

Survival and Mortality of Immature Mordellids (Coleoptera: Mordellidae) Inducing Stem-galls on the Japanese Mugwort¹

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Abstract Mordellid galls were collected from stems of Japanese mugwort, *Artemisia indica* var. *maximowiczii* (Nakai) H. Hara, in early spring at three riverbeds in the Kinki district, central Japan, and reared in the laboratory. Adults of two mordellids, *Mordellistena brevilineata* Nomura (96.2% of the total number of individuals) and *M. fuscoturalis* Nomura (3.8%), emerged from the galls. The galls were simple fusiform swellings in the stems. We could not distinguish the 2 species by gall morphology. Mortality of the immatures mostly could not be determined, but parasitoids (*Eupelmus* sp., *Entedon* sp., and braconids, etc.) accounted for about 25% of the total mortality observed. Survival of immatures tended to be higher and the concomitant parasitism lower in thicker rather than thinner galls, and the galls became thick when they were formed in larger diameter stems. Oviposition and larval establishment in thick stems appeared to be advantageous for the completion of development and avoidance of parasitoid attack.

Key Words gall-inducers, life history, *Mordellistena*, parasitoids, tumbling flower beetles

Plant gall formation is induced by physicochemical interactions between plants and various organisms such as insects, mites, nematodes, fungi, viruses and bacteria (Mani 1964, Meyer 1987). Gall-inducing habits have evolved in six insect orders including Thysanoptera, Hemiptera, Lepidoptera, Coleoptera, Diptera and Hymenoptera (Mani 1964, Meyer 1987, Dreger-Jauffret and Shorthouse 1992). A relatively small number of gall-inducers occur in the Order Coleoptera, with most gall-inducing species in the Family Curculionidae (Mani 1964, Meyer 1987, Morimoto 1996).

The Family Mordellidae, comprising about 1500 described and many undescribed species, is a relatively large family whose larvae are mostly phytophagous and bore into stems and wood (Jackman and Lu 2002). Larvae of the Tribe Mordellistenini bore into herb stems, and several *Mordellistena* species are known as inquiline that have

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no ability to induce galls but feed on gall tissues in the galls (Weis and Abrahamson 1985, Cappuccino 1992). Although gall-inducing mordellid species are rarely found worldwide (Korotyaev et al. 2005), three species (*Mordellistena insignata* Ermisch, *M. brevilineata* Nomura, *M. comes* Marseul) have been recorded to induce stem galls on herbs in Japan (Hukuda 1959, Hayashi 1974, 1986, Morimoto 1996).

Ecological and life history studies of insects that induce plant galls are primarily on gall wasps (Hymenoptera: Cynipidae), gall midges (Diptera: Cecidomyiidae), aphids (Homoptera: Aphididae) and sawflies (Hymenoptera: Tenthredinidae) (Mani 1964, Shorthouse and Rohfritsch 1992). However, life history and survival patterns of immatures in gall-inducing mordellids have rarely been studied. Furthermore, plant traits such as plant organ size affect gall size and subsequently the survival and performance of insects inducing the gall formation (Price and Ohgushi 1995, Prado and Monteiro 1999, Fritz et al. 2000).

We report herein on (1) gall morphology on the Japanese mugwort, *Artemisia indica* var. *maximowiczii* (Nakai) H. Hara, induced by mordellids; (2) parasitism, mortality and survival of the mordellids from gall formation to adult eclosion; (3) the relationship between host plant stem diameter and gall diameter, and (4) the effects of gall diameter on larval survival.

Materials and Methods

Study sites. Mordellid galls on the Japanese mugwort were collected and observed at the following three riverine sites in the Kinki district in central Japan: (1) Kizu River, Yawata City, Kyoto Prefecture (34°53 N, 135°42 E, 20 m above sea level), (2) Yamato River, Osaka City, Osaka Prefecture (34°35 N, 135°30 E, 10 m a.s.l.) and (3) Onosato River, Sennan City, Osaka Prefecture (34°22 N, 135°15 E, 2 m a.s.l.). Detailed site descriptions can be found in Yamazaki et al. (1999) for the Kizu River and Yamazaki and Sugiura (2003) for the Onosato River.

