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# Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots?

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**Summary.** The bud-galling sawfly, *Euura mucronata*, attacked longer shoot length classes on its host, *Salix cinerea*, more frequently than shorter shoots. Shoot length accounted for 76 to 93 percent of the variance in number of galls per 100 shoots in three habitats: forest, watermeadow, and lakeside. The reasons for this pattern were addressed with studies on shoot length in relation to: 1. Number of resources (buds) per shoot; 2. Success in establishment of larvae in galls; 3. Gall size and resources per gall; and 4. Survival of larvae after establishment as influenced by plant resistance and natural enemy attack. The most important factors proved to be success in establishment of larvae, with percent of variance accounted for ranging from 57 to 77 percent in three of four sites where relationships were significant, and survival after establishment of larvae, with variance accounted for ranging from 40 to 54 percent in the same three sites. The pattern of survival was dictated by plant resistance and not by natural enemies. These two additive factors resulted in a general relationship across all sites of increasing emergence of fully developed larvae per cohort as shoot length increased, accounting for 78 percent of the variance. These adaptive advantages to attacking longer shoots are sufficient to account for the pattern of increased probability of shoots being attacked as they increase in length.

**Key words:** Herbivore survival – Plant/insect interactions – Plant quality – *Salix cinerea* – Shoot length

We have established for two species of the willow-galling sawflies, *Euura* (Hymenoptera:Tenthredinidae), that longer shoots are attacked more frequently than shorter shoots within willow individuals, and between plants with different vigor. For the shoot-galling sawfly, *Euura lasiolepis* Smith, in Arizona U.S.A., this has been shown in field populations (Craig et al. 1986), and on experimental plants (Price and Clancy 1986a). For the bud-galling sawfly, *Euura mucronata* (Hartig) Man. (Churchill), very similar relationships occurred in the field in Finland (Price et al. 1987), and in both species as willow branches aged, shoot length declined, and attack declined.

We were therefore interested to know if such an attack pattern is adaptive for the sawflies, and if so, what is the

nature of the advantage to attacking longer shoots in a population of shoots. For the study sites we selected we addressed the following questions. Do *E. mucronata* attack more frequently longer shoots in a shoot population? When the answer was positive, as expected from the earlier study (Price et al. 1987), we asked why this should be, and tested four predictions: 1. That long shoots simply have more resources (buds) on them, so there is a simple increase in attack directly related to increased resource availability.

Unlike this first hypothesis which does not assume that more attack on longer shoots is a consequence of adaptive choices, the next three hypotheses consider possible fitness advantages which could underly the evolution of adaptive utilization of longer shoots. 2. That long shoots produce larger buds, meaning that target size is larger so attack and oviposition is more accurate and more frequently successful. When *E. mucronata* attack, shoots are young and axillary buds are very small and concealed behind the leaf petiole, through which the ovipositor must penetrate. So target size may be a significant factor in successful establishment of a gall, an egg, and a newly hatched larva in the gall. 3. That galls grow to a larger size on longer shoots providing more resources per resident larva. 4. That survival is better in galls on long shoots, for two possible reasons: (a) plant resistance is reduced or (b) natural enemy attack is reduced.

The host plant for *E. mucronata* is *Salix cinerea* L., which grows as a shrub or small tree in pine forests or open sites in watermeadows and lakesides in S.E. Finland. Both plant and herbivore are very common. The bud galler attacks young shoots and stimulates the young bud to swell with undifferentiated parenchymatous tissue on which the larva feeds. The bud scale enlarges and eventually dies leaving a conspicuous swollen dead brown bud, especially prominent after leaf abscission in the fall. The larva feeds in the gall throughout the summer and when fully grown bores through the bud scale and forms a cocoon in the soil where it overwinters (Pschorn-Walcher 1982, Price 1987a).

