

Oviposition Preference and Larval Performance of a Rare Bud-Galling Sawfly (Hymenoptera: Tenthredinidae) on Willow in Northern Arizona

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ABSTRACT Oviposition preference was examined in relation to offspring performance in a bud gall-forming sawfly, *Euura* sp., which attacks the Scouler or fire willow, *Salix scouleriana* (Barratt). The only known locality for this sawfly in Arizona is in the inner basin of the San Francisco Peaks, at 3,100–3,450 m above sea level. A random sample of shoots was taken in October of 1995, 1996, 1997, and 1998 to record shoot length, number of buds per shoot, number of galls per shoot, percent mortality, and overall percent survival for each generation. Oviposition preference was quantified for the first 3 yr, and larval performance was measured over all 4 yr. We found a strong oviposition preference for longer shoots. The longest shoot-length classes contained the smallest proportion of buds, and yet they were attacked more frequently than the short shoot-length classes. Therefore, the rarest shoot-length classes were the most preferred. Larval establishment and survival in galls were used to evaluate offspring performance. No significant correlation existed between larval establishment and shoot length, thus negating the prediction of a preference-performance linkage. Overall survivorship was high in 1995 (77%), 1997 (80%), and 1998 (82%), but drastically dropped in 1996 (16%), possibly because of a severe drought during that year. We discuss two alternative hypotheses to possibly explain these results: (1) all modules (long and short shoots) could provide sufficient nutrients for larvae to survive; and (2) selective pressures acting on female oviposition behavior are independent of larval performance.

KEY WORDS *Euura* sp., *Salix scouleriana*, plant vigor, preference-performance linkage, population dynamics

ONE PATTERN IN PLANT and herbivore interactions that has received considerable attention is the relationship between female ovipositional preference for high-quality plant resources and its link to progeny performance. The prediction has been that female choice should benefit progeny, although this has not been supported as frequently as expected (e.g., Thompson 1988, Courtney and Kibota 1990). Strong evidence for a preference-performance linkage has been found in the gall-inducing sawflies (Hymenoptera: Tenthredinidae: Nematinae: Nematini), involving, as an example, the arroyo willow stem-galling sawfly, *Euura lasiolepis* Smith (Craig et al. 1989). Females prefer to oviposit on long shoots that grow rapidly and on which larvae survive better than on short shoots. This species was the stimulus for the plant vigor hypothesis in which vigorously-growing plants or plant modules are more favorable for herbivore attack and survival than slow-growing plants or modules (Price 1991). We have found evidence for the preference and performance linkage in many gall-inducing sawflies (cf. Price 2003), and we have been interested in testing the

strength and breadth of the general pattern. Broad patterns in nature are the basis for developing hypotheses and theories to explain such patterns, so their discovery is basic to the advance of science.

The nematine galling sawflies include the genera *Euura*, *Pontania*, and *Phyllocolpa*. *Euura* includes stem, petiole, leaf midrib, and bud galls, whereas *Pontania* forms galls on leaves and *Phyllocolpa* forms leaf folds or rolls. Species in the genus *Euura* have shown a largely consistent preference and performance linkage, with 12 species, representing all types of galls in the genus, conforming to the pattern (Price 2003). Related genera of sawflies, *Pontania* and *Phyllocolpa* also conform to the pattern (cf. Price 2003) but have shown some inconsistencies (Price et al. 1999, Kokkonen 2000, Fritz et al. 2003). Only one *Euura* species is known not to conform to the preference-performance pattern, which is the subject of this paper. We show the relationships with its host plant and discuss possible hypotheses on why the species does not fit the pattern.

We studied the bud galler, *Euura* sp., which uses Scouler or fire willow, *Salix scouleriana* Barratt (Salicaceae), as its host plant. We asked the following

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questions. (1) What is the structure and distribution of the available plant resource? (2) Is female oviposition different from random? (3) Do larvae establish and survive better on the resources most frequently chosen by females? In general, we found that female attack pattern was different from random, but larval performance did not show the same pattern. Instead, we found larval establishment and survival to be high across all oviposition sites. We address two alternative hypotheses to possibly explain these results: (1) all modules were providing sufficient nutrients for larvae to survive (Price et al. 1999), and (2) female preference was selected for independently of larval performance.

