

Exploitation of the serpentine leafminer *Liriomyza trifolii* and tomato leafminer *L. bryoniae* (Diptera: Agromyzidae) by the parasitoid *Gronotoma micromorpha* (Hymenoptera: Eucoilidae)

YOSHIIHISA ABE

Laboratory of Applied Entomology, Graduate School of Agriculture, Kyoto Prefectural University, Shimogamo, Kyoto 606-8522, Japan; e-mail: y_abe@kpu.ac.jp

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Abstract. The developmental time and size of a solitary koinobiont parasitoid, *Gronotoma micromorpha* (Perkins) (Hymenoptera: Eucoilidae), were measured in two host species: the serpentine leafminer, *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae) and tomato leafminer, *L. bryoniae* (Kaltenbach). There was no significant difference in the developmental time of *G. micromorpha* in these two hosts. However, significantly larger *G. micromorpha* adults emerged from *L. bryoniae* than from *L. trifolii* puparia. Dissection of larvae revealed that when offered a choice *G. micromorpha* accepted larvae of *L. bryoniae* more often than those of *L. trifolii*. The number of wasps emerging from parasitized hosts did not differ significantly between host species. These results indicate that *L. trifolii* and *L. bryoniae* are both acceptable and suitable hosts for *G. micromorpha*. *Gronotoma micromorpha* may be a useful biological control agent of both *L. trifolii* and *L. bryoniae*.

INTRODUCTION

The serpentine leafminer, *Liriomyza trifolii* (Burgess) and tomato leafminer, *L. bryoniae* (Kaltenbach) often coexist in greenhouses and are serious pests of tomatoes in Europe (Spencer, 1973; Minkenberg & van Lenteren, 1986) and Japan (Abe & Kawahara, 2001). Leaf mining by *Liriomyza* larvae reduces photosynthesis and, as a result, crop yield (Malais & Ravensberg, 1991). The relationship between injury by *L. bryoniae* and yield loss in tomatoes is known (Ledieu & Helyer, 1985).

Liriomyza trifolii is indigenous to the New World (Spencer, 1973), but has extended its geographical range to Asia, Africa and Europe (Saito, 1997). In contrast, *L. bryoniae* is of Palearctic origin (Sasakawa, 1961; Spencer, 1973). *Liriomyza trifolii* and *L. bryoniae* are similar in morphology, so it is not easy for growers to distinguish between them. Both leafminers are polyphagous attacking vegetables and ornamentals (Minkenberg & van Lenteren, 1986). The total developmental times (oviposition to adult emergence) of *L. trifolii* and *L. bryoniae* on kidney bean, *Phaseolus vulgaris* L., are 16.5 and 19.3 days, respectively, at 25°C (Tokumaru & Abe, 2003).

The braconid *Dacnusa sibirica* Telenga and the eulophid *Diglyphus isaea* (Walker), originally used for the biological control of *L. trifolii* and *L. bryoniae* in Europe, have been imported and released in Japanese greenhouses to control *Liriomyza* leafminers (Ozawa et al., 2001). Japanese greenhouses are usually small and kept at high temperatures and humidities (Yano, 1993). The effectiveness of *D. sibirica* may be restricted in Japan, because this wasp is less effective at controlling leafminers on tomato at high temperatures (Minkenberg, 1990).

In contrast to *D. sibirica*, *D. isaea* is a more effective parasitoid at high temperatures (Minkenberg, 1989).

Diglyphus isaea occurs in Japan, where it is the dominant parasitoid attacking the garden pea leafminer, *Chromatomyia horticola* (Gourea) (Takada & Kamijo, 1979). The potential risks of introducing exotic natural enemies has recently received attention and the potential of hybridization needs to be included in risk analysis (van Lenteren et al., 2003). Many naturalists believe strongly that native genotypes should be preserved and that introduction of foreign genes constitutes genetic pollution (Williamson, 1996). Greenhouses in Japan are not completely insect proof (Yano, 1993) so hybridization between European and Japanese populations of *D. isaea* may have occurred.

