

Preference and Performance Linkage in a *Phyllocolpa* Sawfly on the Willow, *Salix miyabeana*, on Hokkaido

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Abstract. A leaf-folding sawfly in the genus *Phyllocolpa* (Hymenoptera: Tenthredinidae) attacking *Salix miyabeana* (Salicaceae) was studied near Sapporo, Hokkaido, along the Ishikari River in 1993. Host plant individuals were young trees 4–7 years old which were growing rapidly, producing some long shoots with large leaves. On a gradient of shoot length classes from 0–5 cm long to over 80 cm long, shoots were much more abundant in the shorter shoot length classes. However, attacks by ovipositing females increased as shoot length increased from 0 attacks on the shortest shoots to 5.17 attacks per shoot on the longest shoots. The frequency of attack per leaf increased from 0 to 0.13 over the same range of shoot lengths. This pattern of attack resulted in a high frequency of larval establishment in feeding sites, between 0.96 and 1.00, in all attacked shoot length categories. However, probability of survival to a late instar larva increased with shoot length and corresponded to the attack pattern, indicating a preference-performance linkage between female ovipositional decisions and larval survival. The patterns found for this *Phyllocolpa* species are similar for galling sawflies in North America and Europe, especially in the genus *Euura*, members of which make stem, bud and leaf midrib galls. Extending the pattern to a *Phyllocolpa* species broadens identification of pattern and ultimately the generality of the emerging theory on populations of galling sawflies.

Key words: leaf-folding sawfly, performance, *Phyllocolpa*, preference, *Salix*.

Introduction

The ecology of galling sawflies in Japan is poorly known, but the importance of such studies has increased because of the growing interest in the comparative ecology of the group (cf. Price and Roininen 1993). Most of the galling sawflies are in the family Tenthredinidae, subfamily Nematinae, and tribe Nematini (Smith 1979). Before dispersal by humans, they were an Holarctic group in arctic and cool temperate climates. Studies on the ecology of the group have been concentrated in North America and Europe, so it is most interesting to explore the extent to which species in Japan conform to general patterns.

The galling sawflies were probably dispersed in cool to cold climates before plate tectonic activity split up Laurasia into North America and Eurasia starting at about 135 million years ago. Therefore, studies in Arizona in the western United States of America and Japan represent the extremes of the galling sawfly range, west to east in Laurasia, and in the present day. We were interested in

the extent to which the sawflies at the ends of their natural distribution, now over 27,000 km apart as the sawflies probably dispersed across Laurasia, conformed or differed in patterns clearly evident for galling sawflies in North America and Europe. It is possible that galling sawflies colonized Japan or North America across the Bering Land Bridge during the Pleistocene, although the critical phylogenetic studies have not been completed. Nevertheless, species in Japan are geographically distant today from both North America and Europe where the sawflies have been studied in some detail. Hence their comparative ecology has great value for testing how general plant-herbivore interactions really are in this group.

On the island of Hokkaido, high populations of certain galling sawflies exist, enabling studies comparable to those conducted in Europe and North America (summarized in Price and Roininen 1993). One sawfly was an unnamed *Phyllocolpa* species, a representative of the genus that causes leaf folds down the edge of willow leaves, resulting from induced swelling of the young leaf through repeated

ovipositor insertion along the leaf edge. Such swelling, or galling, causes the leaf edge to fold under on the abaxial surface, and the larva feeds within the fold.

In studies in Europe and North America, we have found repeatedly strong positive patterns between plant module size and probability of attack and survival of galling sawflies. Especially in the genus *Euura*, which are stem, petiole, bud and leaf midrib galls, we have found an invariable pattern of ovipositional preference among females for long shoots, or buds and leaves on long shoots, and the performance of progeny in relation to higher survival on these long shoots (Price et al. 1995a). Therefore, an equivalent study on another genus of galling sawflies, very distant spatially from the former studies, seemed to be particularly interesting and valuable.

We asked the following questions in this study. 1. Do females, which initiate gall formation, show any preference for large leaves on long shoots, or is attack random? 2. If any preference is shown, is this related to the probability of establishment of larvae in feeding sites and their survival through the feeding period?

