Gall-feeding habits in Lepidoptera of Japan. III: Two leaf galls

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Abstract We report here on lepidopteran larvae associated with two different types of leaf galls. 1) We examined the relationship between the structural features of one type of leaf gall and the feeding preference of two polyphagous caterpillars. On a Distylium racemosum (Hamamelidaceae) tree bearing leaf pouch galls formed by the aphid Neothoracaphis yanonis (Matsumura) (Homoptera, Aphididae) during the spring in an urban park, caterpillars belonging to the species Lymantria dispar (Linnaeus) and L. mathura Moore (Lymantridae) rested on its leaves. The galls were dehiscent, and most alates of the aphids had already escaped the galls. The galls showed no signs of having been attacked by lepidopteran larvae. We brought the larvae back to our laboratory, enclosed them in plastic cups containing D. racemosum galled shoots, and inspected the plant parts on which the larvae had fed. L. dispar and L. mathura larvae fed on normal leaf tissue and dehiscent openings on the underside of the galls but avoided feeding on their round upper surfaces. Since damage by caterpillars feeding on the galls was rare and occurred after alate emergence if at all, the caterpillars posed no negative effects for the aphids. 2) Leaf-roll galls of Phyllocolpa sp. (Hymenoptera, Tenthredinidae) on a Salix eriocarpa (Salicaceae) tree on a riverbank were sampled during the spring. Among them, 1.5% (N=206) had been attacked by the larvae of Clostera anachoreta ((Denis & Schiffermüller) (Notodontidae), Orthosia angustipennis (Matsumura) (Noctuidae) and L. dispar, which are facultative cecidophages (gall-feeders). C. anachoreta and O. angustipennis had invaded and fed on the galls, while L. dispar had grazed on them from the outside. The impact as a result of moth larvae feeding on the survival and development of sawfly larvae was small, since the attack rate was only 1.5% and there was no gall in which sawfly larva died due to cecidophagy feeding activity. The two gall formers in this study exhibited a low mortality attributable to the feeding activity of cecidophagous Lepidoptera. This might be as a result of the roundness and hardness characteristic of pouch galls produced by aphids, which deterred assault by the cecidophages, and because the relatively short developmental period of the sawfly larva reduced the chance of cecidophagy attack.

Key words Leaf galls, facultative cecidophages, Lymantria dispar, Lymantria mathura, Clostera anachoreta, Orthosia angustipennis.

Introduction

Plant galls are usually palatable, and contain more nitrogen, sugar and less defensive chemicals than normal plant tissues, although some exceptions to this exist (Mani, 1964; Abrahamson & Weis, 1987; Price et al., 1987). Leaves are the primary food source for most lepidopteran species (e. g. Young, 1997: 107). Galls that form in leaves are therefore likely to be attacked by lepidopteran larvae. However, records of cecidophagous (gall-feeding) Lepidoptera activity on leaf galls are scarce (but see Ito, 1984; Clancy et al., 1986; Kopelke, 2003; Yoshiasu, 1986).

Leaf galls are classified into several types such as leaf fold, leaf roll, leaf pouch and leaf vein galls (Mani, 1964; Dreger-Jauffret & Shorthouse, 1992; Yukawa & Masuda, 1996), each type being associated with a distinct gall structure. However, the relationship between leaf gall type and cecidophagous lepidopteran faunae is unknown. To analyze these
relationships, more data on the cecidophagous Lepidoptera of leaf galls is required. In this report, the gall-feeding habits of lepidopteran larvae on two different types of leaf galls were examined.

Cecidophages consist of outer and inner feeders. The former feeds on galls from the outside, while the latter invades and feeds on them from the inside. Which type of cecidophage imposes a greater impact on gall formers is a question which has not been examined. But laboratory experiments which examine the feeding preferences of cecidophagous insects are efficient tools for elucidating the feeding habits and impacts of cecidophages on gall formers (Ito & Hattori, 1983; Abe, 1995). Outer cecidophagous caterpillars usually wander over wide ranges on plants, and which species and the extent to which cecidophages impose negative effects on gall formers is unclear. Furthermore, the damage noted results from direct field observations. Therefore, in this study we examined the relationship between the structural features of leaf galls and the feeding preferences of two species of polyphagous caterpillars through a simple laboratory experiment.