Male-biased sex ratios may be common in *Diglyphus* (Heinz & Parrella, 1990). Such male-biased sex ratios need to be carefully monitored and manipulated in the mass production of these parasitoids (Rathman et al., 1991). Moreover, in mass rearing thelytokous wasps do not use expensive hosts for the production of males (Stouthamer, 1993). Thus, thelytokous parasitoids are more suited to mass production than arrhenotokous ones (Abe & Tahara, 2003).

The solitary koinobiont parasitoid, *Gronotoma micromorpha* (Perkins), occurs in subtropical regions, i.e., Okinawa, Florida, Hawaii, Guam and Tahiti (Yoshimoto, 1963; Beardsley, 1988; Abe & Konishi, 2004), and appears to be the dominant parasitoid of *L. trifolii* on Okinawa, Japan (Konishi, 1998), and Guam, USA (Johnson, 1993). Under laboratory conditions, this parasitoid has a high net reproductive rate when it parasitizes the host *L. trifolii* (Abe & Tahara, 2003). *Wolbachia* infection induces thelytoky in this wasp (Arakaki et al., 2001). This thelytokous wasp is an egg-pupal and larval-pupal parasitoid (Abe, 2001). *Gronotoma micromorpha* can develop at most of the temperatures at which *L. trifolii* damages

crops, and the combination of high temperature and short photoperiod found in Japanese greenhouses in winter does not adversely affect its development (Abe & Tahara, 2003). The developmental rate of *G. micromorpha* increases linearly with increasing temperature between 18 and 30°C. The lower thermal thresholds for complete development and oviposition are 11.7°C and approximately 18°C, respectively (Abe & Tahara, 2003). These results indicate that should *G. micromorpha* escape from greenhouses, where they were released for controlling leafminers, they cannot overwinter in Japan, except in the subtropical regions. To clarify the potential of *G. micromorpha* as a biological control agent of *L. trifolii* and *L. bryoniae*, the acceptability and suitability of these two *Liriomyza* species for this parasitoid were determined.

MATERIAL AND METHODS

Insects and plants

Laboratory cultures of *G. micromorpha* and *L. trifolii* were established from parasitized and non-parasitized *L. trifolii* larvae collected in Itoman City, Okinawa Prefecture, Japan, in April 1998 (Abe, 2001). The maintenance of stock colonies, and preparation of hosts and parasitoids for experiments are described in more detail in a previous paper (Abe, 2001). A laboratory culture of *L. bryoniae* was established from individuals collected from leaves of tomato plants in Kamigamo, Kyoto City, Japan, in June 1998. *Phaseolus vulgaris* was used as a host plant for colony maintenance and in all the experiments. Colony maintenance and all experiments were conducted at 25°C under a 15L : 9D photoperiod.

The effects of host (*L. trifolii*) age at oviposition (0 to 4 days = egg to mature larva) on percentage emergence and developmental time of *G. micromorpha* were previously determined in the laboratory (Abe, 2001). There was no significant difference in percentage emergence among host ages. However, the developmental time was significantly shorter in 3- or 4-day-old larvae, suggesting that mature larvae are a more suitable host stage for *G. micromorpha*. The mature larvae of *L. bryoniae* are similarly more suitable than earlier stages as a host for *G. micromorpha* (Abe, Y., unpubl.). Larvae of *L. trifolii* developing on *P. vulgaris* leaves pupate after 5–6 days at 25°C (Abe, 2001), and those of *L. bryoniae* after 6–7 days (Abe, Y., unpubl.). Therefore, 4-day-old *L. trifolii* and 5-day-old *L. bryoniae* larvae were used in the experiments.

Host pupal size

To estimate the size of the pupa of the two *Liriomyza* species, the head width of 15 pupae within their puparia was measured to the nearest 6.7 µm under a binocular stereomicroscope.