Host Plant. *Salix scouleriana* ranges from South Dakota to Alaska and south to New Mexico, Arizona, and California. In Arizona, *S. scouleriana* inhabits mountaintops at elevations ranging from 2,300 to 3,500 m (McDougall 1973). The fire willow grows as a shrub, reaching between 2 and 5 m in height and typically invades burned forest areas (Kearney and Peebles 1942). On the San Francisco Peaks, *S. scouleriana* spreads mostly by vegetative growth, i.e., clonal growth. Clones are distinguished from one another by factors such as sex, stem color, growth patterns, and spatial discreteness.

Sawfly. In Northern Arizona, *Euura* sp. attack the axillary buds of *S. scouleriana*. Oviposition begins during the first week of July and can last for up to 2 wk (unpublished data). Galls are initiated by injection of colleterial fluid during egg deposition by the adult female (Higton and Mabblerley 1994, Kopelke 1999) and consist of undifferentiated parenchymatous tissue that provides resources to the developing larvae. Approximately 7–14 d after oviposition, eggs hatch and, we assume, pass through five instars for males and six instars for females, as in another *Euura* species (Price and Craig 1984). From the second week in October to the end of November, late-instar larvae chew an emergence hole in the gall wall and drop or crawl to the ground, where they spin cocoons and overwinter (unpublished data). They remain in the soil over the winter months and emerge as adults the following summer.

The systematics of the gall-inducing sawflies is in a state of flux. Smith (1968) noted that identification of species would probably have to rely on host plant information and other biological characteristics because morphological criteria were insufficient to separate species (see also Smith 1979, Kopelke 1999). Also, in the recent past, many former gall-forming sawfly species have been divided into host-plant-specific new sibling species using detailed host choice experiments or electrophoretic analysis (e.g., Roininen et al. 1993, Kopelke 1989, 1999), and *Euura mucronata* (Hartig), bud-galling species, is no exception (Kopelke 2001, Nyman 2002). Kopelke (2001) found that 13 species of the *E. mucronata* group in Europe, 8 of which were new based on his studies, were all host species-specific except for one that attacked two closely related willow species. This confirmed the prediction by Price and Roininen (1993)

that sawflies like *E. mucronata* would be revealed as a complex of plant-host-specific sibling species. Therefore, it is probable that the species we studied is an unnamed species and a new species of bud galler that we have not studied before. A new name must await detailed studies such as those by Kopelke (2001) on the European bud-galling species.

Materials and Methods

Study Site. We studied a natural population of *Euura* sp. in the San Francisco Peaks caldera, Coconino Co., AZ, from 1995 to 1998. *S. scouleriana* grows on a steep, north-facing talus slope, which is commonly disturbed by regular avalanche activity during the winter months. Distribution of willows along this slope ranges from 3,100 to 3,450 m and is highly isolated from other populations of *S. scouleriana*. The relatively small size of this population afforded the unique opportunity to examine a natural choice experiment, because all available resources were within the dispersal range of these sawflies (cf. Stein et al. 1994). Voucher specimens of *Euura* sp. have been deposited in the Arthropod Museum at Northern Arizona University and cataloged in the Biological, Environmental, and Cultural Relational Database by NAU CPMAB-gen 2.

Plant Module Vigor. Willow shoot growth was determined by a nondestructive random sample of five shoots from five ramets belonging to 20 different clones ($n = 500$ shoots). All clones were susceptible to sawfly attack so that shoot growth rate could be associated with the probability of attack by *Euura* sp. Shoots were tagged and remeasured every 20–30 d throughout the growing season between June and October. At the end of the season, shoots were divided into short-shoot (0–20.9 cm) and long-shoot (21–55 cm) categories to measure growth rate differences between resource classes. The short-shoot-length category was subsampled to provide an equal sample size to the long-shoot category ($n = 31$). We determined growth rate over time (i.e., vigor) by calculating the difference in mean shoot length from one sampling period to the next for each category. Differences in shoot growth rates were analyzed using repeated measures analysis of variance (ANOVA) on ranks to meet the assumptions of ANOVA (Conover and Iman 1981).

The target size for ovipositing females was estimated by the bud width on shoots. Females oviposit into the axillary buds on the shoot; therefore, the width of the bud indicates the width of the target available to females. We measured bud width with an SPI 2000 dial caliper (Precision Plastic Measuring Instruments, Switzerland) to the nearest millimeter ($n = 7$ shoot-length classes). The relationship between target size and shoot-length class was analyzed using a best fit least-squares regression (Sokal and Rohlf 1995).

