of searching time by the attracted wasps on the plants was shorter than that on the *P. xylostella*-infested plants. Thus, the simultaneous presence of the two herbivore species on the same plant weakens the prey-predator interaction between *P. xylostella* larvae and *C. plutellae*, and such plants are considered to be "enemy-free space" (Jeffries and Lawton 1984; Holt and Lawton 1993; Feder 1995) for *P. xylostella* larvae (see Fig. 6). The indirect interaction between *P. rapae* larvae and *P. xylostella* larvae caused by the positive effect of the former larvae on the parasitism of the latter larvae by *C. plutellae* through chemical information is referred to as "positive infochemical-mediated indirect interaction."

Previous studies of insect-plant interactions have focused primarily on direct or indirect interactions, or both, in a ditrophic and tritrophic context. The present study further shows that one herbivore species affects other tritrophic interactions on the same plant by modifying the chemical information involved in these interactions. Such indirect interactions, which we have referred to as infochemical-mediated indirect interaction, would also affect community persistence and stability of herbivores and natural enemies of herbivores. Field experiments involving the two tritrophic systems we have examined are essential to validate the present findings.

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