**Galls examined, study sites and procedures**

We examined lepidopteran larvae associated with the following types of leaf galls: 1) pouch leaf-galls of the *Distylium racemosum* (Hamamelidaceae) tree formed by the aphid *Neothoracacphis yanonis* (Matsumura) (Homoptera, Aphididae), and 2) leaf-roll galls of the willow *Salix erioarpa* (Salicaceae) produced by the sawfly *Phyllocolpa* sp. (Hymenoptera, Tenthredinidae).

1) *Neothoracacphis yanonis* pouch leaf-galls

*N. yanonis* produces pouch leaf galls on its primary host plant *D. racemosum* in April. The galls were formed around leaf midribs as a result of sucking stimulus associated with stem mothers on newly flushed leaves. The galls swell on the upper and undersides of the leaves. Many alates grow in the galls, and in late spring they exit through dehiscent openings formed on the underside of the galls. They then migrate to their secondary hosts, *Quercus serrata* or *Q. crispula* (Fagaceae) (Moritsu 1983; Yukawa & Masuda 1996).

The gypsy moth *Lymantria dispar* (Linnaeus) and the rosy gypsy moth *L. mathura* Moore (Lepidoptera, Lymantriidae) are major forest pests that defoliate trees such as *Quercus, Prunus, Malus* and *Alnus* (Inoue, 1982). Both *Lymantria* species pass the winter as eggs, hatch in the spring, feed on tree leaves to grow, and eclose in the summer.

We found many *N. yanonis* galls on a *D. racemosum* tree in Oizumi-ryokuchi Park (34°34'N, 135°32'E, 20 m above sea level. For a detailed site description, see Yamazaki & Sugiura, 2003), Sakai City, Osaka Prefecture, central Japan on 12 May 2002. The galls were dehiscent, and the alates had emigrated to their secondary hosts. Furthermore, the galls showed no signs of having been attacked by lepidopteran larvae. We observed one *L. dispar* and two *L. mathura* larvae resting on the leaves of the tree. The developmental stage of all the larvae was judged to be that of the middle instar (2nd–3rd instars) based upon their body length (15–20 mm).

To decide whether these caterpillars fed on galls in the field, we brought larvae samples to our laboratory, and reared them with galled host leaves. Each larva was enclosed in a 200-ml plastic cup with a *D. racemosum* shoot bearing galled and non-galled leaves on 13 May, left until 17 May, and the plant parts on which the caterpillars fed were inspected. Each shoot bore 4–5 galled leaves and 2–7 non-galled leaves, and each galled leaf possessed 1 or 2 galls.
2) *Phyllolclop* sp. leaf-roll galls

The sawfly *Phyllolclop* sp. (same species as *Phyllolclop* sp. E noted in Yukawa & Masuda, 1996) forms roll galls in the leaves of *S. eriocarpa* and several related *Salix* species. The female adult sawfly emerges from mid to late April and inserts her ovipositor into the leaf lamina of her host to lay eggs. Then, as the leaf lamina curls longitudinally as a result of the insertion stimulus, a leaf-roll gall is formed. The larva grazes on the roll gall from the inside during its growth phase, and when it matures after 2–3 weeks it egresses from the leaf roll by cutting through its tip. The mature larva spins its cocoon in the soil and overwinters as a prepupa. Thus, *Phyllolclop* sp. E has a univoltine life cycle (Yukawa & Masuda, 1996; Yamazaki, unpublished data).

We collected the roll galls of *Phyllolclop* sp. E from a *S. eriocarpa* tree along the riverbed (34°53′N, 135°42′E, ca 10 m a. s. l., for detailed site description see Yamazaki *et al.*, 1999) of the Kizu River, Yawata City, Kyoto Prefecture, central Japan on 25 April 2002. In total, 158 shoots with 206 galled leaves were sampled, placed in plastic bags, and brought to our laboratory. The galls were dissected with tweezers to search for cecidophagous lepidopteran larvae and surviving sawfly larvae.

**Results**

1) *Neothoracaphis yanonis* pouch leaf-galls

*L. dispar* and *L. mathura* fed in a similar manner on the normal leaf tissues of galled and non-galled leaves (Table 1). They avoided feeding on the upper surface of the galls (Fig. 1b), but fed on the dehiscent parts of the underside of the galls (Fig. 1a). Thus, although *Lymantria* caterpillars fed on *N. yanonis* galls, the consumed parts were restricted to dehiscent openings, and non-galled leaves and non-galled parts of the galled leaves were preferred over the galls (Table 1).

