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ORIGINAL ARTICLE

Species composition and life histories of shelter-building caterpillars on *Salix miyabeana*

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Abstract

We studied the species composition and life history patterns of shelter-building microlepidoptera on the willow *Salix miyabeana* in Hokkaido, northern Japan. We identified 23 microlepidopteran species across seven families that constructed leaf shelters. Species in Tortricidae and Pyralidae comprised approximately 90% of the total number of sampled shelter-building microlepidoptera that reached adult eclosion in the laboratory. Seasonal changes in the density of leaf shelters showed two peaks: early June and mid-August. In June, caterpillars of *Gypsonoma bifasciata*, *Gypsonoma ephoropa*, *Acleris issikii* and *Saliciphage acharis* were the principal shelter builders, while in August shelters were constructed primarily by caterpillars of *Nephopterix adelphella*, *A. issikii* and *S. acharis*. Approximately 90% of leaf shelters were constructed on the top portions of shoots, suggesting that most shelter-building caterpillars prefer to build leaf shelters here.

Key words: larval occurrence, larval preference, leaf shelter, Pyralidae, Tortricidae.

INTRODUCTION

Most herbivorous insects are exposed to environmental hazards such as adverse weather conditions (Strong *et al*. 1984). To cope with these hazards, some herbivores have adapted concealed feeding behaviors such as galling, mining, boring and shelter building (e.g. Damman 1987; Price *et al*. 1987; Cappuccino 1993). Microlepidopteran larvae often create leaf shelters by rolling, folding and tying leaves together with silk. Living in such shelters has many potential benefits: shelters provide a refuge from natural enemies (Damman 1987; Atlegrim 1989; Cappuccino 1993; Eubanks *et al*. 1997), they protect against adverse microclimatic conditions (Hunter & Willmer 1989; Larsson *et al*. 1997) and they facilitate the acquisition of high quality food (Sagers 1992; Fukui *et al*. 2002).

The genus *Salix* comprises approximately 400 species and more than 200 listed hybrids (Newsholme 1992). These willows are pioneer woody plants that commonly occur on floodplains and provide food for various species of herbivorous insect with different feeding habits (Southwood 1961). Numerous studies have been conducted on herbivorous insects that inhabit willows, including investigation of life history patterns (e.g. Ishihara *et al*. 1999; Nozawa & Ohgushi 2002), relationship between early leaf abscission and larval mortality (e.g. Preszler & Price 1993; Kagata & Ohgushi 2001) and relationship between oviposition preferences and larval performance (e.g. Craig *et al*. 1989; Kagata & Ohgushi 2001; Craig & Ohgushi 2002).

At Ishikari in Hokkaido, northern Japan, leaf shelters made by microlepidopteran caterpillars are frequently found on the dominant willow species, *Salix miyabeana*, which grows along the banks of the Ishikari River. Although shelter-building microlepidoptera comprise one of the most common guilds of herbivorous insects on *S. miyabeana*, detailed biological information on these shelter builders is not yet available. In this study, we investigated the species composition, life history patterns and host plant use of shelter-building microlepidoptera on *S. miyabeana*.

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MATERIALS AND METHODS

Study site and host plant

The study site was located on the banks of the Ishikari River (Ishikari City, Hokkaido). In and around the study site, six willow species (*Salix miyabeana* Seemen, *S. sachalinensis* Fr. Schm., *S. integra* Thunb., *S. hultenii* Floderous, *S. subfragilis* Anders and *S. pet-susu* Kimura) occur sympatrically. This study was conducted on *S. miyabeana*, the most abundant species in the study area (Ishihara *et al*. 1999). Bud break begins in late April and shoot elongation continues until mid-August (Nozawa & Ohgushi 2002). Most leaves become senescent by late October.