The adaptive significance of host selection in herbivorous insects has been studied extensively, and where known the underlying selective factors are very diverse. Safe sites for eggs dictate acceptance of some food plant species and rejection of others by the butterfly, *Euphydryas editha* (Singer 1971). Shifting from one host species to another in heteroecious species seems to maximize food quality in some aphids (Dixon 1973). Host plant phenology and archi-

**Table 1.** Relationships between *S. cinerea* shoot length classes (mm) (X), probability to attack by *E. mucronata* (Y), and number of galls per 100 shoots (Y), in three habitats in which the willow is commonly found

| Location and habitat | Correlation equation | Sample sizes shoots/galls | Number of classes[a] | $r^2$ | Probability |
|---|---|---|---|---|---|
| Probability of attack | | | | | |
| Linnunlahti Forest | $Y = 4.46^{-3}X - 0.21$ | 224/ 52 | 9 | 0.95 | <0.01 |
| Koita River Watermeadow | | | | | |
| Unbrowsed | $Y = 4.05^{-3}X + 0.24$ | 295/304 | 7 | 0.65 | <0.05 |
| Browsed by hare | $Y = 3.48^{-3}X + 0.19$ | 330/358 | 12 | 0.69 | <0.01 |
| Enonkoski Lakeside | $Y = 4.14^{-3}X + 0.26$ | 93/327 | 9 | 0.62 | <0.01 |
| Number of galls per 100 shoots | | | | | |
| Linnunlahti Forest | $Y = 0.84X - 46.70$ | 224/ 52 | 9 | 0.93 | <0.01 |
| Koita River Watermeadow | | | | | |
| Unbrowsed | $Y = 1.84X - 3.13$ | 295/304 | 7 | 0.87 | <0.01 |
| Browsed by hare | $Y = 1.70X - 33.10$ | 330/358 | 12 | 0.91 | <0.01 |
| Enonkoski Lakeside | $Y = 2.72X + 5.49$ | 93/327 | 9 | 0.76 | <0.01 |

[a] Number of shoot length classes used in correlation

tecture was probably more important than nutrition for the herbivore specialist *Uroleucon nigrotibium* (Moran 1984). Host specificity may be dictated less by plant chemistry than by natural enemies associated with potential host plants (e.g. Smiley 1978; Gilbert 1979). Leaf size correlates positively with the probability of gall initiation and fecundity in *Pemphigus betae* (Whitham 1978, 1980), and negatively with defensive chemicals (Zucker 1982). Such diverse plant traits have been implicated in selection for female insect herbivore attack patterns that we felt justified in addressing the four possibilities above.

On the other hand, there is an enigmatic aspect to host selection, suggesting that it may reflect constraints rather than adaptive choice of nutritionally optimal hosts. Specialists do not appear to be more efficient physiologically than generalists in all cases (Smiley 1978; Scriber and Feeny 1979, Futuyma and Wasserman 1981; Futuyma et al. 1984) although for two *Uroleucon* species this was demonstrated (Moran 1986). But seasonal host shifts in *Uroleucon gravicorne* did not provide nutritionally superior food plant species (Moran 1983). The need for good oviposition sites may have been the cause. It is too early to make any generalizations about interspecific or intraspecific host plant utilization by insect herbivores. However, within the genus *Euura* all species we have tested attack longer shoots more frequently than shorter shoots. For *Euura lasiolepis* and *E. mucronata* this relationship is documented (Craig et al. 1986; Price et al. 1987), and future publications will establish the relationships for *E. amerinae, E. atra, E. exiguae* and *Euura* sp. forming petiole galls. These species include shoot gallers, shoot miners, petiole gallers, and bud gallers, and all the modes of plant utilization known in the genus. We are therefore ultimately interested in understanding the adaptive significance of attack on long shoots, and if there are common selective forces on all these species.

## Methods

We studied *E. mucronata* in 1986 on shoots which grew and were attacked in 1985. The term shoot describes the terminal one season of growth on a stem, which in *S. cinerea*

is a simple axis without lateral ramifications. In May and June, when 1985 shoots were sampled, galled buds were prominent because they were dead, brown, and swollen compared to the small, green, unattacked buds.

The three types of habitat in which *S. cinerea* is most typically found were sampled. Forest sites dominated by Scots pine, *Pinus sylvestris* L., were represented by Linnunlahti Forest, a district within the town of Joensuu, in S.E. Finland. The Koita River site, located about 50 km east of Joensuu, represented watermeadows which are flooded in the spring. Enonkoski Lakeside was typical of rocky shorelines colonized by *S. cinerea*, and was about 70 km southwest of Joensuu. When it was found that densities of galls and survival were low in the Linnunlahti Forest another forest site was sampled at Ylämylly about 7 km west of Joensuu, to obtain estimates of sawfly survival.