In previous studies, particularly on *Euura* sawflies, we had found a strong preference-performance linkage, with females ovipositing preferentially on the longer shoots on willows, even though these were uncommon relative to shorter shoots. On the longer shoots larvae established feeding sites in galls more successfully and survived better than on shorter shoots (e.g. Craig et al. 1989; Price 1989). This clear pattern suggested the hypothesis on plant vigor and herbivore attack (Price 1991a), which stated that many herbivore species attack and perform the best on young vigorous plants or modules. This hypothesis was erected to counter a prevalent idea at that time that herbivores were favored by stressed plants (White 1969, 1974, 1976, 1993). In addition, studies on *Euura* sawflies illustrated the need for understanding life history evolution in order to understand population dynamics (Price 1994), called the Phylogenetic Constraints Hypothesis. For the *Euura* sawflies the phylogenetic constraints were a saw-like ovipositor which necessitated insertion into soft plant tissue, and the gall-making habit requiring attack of rapidly developing undifferentiated plant tissue. For a stem galler this necessitated attack of young shoots growing rapidly. These are in short supply, a supply that becomes limiting to population growth, and sets a relatively low carrying capacity for the local population. Hence, populations on a landscape are patchy because they rely on young rapidly growing plants after disturbance, and when disturbance is low the species may become uncommon or rare. However, locally, populations may remain stable over several years if shoot resources are steadily replenished, as with shrubby willows, which regularly generate young juvenile shoots from the root stock (e.g. Price et al. 1995a,b).

Therefore, the study on *Phyllocolpa* described here acts as another test of these hypotheses and the developing theory on galling sawfly population dynamics (e.g. Price et al. 1995a).

Study site and organisms

The low-lying rich land around the mouth of the Ishikari River, near Sapporo, Hokkaido, has been disturbed extensively by development of raised dykes and roads, and land fill. Such disturbance has been colonized frequently by willows, one of the common species being *Salix miyabeana* Seeman. Between the river bank and the parallel dyke and road we found a population of young willows of this species 4 to 7 years of age attacked by an unnamed *Phyllocolpa* species. The host plant grows as a tree, reaching 2-3+ meters in 4-7 years.

The life cycle of members of the genus *Phyllocolpa* starts in the spring as willows are growing rapidly. Oviposition occurs at the base of the fold and the larva emerges and feeds in the fold. Establishment of a feeding larva in the fold can be verified when small brown feeding scars appear and the extent of feeding can be estimated by

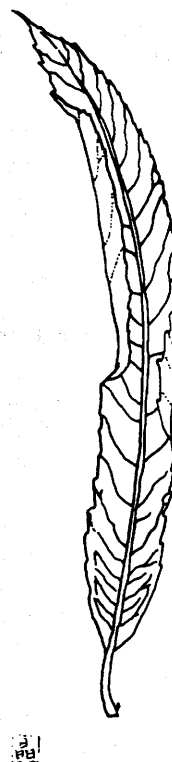


Fig. 1. Underside of a *S. miyabeana* leaf with two leaf folds of a *Phyllocolpa* species. The leaf is about 1 cm in width. Illustration by Akiko Fukui.

the amount of damage in the fold. When feeding is complete the larva descends to the ground, spins a cocoon, pupates, and the emerging adult starts a new generation. Several generations may occur each year. The life cycle of the *Phyllocolpa* species we studied has not been described, but species identity can be confirmed by a combination of the shape of the leaf fold (Fig. 1), and the host plant species, *S. miyabeana*. The most informative research on the ecology of members of the genus has been reported by Fritz and Nobel (1989, 1990) and Fritz and Kaufman (1993).

Methods

Willow module structure

The way in which a willow grows and its architecture provide independent variables which have usually had strong predictive power for the dependent variables, attack and survival, of *Euura* sawflies (e.g. Price 1989; Price et al. 1987a, b, 1995a). Therefore, we measured plant age, shoot lengths, and number of leaves per shoot, and the length and width of the largest leaf per shoot. Trees were aged nondestructively by counting back along the stem the number of winter bud scars visible. This has proved to be a reliable method in other studies (e.g. Craig et al. 1986; Price et al. 1987a). Ten trees with relatively high populations of *Phyllocolpa* were sampled in late September 1993, which grew within an area of about 5×10 m just below and parallel to the dyke or levee. These young trees were 4–7 years old and had been the most rapidly growing in the neighborhood. This was the only stand we could find with a relatively high density of *Phyllocolpa*, so that we could be sure that all trees were within easy cruising range of any female sawfly. Therefore, differences in attack relative to shoot size or leaf size could be attributed to female selection among all modules in the small area sampled. By this time of year the willows had completed growth, so shoot and leaf sizes represented fully developed modules for the 1993 growing season. All shoot lengths were allocated to 5 cm shoot length classes up to 50 cm, and to 10 cm classes above that, and analyses were performed with shoot length classes as the independent variable. In addition, all data on shoot length versus number of leaves per shoot were employed.