Distribution of Resources (Buds). To assess the proportion of resources available to *Euura* sp. females, we compared the distribution of buds and of shoots across all shoot-length classes (1995: $n = 15$; 1996: $n =$

15; 1997: $n = 7$; $n =$ number of shoot-length classes). The distribution of bud resources was quantified by counting the number of buds per shoot. Shoots were grouped in 5-cm increments to make up the shoot-length classes. The number of buds and the number of shoots per shoot-length category were calculated. This provided an expected value of probability of attack, assuming females attacked buds at random, with which the observed value could be compared. Data were obtained from a stratified random sample of shoots from the population of shoots and analyzed with a best fit least-squares regression (Sokal and Rohlf 1995).

Female Preference. To examine female preference, the percent of attacked shoots was recorded in each shoot-length class. A random sample of $\approx 1,000$ shoots was taken from the population of shoots and grouped into shoot-length classes (n) in October 1995 ($n = 14$), 1996 ($n = 15$), and 1997 ($n = 7$). The sample of shoots allowed us to evaluate exactly where a female chooses to lay eggs because females initiate gall formation and larval feeding is not required for gall development. "Attacked" shoots were defined by the presence of at least one gall. Shoot lengths were divided into 5-cm classes, incrementally ranging up to 80 cm. Each shoot-length class had at least five shoots per class to meet linear regression assumptions (Zar 1996). Transformations were made for equality of variances using a square root transform when needed, and all years were analyzed using linear regression to assess the relationship between the percent of shoots attacked and shoot-length class.

Larval Performance. To assess larval performance, we measured the percent of larval establishment and survival on all shoots collected. Because evidence of larval feeding throughout its life is preserved in the gall, we can assess survival and establishment of the entire colonizing population. Larval establishment is defined as individuals that survive past the egg stage and commence feeding. Living or emerged individuals at the end of each year were quantified to provide an estimate of overall larval survivorship for that generation. Establishment of a larva in a safe feeding site is critical in the life cycle and liable to select for female behaviors that maximize establishment. Ultimate survival of larvae in the gall is affected by agencies beyond the mother's control, such as parasitism and predation, and less likely to select for female preference decisions.

Data for larval establishment were obtained from galls on shoots collected in October 1995 ($n = 11$), 1996 ($n = 14$), 1997 ($n = 7$), and 1998 ($n = 7$). The sampling unit, n , represents the number of shoot-length classes. For this part of the study, only two states of the organism were considered: aborted or established. Abortion was defined as a gall formed without any evidence of larval feeding (cf. Preszler and Price 1988 for similar studies on *E. lasiolepis*). Larvae classified as "established" were defined as surviving past the egg stage and establishing a feeding site in the gall. This was before any attack by natural enemies. Linear regression was used to analyze the

relationship between larval performance and shoot-length class.

Survivorship curves were generated using the percent of larvae that lived to each larval period in the sampled galls for 1995 ($n = 136$), 1996 ($n = 880$), 1997 ($n = 182$), and 1998 ($n = 106$). Larvae that established were further categorized into early, mid-, and late larval periods based on larval size, head capsule molts, extent of feeding in the gall, and amount of frass in the gall (cf. Price 1989, Cornell and Hawkins 1995). The gall provides a preserved history of larval activity throughout the season. Therefore, by taking samples at the end of the season, data on timing and type of mortality could be recorded. Estimated time of larval death was based on the extent of feeding and amount of frass in the gall (Price 1989, Woods et al. 1996). Mortality caused by chickadee predation was distinguishable by the remains of a unique tear into the gall.

Gall Structure. Gall size is directly related to the amount of food available to the resident larva as well as possible protection against small parasitoids (Craig et al. 1990). Average gall growth rate was measured to assess differences on long shoots (21–55 cm) in comparison with short shoots (0–20.9 cm) throughout the time of larval development. Gall diameter was measured with a SPI 2000 dial caliper to the nearest mm. A two-way ANOVA was used to analyze time-by-treatment differences. Data were ln-transformed to meet equality of variance assumptions. Pairwise comparisons on time were made with Tukey's post hoc tests. One-way ANOVA and Mann-Whitney U tests with sequential Bonferroni corrections were performed for comparisons between shoot-length classes at each time period depending on conformation to equality of variance (Conover and Iman 1981).

Results

Plant Module Vigor. A significant time and treatment effect was found in the growth rate between short and long shoots (time: $F_{3,180} = 5.86$, $P = 0.001$; shoot: $F_{1,60} = 6.74$, $P = 0.012$; time \times shoot: $F_{3,180} = 1.65$, $P = 0.180$; Fig. 1). Specifically, both shoot-length categories increased over time, but long shoots grew at a relatively faster rate than short shoots. In addition, bud size, i.e., target size for oviposition, increased significantly with shoot length (Fig. 2).