Sampling and rearing of the galls. The Japanese mugwort is ubiquitously distributed in Japan, except northern districts, and abundantly grows in various disturbed and early successional habitats such as urban lots, riverbeds, and mountain paths (Hayashi 1989, Oki 1997). It is a perennial herb, sprouting new shoots in spring and growing to 50-120 cm in height by autumn. During winter, the above-ground portions are killed to the ground (Hayashi 1989, Yamazaki et al., pers. obs.). The mordellid stem-galls appear in early summer. The mordellids overwinter as mature larvae in galls, pupate in spring, and emerge as adults from May onward (Morimoto 1996, Yamazaki et al., pers. obs.). Therefore, stem-galls were collected in April prior to adult emergence. The galls were collected by inspecting the stems of arbitrarily selected host plants. Numbers of galls collected at the Kizu site in 2001 was 162 and 12 in 2002, 64 from the Yamato site in 2001, and 38 from the Onosato site in 2002. The galls and stems were clipped from the dry host plants, transported to the laboratory, individually placed in Zip-lock™ plastic bags, and reared under laboratory conditions until the emergence of either adults or parasitoids. Emerged mordellid adults were identified by the male genitalia and coloration of elytral hairs of both sexes (Nomura 1961). Voucher specimens are deposited in the Osaka Museum of Natural History (Osaka City). Afterward, the diameters of the galls and stems were measured from two different directions with digital calipers to the nearest 0.01 mm, and mean diameters were calculated. Stem diameter was estimated by averaging the diameters of

two stem parts per gall: 10 mm below the base of a gall and 10 mm above the upper side of the gall.

Life table construction and analyses. Additionally, the galls were dissected and inspected to determine developmental stage and cause of death of mordellids that did not emerge. Then, based on the dissection results, a life table from gall formation to adult eclosion was constructed. Developmental stages were classified into early, middle and late-instar larvae, pupae, and adult emergence. Each larval stage was classified based on the positions and amounts of feeding damage (early: only underneath the stem epidermis, middle: attained to vascular bundles, late: middle parts of piths were consumed) and subsidiarily on the sizes of the dead larvae (early: <2 mm in body length, middle: 3-5 mm, late: >5 mm). Although this division may not correspond to an actual instar, we considered that each stage represented a certain developmental stage. Immature mortality was classified into parasitism, fungus infestation, destruction of a gall, miscellaneous death (feeding damage and/or a mordellid remains could be detected but its mortality could not be determined) and failure of emergence of the adult mordellid. Parasitism could be detected not only by parasitoid emergence in the laboratory but also by minute emergence holes made by parasitoids already present. The destruction of galls might be caused by physical disturbances such as river flooding and strong winds.

Logistic regression analyses (Sokal and Rohlf 1995) were used to analyze the effects of gall diameter on survival and parasitism of larvae. Pearson correlation coefficient (Sokal and Rohlf 1995, Zar 1999) was used to evaluate the relationship between stem diameter and gall diameter. These analyses were performed only for the Kizu River in 2001 and the Yamato River in 2001, due to small sample sizes in other site/year samples. The ovipositor lengths of emerged parasitoids were measured using an ocular micrometer under a stereomicroscope to infer whether parasitoids can pierce gall walls with their ovipositors.

To clarify whether the thick walls of some galls prevented adult emergence, gall diameters were compared between galls from which adults emerged ($n = 37$) and those in which adults did not emerge ($n = 20$) using an unpaired *t*-test (Sokal and Rohlf 1995, Zar 1999). All site/year samples were pooled for this comparison.