Species identification of shelter-building caterpillars

To clarify species and numbers of shelter-building caterpillars on *S. miyabeana*, we randomly sampled 20–50 leaf shelters from five to 10 randomly selected trees, three times a month from mid-May to early October 1998. In 1999, we randomly selected 10–15 trees on which we sampled leaf shelters between mid-May and late September. In mid-May and late September, we sampled 50 shelters, because the density of shelters was relatively low, but otherwise we sampled 100 shelters three times per month. In total, we took 627 leaf shelters in 1998 and 1300 in 1999. Because there were many empty leaf shelters (Nakamura & Ohgushi 2003), 240 larvae in 1998 and 354 in 1999 were obtained in sampled leaf shelters. To identify species, each larva within a sampled shelter was individually reared in a plastic cup (90 mm diameter, 60 mm depth) in the laboratory until adult eclosion. The date of adult eclosion was recorded for each larva to determine when caterpillars of each species fed on the willow. Leaves were renewed at 2–3 day intervals.

Seasonal changes in shelter density

To investigate seasonal changes in the density of leaf shelters on *S. miyabeana*, we conducted shelter censuses over 2 years. In 1998, we randomly selected six trees, on each of which we randomly marked 20 1-year shoots. The number of leaf shelters per current-year shoot was then counted twice a week from 21 May to 28 September. In 1999, the same census was conducted from 6 May to 28 September on 15 randomly marked 1-year shoots on each of 12 randomly selected trees. Moreover, the position of each leaf shelter that was newly constructed on a current-year shoot during each interval was recorded in each census. After dividing a current-year shoot into five sections from the base to the top, each leaf shelter was assigned to one of these five sections according to its placement on the shoot. To avoid double counting, each leaf shelter was individually labeled with plastic bands.

RESULTS

Species composition of shelter-building caterpillars

Approximately 55 and 35% of the all larvae in sampled leaf shelters reached adult eclosion in 1998 and 1999, respectively. We identified 23 species of seven families as shelter builders on *S. miyabeana* (Table 1). Approximately 90% of all sampled shelter builders that reached adult eclosion belonged to Tortricidae (78.6%) and Pyralidae (10.1%; Table 1). *Acleris issikii* was the dominant species and comprised 38.1% of the shelter-building species found on *S. miyabeana*.

Seasonal changes in shelter abundance

Seasonal changes in the density of leaf shelters showed two peaks: one in early June and the other in mid-August, both in 1998 and 1999 (Fig. 1). The species composition of shelter builders differed between the peaks (Fig. 2). In the first peak of 1998, caterpillars of two dominant species, *A. issikii* and *Saliciphaga acharis*, were primarily responsible for building leaf shelters. In addition, caterpillars of two other dominant species, *Gypsonoma bifasciata* and *Gypsonoma ephoropa*, constructed leaf shelters in the first peak of 1999. In contrast, shelters in the second peak both in 1998 and 1999 were constructed mainly by caterpillars of three dominant species, *Nephopterix adelphella*, *A. issikii* and *S. acharis*. Although a few caterpillars of *G. bifasciata* and *G. ephoropa* were found in the first peak of 1998 (Table 1), similar patterns in species composition were detected in 1998 and 1999.

Larval preference

Approximately 90% (n = 270) of leaf shelters were constructed in the top sections of shoots (Fig. 3), suggesting that most caterpillars prefer to build leaf shelters on leaves at the upper parts of shoots.

DISCUSSION

Larval preference

Microlepidopteran larvae preferred leaves at the upper portions of shoots for constructing their shelters.

Table 1 Shelter-building lepidopteran species found within sampled leaf shelters on *Salix miyabeana*