Distribution of Resources (Buds). The percent of buds available in each shoot-length class was inversely related to shoot length, such that 88% of buds were on short shoots (0–20 cm), whereas only 12% of all buds in the population were on long shoots (>21 cm; Fig. 3). Additionally, longer shoots were found to be a rare resource in the population of available resources, i.e., the percent of shoots available to ovipositing females significantly decreased as shoot length increased (Fig. 4).

Female Preference. *Euura* sp. females selectively oviposited on the longer shoots in the population of shoots available for oviposition during the first 2 wk in July (Fig. 5). The pattern was clear in all years studied. We can determine from these data that *Euura* sp.

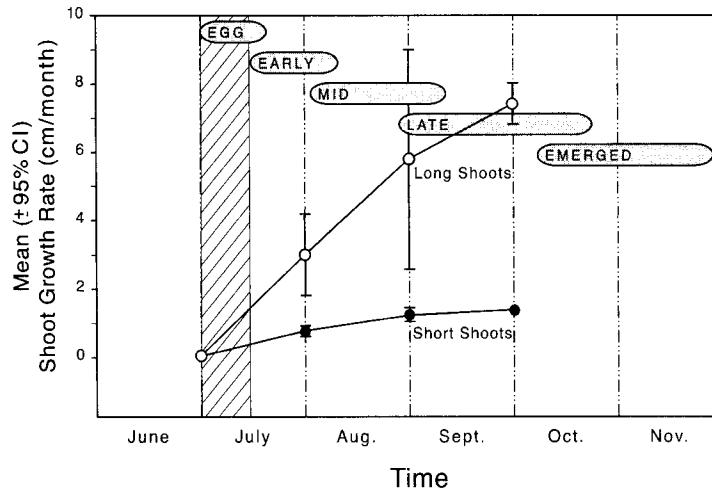


Fig. 1. *Salix scouleriana* shoot growth rate is represented by the difference in mean shoot length between sampling periods. ○, ultimately long shoots (21–55 cm); ●, shoots that ended the season as short shoots (0–20 cm). Dotted and dashed vertical lines delimit the months. Error bars represent 95% CI and are much greater in the long shoots than the short shoots. The range in time of female *Euura* sp. oviposition is represented by the hatched area, which spans ≈2 wk. Larval phenology is represented by the shaded ovals, indicating the larval development stage.

females prefer the more vigorously growing rare shoots in the population. Shoot length significantly predicts bud number per shoot ($y = 0.27x + 5.63$; $r^2 = 0.88$, $P < 0.01$, $n = 114$); therefore, shoot length is a synoptic character that can accurately be used even though the preferred resource is the bud.

Larval Performance. Contrary to the prediction that larvae will perform better on shoots preferred by females, the percent of larvae established in the galls was not significantly correlated with shoot length ($P > 0.05$). However, larval establishment was high across all shoot-length classes except for the longest shoot-length class in 1997 (Fig. 6).

The overall percent survival was high in 1995 (77%), 1997 (80%), and 1998 (82%), but low in 1996 (16%; Fig.

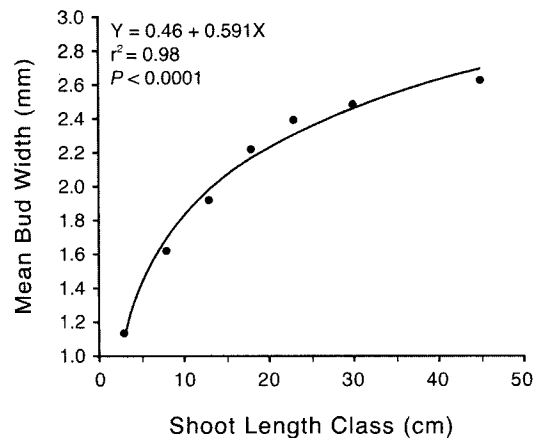


Fig. 2. The mean bud width of *S. scouleriana* represents target size for female oviposition. Long shoots provided significantly larger targets for female oviposition.