Results

Species composition of mordellids and gall morphology. From the galls collected at the three riverine sites, two mordellid species (*Mordellistena brevilineata* Nomura and *M. fuscoturalis* Nomura) emerged (Table 1). However, of the total number of mordellids emerging, *M. brevilineata* accounted for 96.2% (50 individuals) whereas only 2 males (3.8%) of *M. fuscoturalis* emerged.

Fusiform galls were formed in the nodes of main and lateral stems of the host plant (Fig. 1a). Gall morphology of the two *Mordellistena* species was so similar that we could not discriminate between them based on only gall inspection. Gall size was not different between the two mordellid species: the mean (\pm SE) gall length and gall diameter of *M. brevilineata* were 16.1 ± 0.6 mm and 10.8 ± 0.3 mm, respectively, whereas those of *M. fuscoturalis* were 15.7 ± 0.1 mm and 11.4 ± 1.9 mm (Table 2). Because only a few emerged and could not be distinguished the species by their gall morphology, we combined the 2 species for life history analysis. The mean (\pm SE) gall length and diameter of overall galls including galls containing dead larvae were 12.8 ± 0.2 mm and 8.4 ± 0.1 mm, respectively (Table 2).

Table 1. Mordellid adults emerging from stem galls on the Japanese mugwort at three riverine sites in central Japan, 2001-2002

Mordellid species	Sampling site/Year					Total
	Kizu River		Yamato River		Onosato River	
	2001	2002	2001	2002	2002	
<i>M. brevilineata</i>	1♂6♀	1♂1♀	9♂13♀	1♂4♀	7♂7♀	19♂31♀
<i>M. fuscoturalis</i>	1♂	0	0	0	1♂	2♂
No. of galls examined	162	12	64	32	38	308

Individuals destroyed upon dissection of the galls were excluded from the identification.

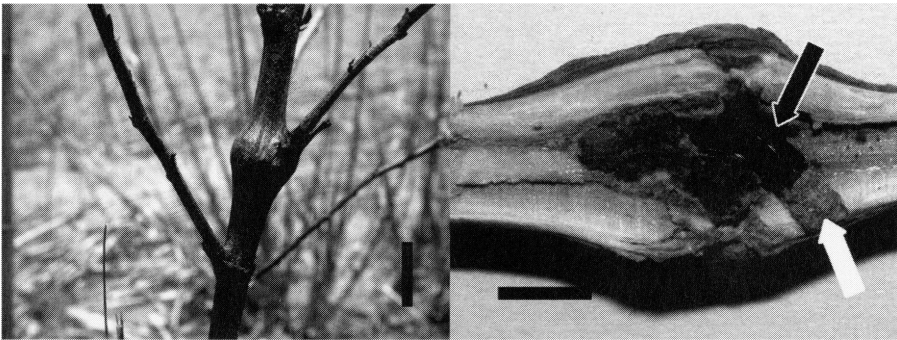


Fig. 1. (A, left) A *Mordellistena* gall formed in a stem of the Japanese mugwort. (B, right) Interior of a *M. brevilineata* gall (cross section). A dead eclosed adult (black arrow) in the gall. The pupal chamber was connected to the gall wall with a channel filled with frass (white arrow). Scale bar: (a) 10.0 mm, (b) 5.0 mm.

Gall dissection revealed internal structures of the galls, feeding activity of the larvae and sites for pupation, resulting in life history construction of the immature mordellids. Each gall contained only one mordellid individual. All galls exhibited signs of feeding activity. Judging from developmental stages of dead larvae and feeding damage, hatched larvae bored and fed under the epidermis of the stem, although the oviposition site was unclear. As larvae grew, they penetrated into the middle part of the stem to feed on the pith. When fully grown, the larva constructed a pupal chamber near the epidermis, overwintered, and pupated in spring. The pupal chamber was connected to the sidewall by a tunnel which was filled with frass and only a thin layer remained to facilitate adult emergence (Fig. 1b). Adults emerged from the galls between early and late May in the laboratory.