Sawfly attack and survival

For each of the 10 trees sampled, starting from the top of the tree, for each stem we measured stem length, and number of leaf folds per stem. For each leaf fold we recorded: 1. If a larva had established feeding, based on small browned feeding scars; 2. If a larva had died and

remained in the fold; 3. If the larva was absent from the fold; 4. If there was a living larva in the fold; or 5. If there was sufficient feeding damage for the larva to have completed feeding, followed by exit for pupation in the ground. We could not determine the cause of death for larvae dead in the fold, or absent after some feeding.

Statistical analyses employed linear regression to test patterns of leaf number and size relative to shoot length, and attack, establishment and survival of sawflies in relation to the independent variable shoot length. Chi-square analysis provided an estimate of the goodness of fit between the observed number of attacks per shoot and per leaf, versus the expected number if attacks were random. When data were grouped into classes, at least 5 samples were represented in each class. Hence, as shoot length classes became longer, and shoots per class were rarer, the class sizes were increased from 5 cm length classes to 10 cm length classes, or longer.

Results

Willow module structure

For shoot length distribution we measured 225 shoots, and for leaf size distribution the sample size was 127 shoots and leaves.

The architecture of *S. miyabeana* was highly organized and predictable based on shoot length. Short shoots were much more common than long shoots, with a strong negative trend (Fig. 2). The number of leaves per shoot increased as shoot length class increased (Fig. 3), although internode length increased also, resulting in a relatively low slope ($b=0.383$) for the correlation. Per unit length,

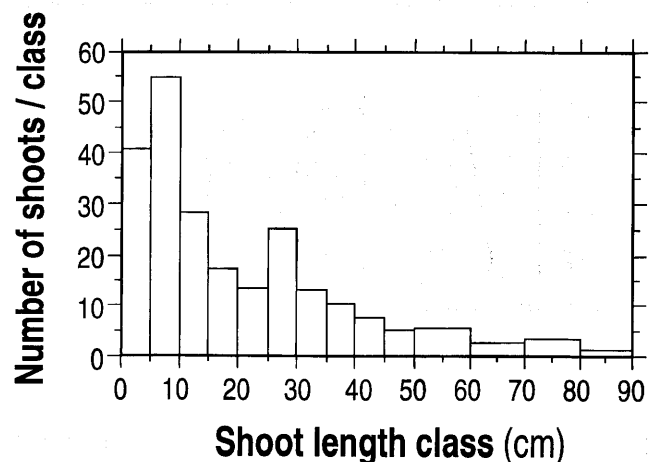


Fig. 2. The pattern of shoot length class and number of shoots per class, showing high numbers of short shoots and low numbers of long shoots.

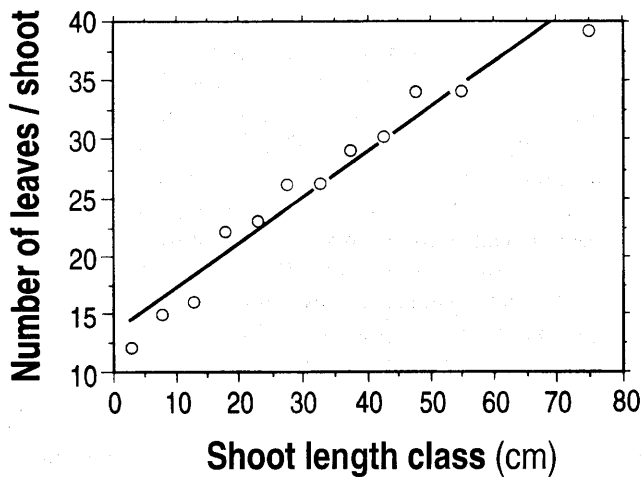


Fig. 3. The correlation between shoot length class and mean number of leaves per shoot ($y = 13.374 + 0.383x$, $n = 12$, $r^2 = 0.95$, $P < 0.0001$). An almost identical pattern was evident when number of leaves per shoot was used with shoot length ($y = 12.801 + 0.402x$, $n = 127$, $r^2 = 0.85$, $P < 0.0001$).

short shoots had more leaves than long shoots.

Leaf size increased significantly as shoot length increased ($y = 7.84 + 0.12x$, $n = 14$, $r^2 = 0.91$, $P < 0.01$), with mean length per shoot length class ranging from 6.6 cm on shoots up to 5 cm long, to 17.0 cm on shoots 81–90 cm long. Leaf width also increased with a range of 1.2–2.4 cm ($y = 1.25 + 0.01x$, $n = 14$, $r^2 = 0.78$, $P < 0.01$). With shoot length a good predictor of leaf size, it is possible to employ shoot length classes as the independent variable in evaluating patterns of attack by the sawflies and subsequent survival.