7A). Survivorship curves were not significantly different for long and short shoots; therefore, we combined these shoot-length classes. Mortality in the egg stage averaged 7% during 1995, 1997, and 1998. This yielded over 90% larval establishment in galls for these years. However, during 1996, 20% of the cohort died in the egg stage. Death during the egg stage implies plant-induced resistance (Price et al. 1999) or a bottom-up mortality factor, whereas chickadee predation or parasitoid attack caused mortality in mid- and late larval periods. Top-down forces resulted in an average of 13% mortality in mid- and late larval periods during 1995, 1997, and 1998, and 64% mortality during 1996. Even during high mortality in 1996, survival rates were not significantly different among shoot types. Additionally, parasitoid attack accounted for 4% of mortality during 1996 (Fig. 7B). The twofold increase in egg-stage mortality during 1996 is probably a response to severe drought conditions in northern Arizona, similar to the response by the shoot galler, *E. lasiolepis* (Price and Clancy 1986). Winter precipitation recordings for the inner basin, San Francisco Peaks, AZ, confirm a significant decrease in 1996 relative to other years (1995 = 862.58 mm, 1996 = 430.53 mm, 1997 = 596.9 mm, and 1998 = 751.84 mm). Furthermore, the outstanding chickadee predation in 1996 may be explained under the same premise of drought, such that resources for the chickadees were scarce across the landscape, thus, causing the birds to forage more than normal on the sawfly population.

Gall Structure. As expected, galls significantly increased in size throughout the growing season on both long and short shoots (time: $F_{3,182} = 95.77$, $P < 0.01$). The longer shoots did have significantly larger gall diameters than short shoots (shoot: $F_{1,182} = 24.34$, $P <$

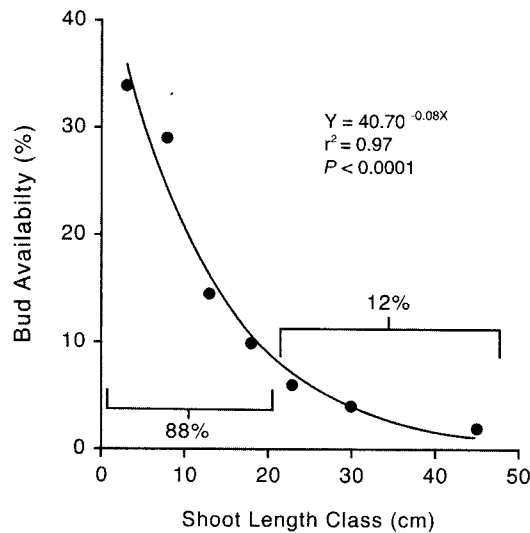


Fig. 3. The percent of buds available to the ovipositing *Euura* sp. female significantly decreased as shoot length increased; 88% of all buds were distributed among shoot lengths <20 cm and only 12% were distributed among shoot lengths >21 cm.

0.01). However, there was an interaction effect, meaning that gall diameters increased at different rates throughout the growing season depending on shoot length (shoot \times time: $F_{3,182} = 5.31$, $P < 0.01$). Therefore, post hoc tests revealed that gall diameters between shoot-length classes were only significantly different during July and converged in size over the rest of the growing season (July: $F_{1,35} = 31.7$, $P < 0.001$; Fig. 8). This suggests that shoot length may influence initial gall size but is not a good predictor of final gall size.

Discussion

Females showed a strong preference for modules on vigorously growing shoots even though these resources were rare in the population (Figs. 3–5). However, we rejected the preference-performance linkage hypothesis because larvae did not necessarily establish or survive better in the buds on vigorously growing shoots (Fig. 6). However, other aspects of fitness that were not examined in this study such as larval weight and sex ratio could show enhanced performance on longer shoots.

Alternative explanations for mechanisms driving female preference for long shoots and high larval survival across all shoots need consideration. They include (1) all modules were providing sufficient nutrients for larvae to survive (Price et al. 1999), and (2) female preference was selected for independently of larval performance.

The first alternative hypothesis predicts that shoots in all size classes may have provided sufficient nutrients for larval development. Data from this study were not gathered in enough detail to fairly evaluate the