Family	Species	Number 1998	Number 1999	Number Total	Proportion (%)
Tortricidae					78.6
	Saliciphaga acharis (Butler)	15	15	30	
	Gypsonoma bifasciata (Kuznetzov)	7	14	21	
	Gypsonoma ephoropa (Meyrick)	5	14	19	
	Olethreutes cacuminana (Kennel)	1	1	2	
	Archips breviplicanus (Walsigham)	6	2	8	
	Archips fuscocupreanus (Walsingham)	–	1	1	
	Adoxophyes orana (Fischer von Roslerstamm)	–	1	1	
	Acleris issikii (Oku)	75	23	98	
	Ptycholoma lecheana (Linnaens)	1	1	2	
	Hoshinoa longicellana (Walsigham)	6	2	8	
	Hedya vicinana (Ragonot)	–	2	2	
	Pandemis heparana (Denis & Schiffermuller)	4	6	10	
Pyralidae					10.1
	Nephopterix adelphella (Fischer von Roslerstamm)	10	15	25	
	Botyodes diniasalis (Walker)	–	1	1	
Gelechiidae					6.2
	Gelechia sp.	1	9	10	
	Anacampsis populella (Clerck)	–	2	2	
	Posricoptera triorthias (Meyrick)	–	4	4	
Noctuidae					3.1
	Parastichtis suspecta (Hubner)	–	3	3	
	Ipimorpha retusa (Linnaeus)	–	4	4	
	Earias pudicana (Staudinger)	–	1	1	
Notodontidae					0.8
	Clostera anachoreta (Denis & Schiffermuller)	1	1	2	
Oecophoridae					0.8
	Agonopterix ibarai (Fabricius)	1	1	2	
Gracillariidae					0.4
	Caloptilia sp.	–	1	1	
Total		133	124	257	

Because these upper leaves are young and tender, caterpillars may easily manipulate them in making their shelters. Furthermore, young leaves are more likely to have a greater nutritional value in terms of nitrogen and amino acids (Scriber 1977; Scriber & Feeny 1979; Rausher 1981). Thus, the larval preference for upper leaves may be due to better food quality.

One could argue that distribution of leaf shelters may be limited in upper parts of shoots if adult females have a strong oviposition preference for them. However, this is unlikely, as some authors have reported that females of shelter-building microlepidoptera oviposit on or near pre-existing leaf shelters on the lower parts of shoots (Carroll & Kearby 1978; Carroll *et al.* 1979), where survivorship of their newly hatched larvae is greater than on leaves without leaf shelters (Cappuccino 1993).

Synchronization between plant phenology and larval performance

Nozawa and Ohgushi (2002) reported that spring shoot growth of *S. miyabeana* at Ishikari occurred vigorously up to mid-June; thereafter, secondary shoot growth occurred from mid-July to mid-August in 1999. These seasonal changes in shoot growth are accorded to seasonal changes in shelter density. Synchronization between shoot development and shelter density suggests that leaf flushing enables caterpillars to easily manipulate young leaves for shelter building. Therefore, larval preference for newly flushed leaves may result in shelter construction on upper leaves (Fig. 3). Similarly, leaf phenology of the host plant is an important factor in performance of other insect herbivores (Feeny 1970, 1976). For example, Feeny (1976) showed that newly hatched larvae of the lepidopteran *Operophthera brumata* L. were able to attack leaves of the oak *Quercus robur* only just after bud break, because increasing leaf toughness prevented larvae from feeding.

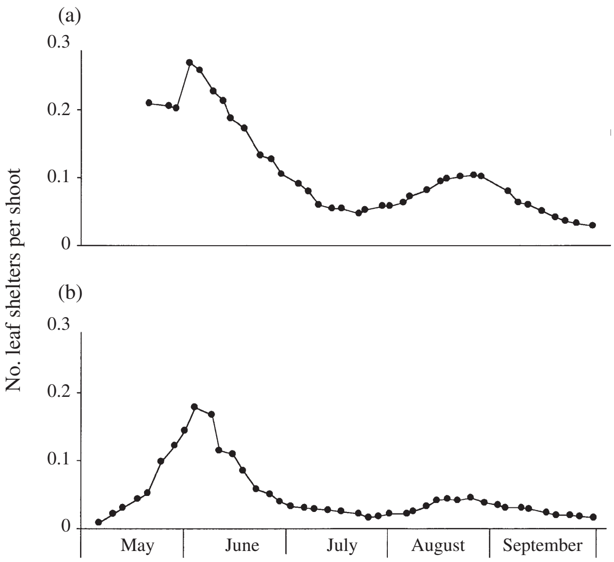

Figure 1 Seasonal changes in the number of microlepidopteran leaf shelters on *Salix miyabeana* per current-year shoot in (a) 1998 and (b) 1999.