Host suitability

The base of the stem of a *P. vulgaris* plant with two true leaves infested with approximately 20–30 4-day-old larvae of *L. trifolii* or 5-day-old larvae of *L. bryoniae* was immersed in water in a 10-ml glass vial attached to the inside bottom of a cylindrical glass tube (6.4 cm diameter, 22 cm high). The top of the tube was covered with organdy and the bottom with Kimwipe®. Undiluted honey was streaked on the inside of the tube as a food source for the wasps. Immediately thereafter, one naive female *G. micromorpha* (0–24 h old) was released into the tube and allowed to parasitize the *Liriomyza* larvae for 24 h before removal from the tube. Fifteen wasps were used for each *Liriomyza* species. After removal of the wasp, the two leaves were detached from each plant by cutting the petioles and then

placed in a 250-ml plastic cup. The immatures of *Liriomyza* were reared and the emergence of *G. micromorpha* wasps recorded. The hind tibial lengths of 20 randomly selected wasps emerging from each host species were measured to the nearest 6.7 µm under a binocular microscope.

Host acceptance

Phaseolus vulgaris plants with two true leaves were infested with mature larvae of *L. trifolii* or *L. bryoniae* as in the previous experiment. Just before the experiment, one of the two true leaves was cut from each plant. The stems of one plant with mature larvae of *L. trifolii* and one with mature larvae of *L. bryoniae* were immersed in water in a 10-ml glass vial attached to the bottom of a glass tube (as above). Immediately after transfer of the plants, one 0–24 h-old naive female *G. micromorpha* was introduced into the tube and allowed to oviposit into *L. trifolii* and *L. bryoniae* larvae for 24 h before removal. After removal of the wasp, all host larvae were transferred from the leaves into Ringer's solution and dissected with minute pins under a binocular microscope to see whether they contained parasitoid eggs or not. Twenty replicates were performed. The ratio of the number of the two host species (*L. trifolii* / *L. bryoniae*) per replicate ranged from 0.54 to 2.12.

Host acceptance and larval survival

The experimental design was the same as in the host acceptance experiment, except that the host larvae were reared after exposure to *G. micromorpha* and the emergence of adult parasitoids was recorded. After the end of adult emergence, host puparia with no exit holes were dissected under a binocular microscope to record mortality of *L. trifolii* and *L. bryoniae* pupae, and larval, pupal, or adult mortality of *G. micromorpha*. Twenty replicates were performed. The ratio of the two host species (*L. trifolii* / *L. bryoniae*) per replicate ranged from 0.72 to 3.33.

Data analysis

One-way ANOVA was used to detect differences in pupal head width between *L. trifolii* and *L. bryoniae*. Effects of host species on developmental time and body size of *G. micromorpha* were analyzed using the same statistical tests. Host acceptance and combined effects of host acceptance and larval survival of *G. micromorpha* were analyzed in paired T-test after weighting data for proportional availability of hosts. The significance level for all statistical tests was set at $P = 0.05$.

RESULTS

Host pupal size

The mean (\pm SE) pupal head widths of *L. trifolii* and *L. bryoniae* were significantly different: 0.590 (\pm 0.013) mm and 0.655 (\pm 0.014) mm, respectively (ANOVA, $F = 11.802$, d.f. = 1, $P < 0.01$).

Host suitability

All the wasps that emerged were females. No significant difference was found in the developmental time of *G. micromorpha* (measured from oviposition to adult emergence) between *L. trifolii* and *L. bryoniae* (Table 1, ANOVA, $F = 3.206$, d.f. = 1, $P > 0.05$). The hind tibiae of wasps emerging from *L. bryoniae* puparia were significantly longer (difference = 0.024 mm) than those emerging from *L. trifolii* puparia (Table 1, ANOVA, $F = 7.659$, d.f. = 1, $P < 0.01$).

TABLE 1. Effect of host species on developmental time (mean \pm SE) and hind tibial length (mean \pm SE) of *Gronotoma micromorpha*.

Host species	Developmental time (egg-adult) in days	Hind tibial length (mm)
<i>L. trifolii</i>	19.3 \pm 0.1 (n = 217)a	0.412 \pm 0.006 (n = 20)a
<i>L. bryoniae</i>	19.1 \pm 0.1 (n = 156)a	0.436 \pm 0.006 (n = 20)b

Means with the same letter were not significantly different in one-way ANOVA ($P > 0.05$).

Host acceptance

Significantly more *L. bryoniae* than *L. trifolii* larvae were parasitized by *G. micromorpha* (Table 2, paired T-test, $t = -2.818$, d.f. = 19, $P = 0.01$).