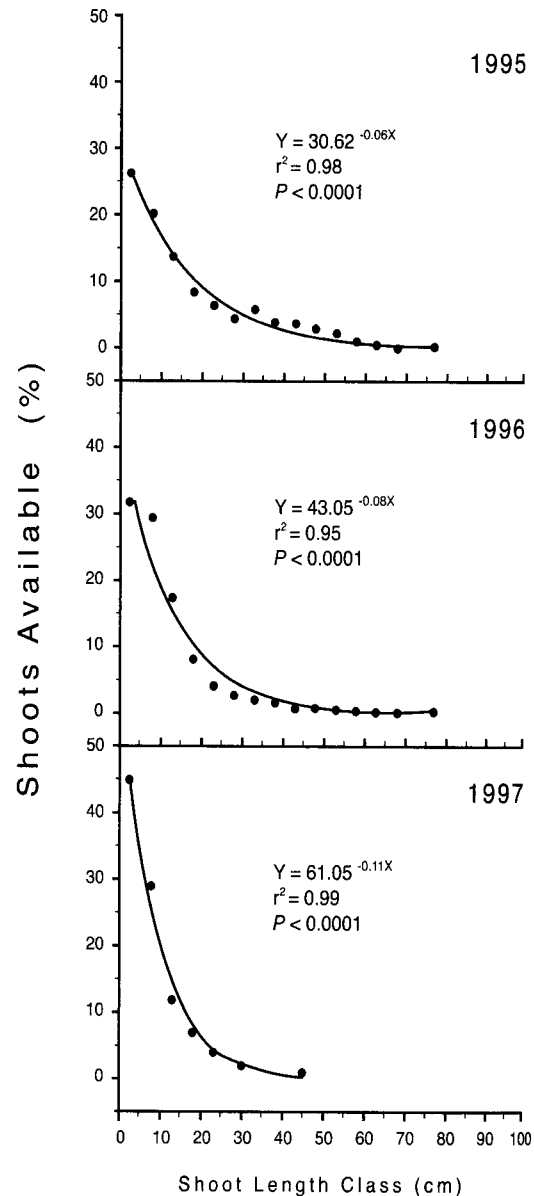


Fig. 4. The percentage of shoots available in each shoot-length class of *S. scouleriana* diminished in the longer shoot-length classes.

strength of this prediction. However, some generalizations can be made on parameters that were indicative of increased larval survival in other studies. These parameters are shoot growth rate, gall growth rate, and overall gall size per shoot-length class. The plant vigor hypothesis predicts that higher shoot growth rates will favor larval performance compared with that on slower-growing shoots (Price 1991). Additionally, fast-growing galls and overall larger galls have been found to promote higher larval survival as a result of parasitoid exclusion (Price and Clancy 1986,

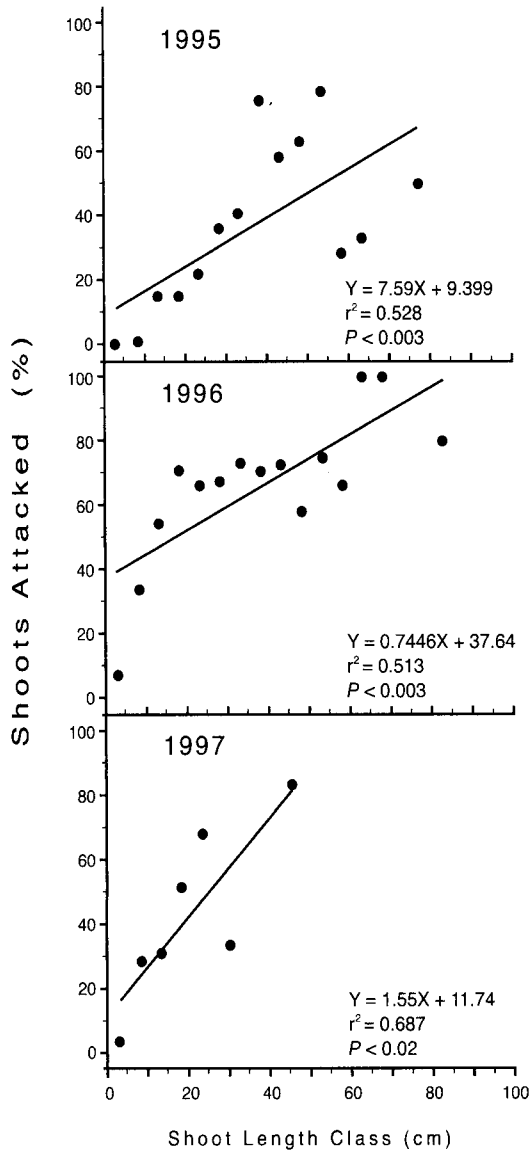


Fig. 5. *Euura* sp. female preference is represented by the percent of *S. scouleriana* shoots attacked (y) in each shoot-length class (x). There was a higher frequency of attack in the longer shoot-length classes.

Craig et al. 1990, Price 1992). Our results only showed a difference in growth rate for shoots and galls during female oviposition and larval establishment, respectively. During the critical time of larval development, all shoots were providing equivalent resources for larvae (Figs. 1 and 8).