Mechanism of coexistence of shelter-building species

Price (1992) proposed a hypothesis to explain the coexistence of multiple species of herbivorous insect on a single plant. He suggested that rapidly increasing resources, such as deciduous trees in temperate climate regions, usually increase faster than resources that are consumed by herbivores. As a result, interspecific competition is unlikely to occur. *Salix miyabeana* is a temperate deciduous tree and grows rapidly. Furthermore, the density of shelters it contained was very low (<0.3 shelters per shoot; Fig. 1), which is far below the level at which interspecific competition would occur among shelter builders. These findings suggest the possibility that rapid growth of the willow may increase the probability of coexistence of multiple species of shelter-building insects through reduced interspecific competition.

This study determined species composition and larval occurrence of shelter-building microlepidoptera on *S. miyabeana*, as well as illustrating larval preference for the upper leaves of shoots. Because shelter-building caterpillars comprise one of the most common guilds of herbivorous insects on *S. miyabeana*, our results will contribute to understanding of insect–plant interactions on the willow. Specifically, our data suggest that the relationship between insect behavior and plant growth pattern is an important factor in determining insect guild structure.

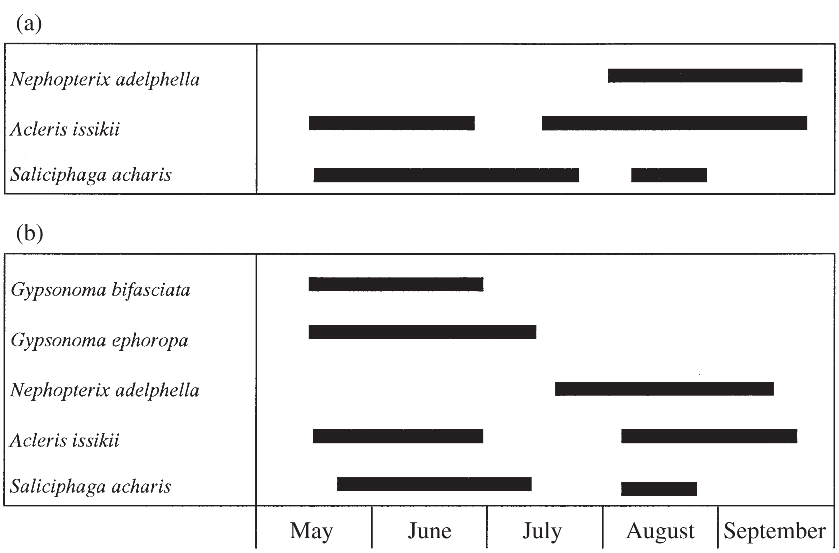

Figure 2 Larval occurrence of dominant species (>10 individuals) of shelter-building microlepidopterans on *Salix miyabeana* in (a) 1998 and (b) 1999. Data are from shelter sampling and larval rearing in the laboratory.

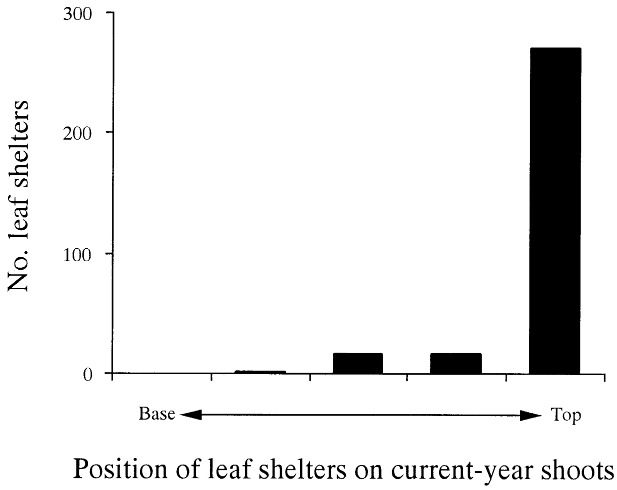

Figure 3 Position of newly constructed leaf shelters (n = 303). Each leaf shelter was assigned to one of the five positions from the base to the top of the shoot.

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