Life table of immature mordellids. Table 3 shows life table of the mordellids from gall formation to adult emergence in all site/year samples. Mortality was relatively high from middle larval stadium to adult emergence, whereas that during early larval

Table 2. Mean (\pm SE) gall size induced by two mordellid species on the Japanese mugwort at three riverine sites

Species/Gall size	Sampling site/Year						Total
	Kizu River		Yamato River		Onosato River		
	2001	2002	2001	2002	2002	2002	
<i>M. brevilineata</i>							
Gall length* (mm)	13.1 \pm 1.0 (9)	18.4 \pm 5.2 (2)	16.9 \pm 1.0 (23)	14.5 \pm 0.6 (7)	17.3 \pm 1.0 (14)	16.1 \pm 0.6 (55)	
Gall diameter* (mm)	8.8 \pm 0.7 (9)	12.1 \pm 2.3 (2)	10.8 \pm 0.5 (23)	10.4 \pm 0.2 (7)	12.1 \pm 0.5 (14)	10.8 \pm 0.3 (55)	
<i>M. fuscoturalis</i>							
Gall length (mm)	15.7 (1)	—**	—	—	15.8 (1)	15.7 \pm 0.1 (2)	
Gall diameter (mm)	9.5 (1)	—	—	—	13.2 (1)	11.4 \pm 1.9 (2)	
Overall galls sampled							
Gall length* (mm)	11.4 \pm 0.2 (162)	14.5 \pm 1.2 (12)	14.5 \pm 0.6 (64)	13.1 \pm 0.4 (32)	15.0 \pm 0.7 (38)	12.8 \pm 0.2 (308)	
Gall diameter* (mm)	7.2 \pm 0.2 (162)	8.4 \pm 0.9 (12)	9.4 \pm 0.3 (64)	9.4 \pm 0.3 (32)	11.1 \pm 0.4 (38)	8.4 \pm 0.1 (308)	

* Gall length and diameter were measured on galls from enclosed mordellids and as well as total galls sampled. Gall diameter was measured from two directions and averaged for each gall. Sample sizes are presented in parentheses.

** - denotes no eclosion.

Table 3. Life table of mordellids inducing stem galls on the Japanese mugwort at three riverine sites

Developmental stage	Year	Mortality factor	Kizu River		Yamato River		Onosato River		Total
			2001	2002	2001	2002	2001	2002	
			Survival rate		Survival rate		Survival rate		
Early instar larva		Survival rate	100	100	100	100	100	100	100
		Braconid parasitism	0	0	1.6	0	0	0	0.3
		Unknown parasitoids	1.2	0	0	0	0	0	0.6
		Unknown death	11.7	0	7.8	0	2.6	0	8.1
Intermediate instar larva		Survival rate	87.0	100	90.6	100	97.4	97.4	90.9
		Braconid parasitism	4.9	0	4.7	3.1	0	0	3.9
		<i>Entedon</i> sp.	0.6	0	0	0	0	0	0.3
		Unknown parasitoids	11.1	0	4.7	6.3	0	0	7.5
Late instar larva and pupa		Destruction of a gall	3.7	0	1.6	3.1	0	0	2.6
		Unknown death	37.0	25	21.9	40.6	31.6	31.6	29.9
		Survival rate	29.6	25.0	57.8	46.9	65.8	65.8	46.8
		Braconid parasitism	3.7	8.3	6.3	9.4	0	0	4.5
Eclosed as adult		<i>Entedon</i> sp.	0.6	0	0	0	0	0	0.3
		<i>Eupelmus</i> sp.	1.9	0	1.6	3.1	0	0	1.6
		Unknown parasitoids	4.9	16.7	6.3	6.3	5.3	5.3	5.8
		Fungus infestation	0.6	0	0	0	0	0	0.3
Emerged from the gall		Destruction of a gall	0	0	0	0	0	0	0.6
		Unknown death	11.7	33.3	7.8	6.3	15.8	15.8	11.7
		Survival rate	6.2	16.7	35.9	21.9	39.5	39.5	21.8
		Death in a gall	3.1	0	26.6	12.5	28.9	28.9	12
% parasitism		Survival rate	3.1	16.7	9.4	9.4	10.5	10.5	9.7
		No. of galls examined	29.0	25.0	25.0	28.1	5.3	5.3	25.0
			162	12	64	32	38	38	308