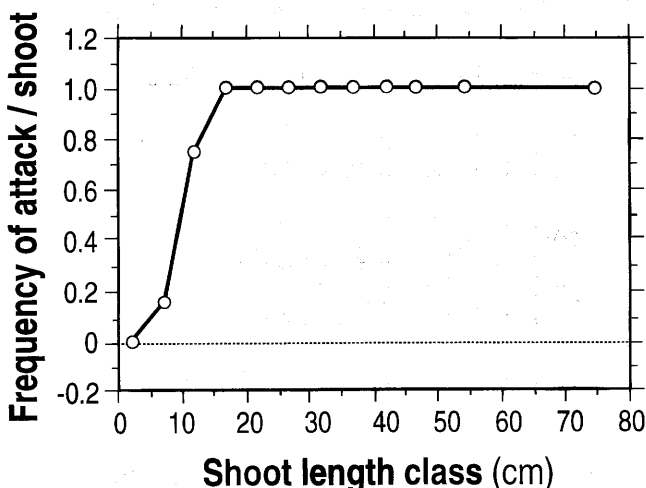


Fig. 4. Frequency of attack per shoot in each shoot length class increased rapidly to a maximum in the 16–20 cm shoot length class.

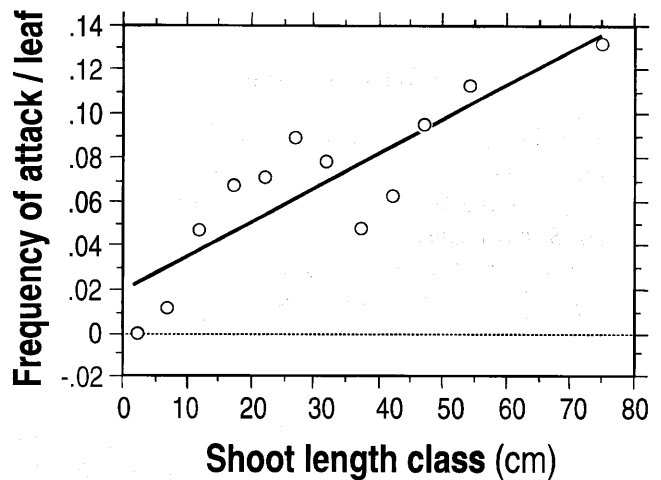


Fig. 5. Frequency of attack per leaf in each shoot length class. The relationship was highly significant ($y = 0.018 + 0.002x$, $n = 12$, $r^2 = 0.76$, $P < 0.0002$).

Phyllocolpa attack

We recorded 252 leaf folds on 225 shoots from the 10 trees studied. The frequency of attack per shoot in shoot length classes increased rapidly, until all shoots longer than 15 cm were attacked (Fig. 4). This was not a simple response to more leaves on the longer shoots, because the frequency of attack per leaf increased significantly as shoot length class increased (Fig. 5). This frequency increased from 0 to 0.13, while leaf size increased by less than three times, and the frequency increased even though large leaves were much rarer than smaller leaves. Female sawflies clearly demonstrated an increasing preference for leaves on longer shoots. Compared to random attack per shoot and per leaf, the observed attacks were much higher than expected in the long shoot categories and much lower than expected in the low shoot length categories (attacks/shoot: $\chi^2 = 288.77$, $n = 12$, $P < 0.001$; attacks/leaf: $\chi^2 = 111.88$, $n = 12$, $P < 0.001$). These patterns resulted from a strong increase in the mean number of attacks per shoot as shoot length class increased ranging from 0 attacks per shoot to 5.17 attacks per shoot ($y = -0.14 + 0.07x$, $n = 12$, $r^2 = 0.90$, $P < 0.01$).

Phyllocolpa establishment and survival

In all shoot length classes on which attacks occurred, the frequency of establishment of feeding in the leaf fold was very high. Frequency of establishment ranged between 0.96 and 1.00 in all shoot length classes above the 0–5 cm class.