2) *Phyllolclop* sp. leaf-roll galls

Among 206 roll galls examined, three galls were fed on by lepidopteran larvae (attack rate=1.5%): i) One gall possessed two *Clostera anachoreta* ([Denis & Schiffermüller]) (Lepidoptera, Notodontidae) middle-instar larvae inside its roll. In the roll gall, a mature *Phyllolclop* larva coexisted with these notodontid larvae (Fig. 2). ii) An *Orthosia angustipennis* (Matsumura) (Lepidoptera, Noctuidae) middle-instar larva fed on a leaf roll from the inside. There was no *Phyllolclop* larva present in the leaf roll. Judging from the

<table>
<thead>
<tr>
<th>Examined larvae</th>
<th>L. dispar</th>
<th>L. mathura No.1</th>
<th>L. mathura No.2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Non-galled leaves</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of leaves eaten/provided</td>
<td>5/5</td>
<td>2/2</td>
<td>5/7</td>
</tr>
<tr>
<td><strong>Galled leaves</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of leaves eaten (only leaves)/provided</td>
<td>1/5</td>
<td>2/4</td>
<td>2/5</td>
</tr>
<tr>
<td>No. of leaves eaten (both leaves and galls)/provided*</td>
<td>1/5</td>
<td>1/4</td>
<td>2/5</td>
</tr>
<tr>
<td>No. of leaves eaten (only galls)/provided*</td>
<td>0/5</td>
<td>0/4</td>
<td>1/5</td>
</tr>
</tbody>
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*The consumed gall parts were restricted to dehiscent openings from which alates exit.*

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feeding traces left by the sawfly larva, the early stage larva appeared to have died of an unknown cause. iii) A gypsy moth middle-instar larva fed on the roll gall from the outside. There was a penultimate instar sawfly larva present in the roll.

The developmental stages of *Phyllocolpa* larvae found in the rolls were 22 last instar (22.7%), 32 penultimate instar (33.0%) and 43 middle instar larvae (44.3%) (N=97). In the roll galls, predacious arthropods such as *Lasius sakagamii* Yamauchi & Hayashida ants that attended the aphid *Chaitophorus saliniger* Shinji and two clubionid spiders and a lacewing larva were present.

**Discussion**

1) *Neothoracaphis yanonis* pouch leaf-galls

*Lymantria dispar* and *L. mathura* fed on normal leaf tissue and the dehiscent openings of
pouch galls, but avoided feeding on the upper surface of the galls (Table 1, Figs 1a, b). We believe that this feeding preference occurs because the upper surface of the galls is so round and hard that the caterpillars cannot pierce the galls from the upper side using their mandibles. However, the dehiscent parts of the galls are soft enough to graze on. Since attack by *Lymantria* caterpillars on the galls was rare in the field and only occurred after the alates had escaped, the caterpillars imposed no adverse effects on *N. yanonis*. Although we reported on the gall-feeding habits of various lepidopteran species in a series of articles (Yamazaki & Sugiura, 2003a, b), feeding avoidance by cecidophages may be crucial for the survival of gall-formers (Schultz, 1992). The round and hard surface characteristics of this aphid gall may inhibit attacks by cecidophages, especially before alate emergence. However, Ito (1984) reported that the larvae of an obligate cecidophagous moth, *Nola innocua* Butler (Lepidoptera, Noctuidae, Nolinae) attack *N. yanonis* galls before alate emergence. *Nola innocua* larvae bore into the galls and feed on their inner walls (Ito, 1984). Therefore, the round and hard physical characteristics of *N. yanonis* galls cannot completely prevent attacks by various cecidophages.

2) *Phyllocolpa* sp. leaf-roll galls

The feeding impact by lepidopteran larvae on the survival and development of sawfly larvae was low; the attack rate was only 1.5% and there was no gall in which sawfly larva died as a result of cecidophagous feeding activity. This attack rate might be attributed to the relatively short developmental period (2–3 weeks) of the *Phyllocolpa* sawfly, which appears to reduce the chance of attack by cecidophages. However, the degree of impact by gall-feeding Lepidoptera on *Phyllocolpa* larvae varies depending upon year and site: Yamazaki observed that many *Clostera anastomosis* (Linnaeus) (Lepidoptera, Notodontidae) caterpillars fed on *Phyllocolpa* sp. E leaf rolls on *S. eriocarpa* trees at the study site in the spring of 1994. In addition, frequent outbreaks of *Chrysomela vigintipunctata* (Scopoli) and *Plagiodera versicolor* (Laicharting) (Coleoptera, Chrysomelidae) willow leaf beetles occur on *Salix* trees, which defoliate most leaves including *Phyllocolpa* galls along riverbanks in central Japan (Yamazaki, personal observations).