The values are percentages. Two mordellid species, *M. brevilineata* and *M. fuscocuturalis*, were combined.

stadium was low. The most frequent (49.7% of total mortality) mortality factor was unknown. On average, parasitoids were responsible for 0.9% mortality of early instars ($n = 28$), 11.7% of intermediate instars ($n = 136$), and 12.2% of late instars ($n = 77$) (Table 3). The parasitoids that emerged from the galls were *Eupelmus* sp. (Hymenoptera: Eupelmidae), *Entedon* sp. (Hymenoptera: Eulophidae), *Rhaconotus* sp., and *Bracon* sp. (Hymenoptera: Braconidae). In addition, parasitoids had already emerged from 53 galls before gall collection, some of which contained empty braconid cocoons. The destruction of galls by physical disturbances and fungus were of minor importance (Table 3). The number of adults emerged in pupal chambers but that died in the galls was 12.0% (Table 3). Overall, the percentage of adult emergence was highest at the Kizu River in 2002, and lowest at the Kizu River in 2001 (Table 3).

Effects of gall size on immature survival and parasitism. For both Kizu River (2001) and Yamato River (2001), the immature mordellids survived more frequently as the gall diameter became larger (Logistic regression analyses, $df = 1$, $\chi^2 = 6.211$, $P = 0.0127$ for Kizu River in 2001 and $\chi^2 = 10.973$, $P = 0.0009$ for Yamato River in 2001). At the Kizu River in 2001, the gall diameter did not affect parasitism rate (Logistic regression analysis, $df = 1$, $\chi^2 = 1.281$, $P = 0.2577$), whereas at the Yamato River in 2001, the mordellids in larger galls had less parasitism ($\chi^2 = 6.551$, $P = 0.0105$).

The ovipositor lengths of emerged parasitoids were 0.48-0.56 mm ($n = 3$) in *Eupelmus* sp., 0.68-0.92 mm ($n = 4$) in *Bracon* sp. and 1.40 mm ($n = 1$) in *Rhaconotus* sp. However, in *Entedon* sp., no ovipositors could be seen from the dorsal view ($n = 5$). The thicknesses of the normal stem and gall epidermis (the diameter of the gall was 12 mm) were approx. 0.3 mm and >1.0 mm, respectively.

Stem diameter was positively correlated with gall diameter in both samples (Pearson correlation analyses, $R = 0.888$, $P < 0.0001$ for Kizu River, 2001, $R = 0.874$, $P < 0.0001$ for Yamato River, 2001). The gall diameters were not significantly different between the galls from which adults emerged and those in which adults died (unpaired t -test, $t = 0.468$, $P = 0.6415$), reflecting that variations in thickness of gall walls did not account for the success or failure of adult emergence from the galls.

Discussion

Species composition of mordellids inducing stem-galls on the Japanese mugwort. In this study, two mordellid species, *M. brevilineata* and *M. fuscoturalis*, emerged from the galls on the Japanese mugwort (Table 1). Although *M. insignata* has been considered as a common mordellid inducing stem-galls on the Japanese mugwort (Hukuda 1959, Morimoto 1996), it did not emerge in this survey. There are no recent reliable records of *M. insignata* that were identified by inspecting the male genitalia. We, therefore, conclude that the most common mordellid species inducing stem galls on the Japanese mugwort is *M. brevilineata*.