To address the second alternative hypothesis, that female preference was selected for independently of larval performance, we considered shoot growth rate for long and short shoots during the time of female oviposition to explain possible mechanisms of female

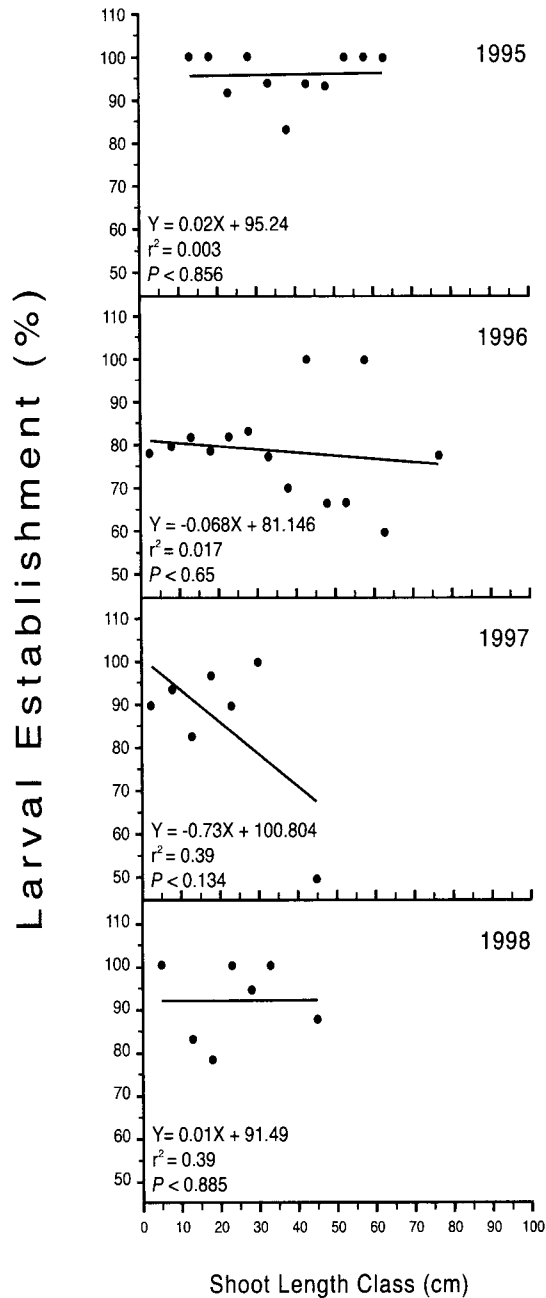


Fig. 6. The percent of *Euura* sp. larvae established in the galls (y) are used as a measurement for larval performance. Larvae showed no significant trend in establishment in galls across all shoot-length classes (x).

preference. The saw-like ovipositor of sawflies is very delicate and can suffer from serious wear (Benson 1963) because they are inserted through plant tissue and flexed to allow accurate maneuvering (Smith 1968). Therefore, the toughness of the plant tissue