Host acceptance and larval survival

There was no significant difference in rate of emergence of *G. micromorpha* between *L. trifolii* and *L. bryoniae* (Table 3, paired T-test, $t = -0.394$, d.f. = 19, $P > 0.05$). No dead larvae, pupae, or adults of *G. micromorpha* were found in the dissected host puparia. These puparia contained only dead host pupae.

DISCUSSION

Gronotoma micromorpha completed its development successfully in both *L. trifolii* and *L. bryoniae*. No signifi-

cant difference was found in the developmental time of this wasp in the two host species. However, larger *G. micromorpha* adults emerged from *L. bryoniae* than from *L. trifolii* puparia. Developmental time (or developmental rate) and body size are both important traits for evaluating fitness of parasitoids (Roitberg et al., 2001). In solitary koinobiont parasitoids, the size of the offspring is often influenced by the host species from which it emerged (Visser, 1994). Pupae of *L. trifolii* and *L. bryoniae* can be regarded as fixed host resources available for offspring development of *G. micromorpha*, because the parasitoid is in the 1st instar when the host pupates (Abe, Y., unpubl.). Pupae of *L. bryoniae* were significantly larger than those of *L. trifolii*. Large hosts presumably contain more resources and, therefore, should be of relatively higher quality than small hosts (Nicol & Mackauer, 1999). Consequently, the difference in body size of *G. micromorpha* is probably due to the difference in the size of pupae of the two host species. Similarly, no significant difference was found in female developmental time of *D. sibirica* in *L. trifolii* and *L. bryoniae*, and larger parasitoid females emerged from *L. bryoniae* than from *L. trifolii* puparia (Abe et al., 2005). This difference in female size might be also explained by the higher quantity of food available in *L. bryoniae*.

TABLE 2. Acceptability of *L. trifolii* and *L. bryoniae* as hosts for *G. micromorpha*.

Replicate	Number of larvae parasitized / Number of larvae exposed		Proportional availability of hosts		Number of larvae parasitized / Proportional availability of hosts	
	<i>L. trifolii</i>	<i>L. bryoniae</i>	<i>L. trifolii</i>	<i>L. bryoniae</i>	<i>L. trifolii</i>	<i>L. bryoniae</i>
1	5 / 29	12 / 23	0.558	0.442	8.96	27.15
2	18 / 19	8 / 13	0.594	0.406	30.30	19.70
3	11 / 45	11 / 26	0.634	0.366	17.35	30.05
4	4 / 21	14 / 39	0.350	0.650	11.43	21.54
5	10 / 19	3 / 9	0.679	0.321	14.73	9.35
6	14 / 27	5 / 14	0.659	0.341	21.24	14.66
7	5 / 20	12 / 33	0.377	0.623	13.26	19.26
8	9 / 23	13 / 27	0.460	0.540	19.57	24.07
9	12 / 22	16 / 27	0.449	0.551	26.73	29.04
10	19 / 25	9 / 12	0.676	0.324	28.11	27.78
11	9 / 15	11 / 14	0.517	0.483	17.41	22.77
12	3 / 21	16 / 35	0.375	0.625	8.00	25.60
13	14 / 29	9 / 21	0.580	0.420	24.14	21.43
14	4 / 25	18 / 24	0.510	0.490	7.84	36.73
15	4 / 17	17 / 24	0.415	0.585	9.64	29.06
16	9 / 23	9 / 16	0.590	0.410	15.25	21.95
17	10 / 21	8 / 13	0.618	0.382	16.18	20.94
18	4 / 26	13 / 15	0.634	0.366	6.31	35.52
19	11 / 21	5 / 11	0.656	0.344	16.77	14.53
20	9 / 26	6 / 15	0.634	0.366	14.20	16.39

Mean (\pm SE) of the number of larvae parasitized/proportional availability of hosts for *L. trifolii* and *L. bryoniae* were 16.37 (\pm 1.56) and 23.38 (\pm 1.56), respectively. There was a significant difference in acceptability of these two hosts (paired T-test, $t = -2.818$, d.f. = 19, $P = 0.01$).

TABLE 3. Combined effects of host acceptability and offspring survival on the number of *G. micromorpha* that emerged from *L. trifolii* and *L. bryoniae*.