From North America, *M. convicta* LeConte was reported as an inquiline of the tephritid fly, *Eurosta solidaginis* (Fitch), on goldenrods (Weis and Abrahamson 1985, Abrahamson et al. 1989, Ford and Jackman 1996). In addition, Tooker and Hanks (2004) revealed that *M. aethiops* Smith larvae facultatively preyed on gall wasp larvae and other endophytic insects and fed on gall tissues. The Japanese mugwort harbors diversity of gall-inducing insects such as cecidomyiids and tephritids (Yukawa and Masuda 1996).

It is unlikely that both *Mordellistena* species are inquilines of other insects on the

Japanese mugwort, because (1) there were only a small number of stem galls induced by an unidentified gall midge on the Japanese mugwort (K. Yamazaki, pers. observ.), (2) the positioning of galls by the gall midge (basal parts of lateral stems) were different from those made by the mordellids (nodes of lateral and main stems) (K. Yamazaki, pers. observ.), and (3) there were no signs of feeding activity and remains of gall-inducers other than mordellids and parasitoids in the dissected galls. Therefore, *M. brevilineata* is a unique gall-inducer. Its gall-inducing habits have rarely been reported worldwide for the Mordellidae (Korotyaev et al. 2005). However, in this study *M. fuscoturalis* was rarely observed, and the gall morphology of *M. fuscoturalis* was similar to that of *M. brevilineata*. There is an unpublished record that *M. fuscoturalis* eclosed from the normal stems of *Artemisia* sp. on Hokkaido, northern Japan (Tsuru, pers. comm.). Therefore, *M. fuscoturalis* may be an inquiline of *M. brevilineata* galls.

Immature survival process and mortality factors of the mordellids. All galls exhibited feeding damage characteristic of mordellid larvae. This indicates that mordellid galls are induced by the feeding activity of these larvae. If oviposition induced gall formation in mordellid beetles, there would have been some galls that had no larval feeding damage because of death during the egg stage. Galls with no eggs or signs of larval feeding activity can frequently be detected in sawfly galls, in which the galls are primarily induced by oviposition by adult females (Price and Roininen 1993).

The most frequent mortality factor could not be determined (Table 3). Conceivably, several factors were involved: plant resistance to early-instar larvae, dessication, and winter cold against late-instar larvae. Four or more parasitoid species emerged from the galls. Although diverse parasitoid complexes (more than 10 species) are frequently reported in cecidomyiid and cynipid galls (e.g., Yasumatsu and Kamijo 1979, Hawkins and Goeden 1984), coleopteran galls harbor relatively poor parasitoid faunas (Hawkins 1994).

The number of adults eclosed in pupal chambers that died in the galls was not negligible (Table 3), but gall diameter (possibly positively related to the thickness of the gall walls) did not account for the success or failure of adult emergence from the galls. Therefore, eclosed adults in the galls might not fail to exit from the galls because of thick gall walls. Mature mordellid larvae made pupal chambers and channels from the chambers to side walls with only a thin layer remaining to facilitate adult emergence (Fig. 1b). This finding also supports the hypothesis that gall thickness does not hinder adult emergence. The channels leading to side walls were usually filled with compact frass (Fig. 1b), that may have prevented adult emergence from the galls.

Effects of gall size on immature survival and parasitism. The immature survival rate was higher and the parasitism rate was lower for thicker galls. For several gall-inducing insects, large and thick galls reduce the parasitoid attack rate, because a thick gall wall prevents penetration of the ovipositors of parasitoids (Weis and Abrahamson 1985, Price and Clancy 1986, Price 1988, Abrahamson et al. 1989). In the present study, the ovipositor lengths of most emerged parasitoids were less than 1.0 mm. Therefore, a thick gall epidermis (>1.0 mm) of thick galls (diam. >12 mm) might prevent the penetration of parasitoid ovipositors through the gall epidermis. Thus, variation in gall size seems to affect the parasitism rate. However, because these parasitoids, except for *Entedon* sp., are idiobiont ectoparasitoids (Goulet and Huber 1993), host larvae immediately die or are paralyzed by parasitoid attack which is followed by gall growth arrest. On the other hand, galls not-attacked continue to

grow. Thus, difference in gall sizes between parasitized and unparasitized galls in this study may have been caused by two factors, the thickness of gall epidermis and the developmental stages of mordellid larvae that died.