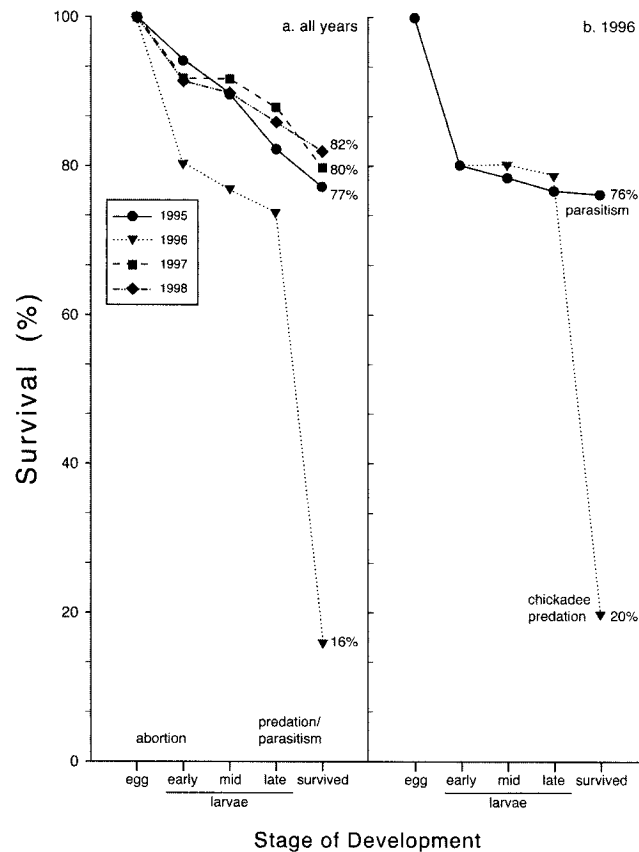


Fig. 7. *Euura* sp. survivorship curves for 1995, 1996, 1997, and 1998 (a) on *S. scouleriana* show the percent mortality at each life period as well as overall survival of that generation. Overall survival was high in 1995, 1997, and 1998. During the 1996 generation, survival fell to 16% (coinciding with a 100-yr drought). Mortality occurrences at the egg stage (1995 = 6%; 1996 = 20%; 1997 = 8%; 1998 = 8.5%) were caused by abortion of the egg, and in the mid- and late stages (1995 = 17%; 1996 = 64%; 1997 = 12%; 1998 = 9.5%) mortality was caused by predation or parasitism. Mortality in the mid- and late instar stages is broken down into the percentages caused by parasitism and chickadee predation for 1996 (b). Results showed that after the 20% mortality caused by abortion, 4% of larvae died as a result of parasitism, and 60% died as a result of chickadee predation.

being penetrated plays a critical role in a female sawfly's life. Plant tissue with increased growth rates are known to have lower toughness measures than tissue with slower growth rates (Coley and Kursar 1996). Therefore, rapid shoot growth is a resource necessary for female oviposition, thereby constraining the female to oviposit on these modules (Price 1994). Additionally, higher oviposition stimulus levels (i.e., phenolic glucosides) have been found in longer, more vigorously growing shoots for two species of stem gallers, *E. amerinae* (Kohlemainen et al. 1994) and *E. lasiolepis* (Roininen et al. 1999). The prediction is that increased shoot growth rate at the time of oviposition determines female preference because of possible decreased tissue toughness and increased levels of oviposition stimulus. Our data show that long shoots grew faster than short shoots during the time of female oviposition, indicating support for this hypothesis (Fig. 1). Thus, female oviposition preference may be selected for based on ease of injection of her saw-like

ovipositor that may be stimulated by higher phenolic glucoside levels.

Additionally, we considered the relative target size for ovipositing females. Females begin oviposition early in the season when shoots are young and buds are very small, and successful oviposition in the nematodes requires the exact positioning of the egg in the host tissue (McCalla et al. 1962, Price et al. 1987, Kopelke 1990). This dependence on precise female accuracy means that target size differences between shoot lengths could restrict the range of available resources for a female sawfly (Nyman 2000). The prediction follows that increased target size determines oviposition success. We found that *S. scouleriana* buds became significantly wider as shoots increased in length, thus producing larger targets for females (Fig. 2). This suggests that longer shoots enabled more successful attack because enlarged target size facilitated increased female oviposition accuracy.

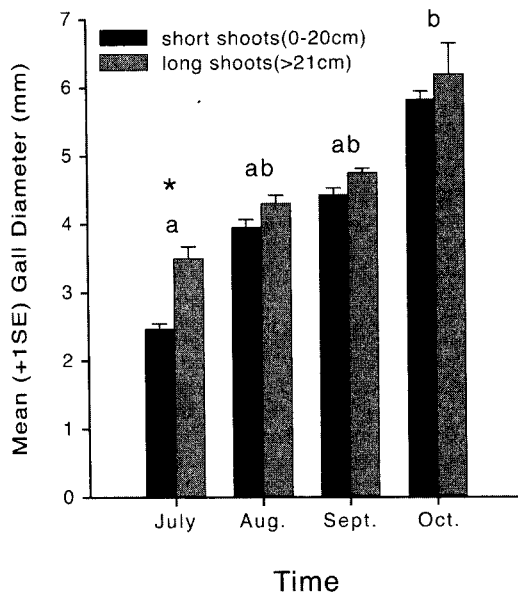


Fig. 8. Gall growth rates were significantly different between the short shoot-length class and the long shoot-length class in July (*), but did not differ during the rest of the season. Overall gall size significantly increased from July to October for both shoot-length classes. Bars represent \pm SE.

Therefore, selection for female preference might be independent of larval performance.

Although *Euura* sp. deviates from the preference-performance pattern, the preference for vigorously growing shoots has still been retained. Similarly, this pattern has been found in four *Pontania* species (Price et al. 1999, Kokkonen 2000) and *Phyllocolpa leavitti* (Fritz et al. 2003). While the mechanisms of deviation from such a pattern may differ, exploitable resources are still limiting, suggesting that bottom-up effects are most important in structuring the distribution, abundance, and population dynamics of the nematine sawflies (Price 2003).

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