Replicate	Number of wasps emerging / Number of larvae exposed		Proportional availability of hosts		Number of wasps emerging / Proportional availability of hosts	
	<i>L. trifolii</i>	<i>L. bryoniae</i>	<i>L. trifolii</i>	<i>L. bryoniae</i>	<i>L. trifolii</i>	<i>L. bryoniae</i>
1	14 / 24	7 / 32	0.429	0.571	32.63	12.26
2	15 / 16	9 / 13	0.552	0.448	27.17	20.09
3	6 / 16	10 / 15	0.516	0.484	11.63	20.66
4	11 / 16	7 / 17	0.485	0.515	22.68	13.59
5	16 / 18	8 / 12	0.600	0.400	26.67	20.00
6	17 / 27	5 / 12	0.692	0.308	24.57	16.23
7	4 / 13	6 / 15	0.464	0.536	8.62	11.19
8	5 / 13	8 / 16	0.448	0.552	11.16	14.49
9	5 / 18	5 / 25	0.419	0.581	11.93	8.61
10	10 / 14	8 / 11	0.560	0.440	17.86	18.18
11	13 / 33	8 / 30	0.524	0.476	24.81	16.81
12	0 / 24	13 / 23	0.511	0.489	0	26.58
13	7 / 25	6 / 20	0.556	0.444	12.59	13.51
14	5 / 15	6 / 8	0.652	0.348	7.67	17.24
15	6 / 34	6 / 20	0.630	0.370	9.52	16.22
16	7 / 30	4 / 9	0.769	0.231	9.10	17.32
17	4 / 23	4 / 19	0.548	0.452	7.30	8.85
18	6 / 33	7 / 14	0.702	0.298	8.55	23.49
19	13 / 23	3 / 21	0.523	0.477	24.86	6.29
20	0 / 21	9 / 20	0.512	0.488	0	18.44

Mean (\pm SE) of the number of wasps emerging / proportional availability of hosts for *L. trifolii* and *L. bryoniae* were 14.97 (\pm 2.11) and 15.87 (\pm 1.19), respectively. There was no significant difference in the number of wasps emerging from these two host species (paired T-test, $t = -0.394$, d.f. = 19, $P > 0.05$).

A female parasitoid can influence the fitness of her offspring through her choice of a host, since the quality of the host can directly affect offspring fitness (Luck & Nunney, 1999). Thus, it is predicted that foraging female parasitoids that encounter hosts of different species should select the most suitable. Female *G. micromorpha* exhibited a significant preference for *L. bryoniae* larvae. However, no significant difference was found in the number of wasps emerging between *L. trifolii* and *L. bryoniae*. These results indicate that *G. micromorpha* immatures parasitizing *L. bryoniae* had a higher mortality rate than those parasitizing *L. trifolii*. Why do female *G. micromorpha* prefer *L. bryoniae* larvae, which are of a lower quality than *L. trifolii* larvae in terms of their offspring's survival? It is possible that *L. bryoniae* larvae are a better quality host than *L. trifolii* larvae in terms of the fecundity of wasp's offspring. In general, large parasitoids are more fecund than small ones (King, 1987; Visser, 1994). Provided the size and fecundity of female *G. micromorpha* are positively correlated, as in female *D. sibirica* (Croft & Copland, 1993), female *G. micromorpha* emerging from *L. bryoniae* puparia would have a higher fecundity than those from *L. trifolii* puparia. Further study is needed to clarify the relationship between the size and fecundity in female *G. micromorpha*.

The geographical distributions of *L. bryoniae* and *G. micromorpha* do not overlap. However, the present study reveals that *L. bryoniae* is as good as *L. trifolii* as a host for *G. micromorpha* in terms of larval development and survival and is the preferred host for oviposition. These three factors are important for biological control because they influence a parasitoid's parasitism rate and its numerical response. In addition to the wide range of host stages (egg to mature larvae) suitable for oviposition (Abe, 2001), the reproductive capacity and no adverse effect of high temperature or short photoperiod on development (Abe & Tahara, 2003), the present results indicate that *G. micromorpha* could be an effective biological control agent of *L. trifolii* and *L. bryoniae* in greenhouses.

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