Thick galls were formed in thick stems, suggesting that oviposition and larval establishment at thick stems is advantageous to complete immature development. This finding is consistent with the Plant Vigor Hypothesis, which argues that many herbivore species preferentially feed on and grow well on large vigorous plants or in plant organs (Price 1991). However, many galls were formed on thin lateral stems, but in these cases the main stems also had galls (K. Yamazaki, pers. observ.). Therefore, intraspecific competition for galling sites may affect the within-plant distribution of galls in the mordellids.

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References Cited

- Abrahamson, W. G., J. F. Sattler, K. D. McCrea and A. E. Weis. 1989.** Variation in selection pressures on the goldenrod gall fly and the competitive interactions of its natural enemies. *Oecologia* 7: 15-22.
- Cappuccino, N. 1992.** Adjacent trophic-level effects on spatial density dependence in a herbivore-predator-parasitoid system. *Ecol. Entomol.* 17: 105-108.
- Dreger-Jauffret, F. and J. D. Shorthouse. 1992.** Diversity of gall-inducing insects and their galls, Pp. 8-33. *In* J. D. Shorthouse and O. Rohfritsch [eds.], *Biology of Insect-Induced Galls*, Oxford University Press, New York.
- Ford, E. J. and J. A. Jackman. 1996.** New larval host plant associations of tumbling flower beetles (Coleoptera: Mordellidae) in North America. *Coleopt. Bull.* 50: 361-368.
- Fritz, R. S., B. A. Crabb and C. G. Hochwender. 2000.** Preference and performance of a gall-inducing sawfly: a test of the plant vigor hypothesis. *Oikos* 89: 555-563.
- Goulet, H. and J. T. Huber. 1993.** Hymenoptera of the World: An Identification Guide to Families. Agriculture Canada, Ottawa.
- Hawkins, B. A. 1994.** Pattern and Process in Host-Parasitoid Interactions. Cambridge University Press, Cambridge.
- Hawkins, B. A. and R. D. Goeden. 1984.** Organization of a parasitoid community associated with a complex of galls on *Atriplex* spp. in southern California. *Ecol. Entomol.* 9: 271-292.
- Hayashi, E. 1989.** Wild Flowers of Japan: Plains, Seaside and Hills. Yama-kei, Tokyo.
- Hayashi, N. 1974.** Ecological notes on *Mordellistena* (Mordellidae, Coleoptera). *Saisyû to Shiiku* 36: 180-181.
- 1986.** Life of Coleoptera: Exploring Habits of Beetle Larvae. Chikuji-shokan, Tokyo.
- Hukuda, A. 1959.** *Mordellistena insignata* Ermisch, p. 488. *In* T. Esaki *et al.* [eds.], *Illustrated Insect Larvae of Japan*, Hokuryukan, Tokyo.
- Jackman, J. A. and W. Lu. 2002.** Mordellidae Latreille 1802, Pp. 423-430. *In* R. H. Jr. Arnett, M. C. Thomas, P. E. Skelley, and J. H. Frank [eds.], *American Beetles, Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea*, CRC Press, Boca Raton.
- Korotyaev, B. A., A. S. Konstantinov, S. W. Lingafelter, M. Y. Mandelshtam and M. G. Volkovitch. 2005.** Gall-inducing Coleoptera, Pp. 239-271. *In* A. Raman, C. W. Schaefer, and T. M. Withers [eds.], *Biology, Ecology, and Evolution of Gall-inducing Arthropods Volume 1*, Science Publishers, Entfield.