However, frequency of survival to a late instar larva increased significantly with shoot length class (Fig. 6). Given that the number of attacks per shoot increased from

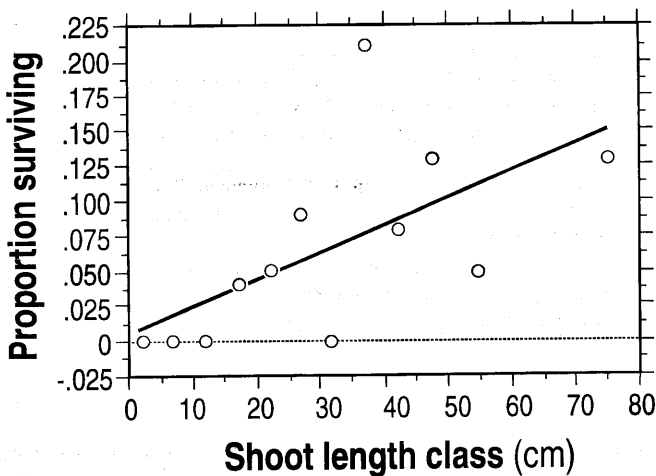


Fig. 6. Proportion of larvae surviving per attack, by shoot length class ($y=0.004+0.002x$, $n=12$, $r^2=0.38$, $P<0.03$).

0–5.17 over the range of shoot length classes, and the proportion surviving increased significantly over the same range, there is a clear correspondence between preference and performance in this leaf-folding sawfly.

The causes of the radically reduced survival relative to establishment in the lower shoot length categories cannot be evaluated adequately. Of those that established feeding sites in the leaf fold, 98 percent were absent from the fold. Some could have been removed by predators, because anthocorids were present in a small number of folds. Others could have died from poor nutrition. Clear evidence of parasitoid attack was observed only once. Hence, the causes driving the pattern of increased survival with shoot length class are in need of more detailed study in the future. At this time it is clear only that smaller leaves on shorter shoots provide poor resources or protection for sawfly larvae.

Discussion

The patterns discovered for this sawfly and its host plant are similar to those we have found in the genus *Euura* (cf. Price et al. 1995a). (1) The willow plant grows in a predictable and integrated way, with a large number of shorter shoots with smaller leaves, and relatively rare long shoots with large leaves. This is true even when the most vigorous populations of willows in an area are studied. (2) The distribution of sawflies is patchy and depends on the availability of young, rapidly growing plants. (3) Especially when galling sawflies attack tree species in the genus *Salix*, there is a narrow window in time when individual plants are susceptible to attack (cf. Roininen et al. 1993, 1995; Price et al. 1995b). (4) Females oviposit preferentially on the relatively rare long shoots. (5) Larvae perform

best where attack is concentrated, showing a preference-performance linkage. (6) Tree age and growth rate are critical factors in the presence and abundance of galling sawflies. Usually it has been possible to show that natural enemies in the system are not important in generating the observed patterns, but in this *Phyllocolpa* species we have been unable to discount their importance.

The leaf fold of *Phyllocolpa* makes it more difficult to detect the fate of larvae than in the other genera which form enclosed galls. In *Phyllocolpa* a larva can leave the fold or be removed without leaving evidence of the cause, while in *Euura* and the leaf galls in the genus *Pontania*, entry by predators or exit by larvae leave a record in the gall wall. High mortality in *Phyllocolpa* has been recorded in several species (Fritz and Nobel 1990; Fritz and Kaufman 1993). Both egg death, including parasitoid attack, and larval death were important, with the latter unexplained or uncategorized in our study. A major difference in mortality between the *Phyllocolpa* on Hokkaido and those in North America was that establishment of feeding larvae was so high in the former, indicating very little egg death caused by parasitoids or other factors. It is possible that around Sapporo, new host populations were developing, with new colonization of sawflies in the absence of close tracking by parasitoids. In Arizona and New York states where Fritz and associates worked, *Phyllocolpa* populations had been residents for many years.

This study supports the plant vigor hypothesis (Price 1991a) and the phylogenetic constraints hypothesis (Price 1994). The proximate mechanistic explanation of why females attack long shoots preferentially is not available (meaning how they actually identify large leaves on long shoots), although the ultimate evolutionary explanation appears to be the higher survival of larvae. If this were a general pattern, females able to detect longer shoots for oviposition would be favored by natural selection as more progeny would survive. Females may well evolve to detect phenolic glucoside patterns in shoots which provide information on shoot length, as in the stem galler *Euura amerinae* (Kolehmainen et al. 1995). Whatever the details are which enable a female to select large leaves, it is clear that such leaves result in larger leaf folds, and more food for a larva per fold. Therefore, there is a direct advantage to female preference in relation to larval performance.

The discovery of the kinds of patterns mentioned above is important in the development of empirically based factual theory in ecology (e.g. Tilman 1989; Price 1991b). Adding another example, especially in another genus, to the patterns well defined for *Euura*, enables the pattern to be broadened, resulting ultimately in a broader theory. Therefore, studies on other *Phyllocolpa*, *Pontania* and *Euura* species in Japan can contribute importantly to the development of theory in ecology.

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