Three lepidopteran larvae which feed on *Phyllocolpa* galls are facultative cecidophages: *Clostera anchoreta* ties salicaceous leaves together and feeds on them (Arisawa & Nishiguchi, 1965; Sugi, 1982); *Orthosia angustipennis* feeds externally on the leaves of various broad-leaf trees (Teramoto, 1996); and *Lymantria dispar* is a generalist external defoliator as mentioned above (Inoue, 1982). These larvae use leaf-roll galls as shelters and/or nutritious food sources. A sawfly larva can complete its growth within a gall by feeding on half of a leaf lamina, suggesting nutritional improvement in the leaf roll. The inhabitants of leaf shelters (such as leaf rolls) generally benefit from a favorable microhabitat, reduction in antiherbivore defense, and protection from natural enemies (Fukui, 2001). However, leaf shelters often act as cues for natural enemies that search for shelter users as prey (Fukui, 2001). In this study, since ants, spiders and lacewing larva were found in the roll-galls, these predators might prey on cecidophages as well as gallmakers.

The present study found that two leaf galls were fed on by lepidopteran larvae, but that the gall formers suffered low mortality as a result of this feeding activity. This appears to be due to the round and hard characteristics of pouch galls produced by aphids, and the relatively short developmental period of sawfly larva.
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References

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摘 要

日本の鱗翅目におけるゴール食の習性3.—2種の葉ゴール—(山崎一夫・杉浦真治)
本論文では、2種のタイプの異なる葉ゴールを観察する鱗翅目幼虫の食性や攻撃率に関して報告する。
1) 2種の多食性鱗翅目幼虫において、葉ゴールの構造特性と摂食選好性の関係を調査した。大阪府壺市の都市緑地(大泉緑地)において、春に、多くのイスノキハハマフシ(イスノキ葉のヤノイアブラムシ Neothoracaphis yanonis (Matsumura) (同翅目アブラムシ科) によるゴール)を擁するイスノキの葉上に、マイマイガ Lymantria dispar (Linnaeus) とカシワママイ L. mathura Moore (いずれもドクガ科)の中間幼虫が静止しているのを見出した。全てのゴールは裂開し、アブラムシ有翅虫はすでにゴールから脱出していった。このとき、ゴールに鱗翅目幼虫に攻撃された形跡は認められなかった。そこで、これらの幼虫を実験室に持ち帰り、ゴールの形成されたシートと共に容器に入れておき、幼虫が摂食する部位を記録した。これらの幼虫は、イスノキの果実の葉組織と葉裏のゴールの裂開部分を摂食したが、ゴールの葉表の部分は摂食しなかった。鱗翅目幼虫によるゴールへの攻撃は稀であり、たとえあっても、アブラムシ有翅虫の脱出後の裂開部分に限られるので、幼虫はアブラムシに負の影響は与えていないと考えられた。

2) 京都府八幡市木津川河岸において、春季に、ジャヤナギハマキフシ(ジャヤナギ葉のハマキハバチの一種 Phyllocopa sp. (膜翅目ハバチ科) による葉巻型ゴール)をサンプリングして調べると、ツマアカシャホココ Clostera anchoreta ((Denis & Schiffermüller)) (シャホコポドガ科)、ホソバキリガ Orthosia angustipennis (Matsumura) (ヤガ科)、マイマイガの幼虫がゴールを摂食していた。これらの幼虫は機会的えい食者と判断された。ツマアカシャホココとホソバキリガは内部から、マイマイガは外部からゴールを摂食していた。これら鱗翅目幼虫の攻撃率は1.5%と小さく、ゴール食の被害によって死亡したハバチ幼虫はいなかったことから、鱗翅目幼虫の摂食によるハバチ幼虫へ与える影響は非常に小さいと考えられた。

本研究で扱った2種の葉ゴールでは、ゴールは鱗翅目幼虫によって摂食されたがそれに起因する死亡率はわずかであった。これは、アブラムシのゴールでは丸く堅固なゴールの外部形態がゴール食者からの攻撃を防い、ハバチのゴールでは比較的短い幼虫の発育期間によってゴール食者の攻撃の機会を減少させていた可能性がある。

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