- Mani, M. S. 1964.** Ecology of Plant Galls. Dr W Junk, The Hague.
- Meyer, J. 1987.** Plant Galls and Gall Inducers. Gebruder Borntraeger, Berlin.
- Morimoto, K. 1996.** Stem-galls on *Cannabis sativa* by *Mordellistena comes* Marseul, Elongate stem-galls on *Artemisia princeps* by *M. insignata* Ermisch, Mordellidae, Coleoptera, Pp. 188, 303-304, 370-373. In J. Yukawa and H. Masuda [eds.], Insect and Mite Galls of Japan in Colors, Zenkoku Nôson Kyôiku Kyôkai, Tokyo.
- Nomura, S. 1961.** Some new species of the Coleoptera from Japan. Toho-Gakuho 11: 70-89.
- Oki, Y. 1997.** *Artemisia indica* var. *maximowiczii*, p. 68. In S. Okuda [ed.], Wild Plants of Japan, Shogakkan, Tokyo.
- Prado, P. I. K. L. and E. Monteiro. 1999.** The interplay between plant traits and herbivore attack: a study of a stem galling midge in the neotropics. Ecol. Entomol. 24: 80-88.
- Price, P. W. 1988.** Inversely density-dependent parasitism: The role of plant refuges for hosts. J. Anim. Ecol. 57: 89-96.
- 1991.** The plant vigor hypothesis and herbivore attack. Oikos 62: 244-251.
- Price, P. W. and K. M. Clancy. 1986.** Interactions among three trophic levels: Gall size and parasitoid attack. Ecology 67: 1593-1600.
- Price, P. W. and T. Ohgushi. 1995.** Preference and performance linkage in a *Phyllocolpa* sawfly on the willow, *Salix miyabeana*, on Hokkaido. Res. Popul. Ecol. (Kyoto) 37: 23-28.
- Price, P. W. and H. Roininen. 1993.** Adaptive radiation in gall induction, Pp. 229-257. In M. R. Wagner and K. F. Raffa [eds.], Sawfly Life History Adaptation to Woody Plants, Academic Press, New York.
- Shorthouse, J. D. and O. Rohfritsch. 1992.** Biology of Insect-Induced Galls. Oxford Univ. Press, Oxford.
- Sokal, R. R. and F. J. Rohlf. 1995.** Biometry: The Principles and Practice of Statistics in Biological Research, 3rd Edition. W. H. Freeman and Co., New York.
- Tooker, J. F. and L. M. Hanks. 2004.** Trophic position of the endophytic beetle, *Mordellistena aethiops* Smith (Coleoptera: Mordellidae). Environ. Entomol. 33: 291-296.
- Weis, A. E. and W. G. Abrahamson. 1985.** Potential selective pressures by parasitoids on a plant-herbivore interaction. Ecology 66: 1261-1269.
- Yamazaki, K. and S. Sugiura. 2003.** Biological notes on *Hyperaspis asiatica* (Coleoptera, Coccinellidae). Elytra 31: 87-92.
- Yamazaki, K., S. Sugiura and K. Kawamura. 1999.** Overwintering ground beetle assemblages along the Kizu River. Kyoto. Entomol. Sci. 2: 33-40.
- Yasumatsu, K. and K. Kamijo. 1979.** Chalcidoid parasites of *Dryocosmus kuriphilus* Yasumatsu (Cynipidae) in Japan, with descriptions of five new species (Hymenoptera). Esakia 14: 93-111.
- Yukawa, J. and T. Masuda. 1996.** Insect and Mite Galls of Japan in Colors. Zenkoku Nôson Kyôiku Kyôkai, Tokyo.
- Zar, J. H. 1999.** Biostatistical Analysis, 4th Edition. Prentice Hall, New Jersey.