At each site about 100–300 shoots were taken haphazardly from all parts of *S. cinerea* plants. Each shoot length and basal diameter was measured and the number of buds and galls counted. All galls present were measured for diameter through the adaxial-abaxial orientation of the gall, providing an index of gall size, particularly relevant to the attack from the gall surface by small chalcid parasitoids. All galls were then opened and the contents recorded in one of the following categories: 1. No egg laid or dead egg, but with some gall formation, although frequently the gall did not form adequately. It was very difficult to determine if an egg had been laid so both categories were combined; 2. Dead larva just after hatching; 3. Mid-sized larva dead, which may have died because of some aspect of plant resistance (3a), or from chalcid parasitoid attack by *Eurytoma salicis* when a parasitoid larva would be present (3b); 4. Dead large larvae which died from plant-induced causes (4a) or from bird predation (4b). In the latter case a clear peckhole was visible. 5. Larva emerged from the gall leaving a clearly visible emergence hole.

At the Koita River site extensive browsing by mountain hare, *Lepus timidus*, occurred on some plants in 1984 and earlier. Therefore, samples were taken from unbrowsed and browsed parts of willow plants and the relationship between shoot length and probability of attack was tested separately.
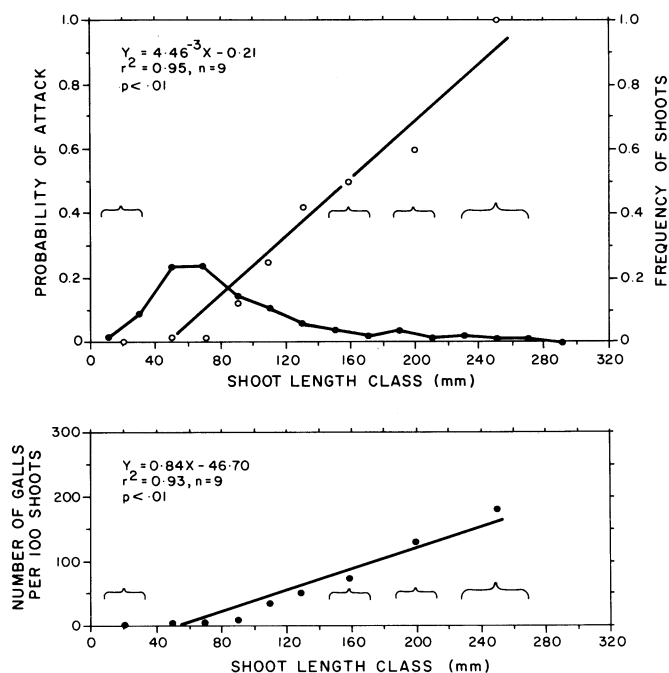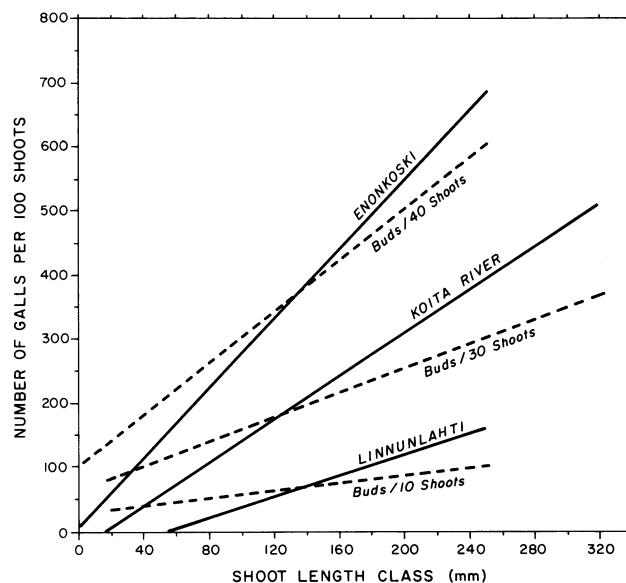
**Fig. 1.** Relationships between shoot length classes, the probability of attack by *E. mucronata*, the frequency of shoots in each class (*above*), and the number of galls per 100 shoots (*below*). Probability of attack is given in open circles and the linear regression line is described by the equation $Y = 0.0045X - 0.21$, $n = 9$, $r^2 = 0.95$, $P < 0.01$. Frequency of shoots is given in solid circles. Number of galls per 100 shoots is accounted for by the equation $Y = 0.84X - 46.70$, $n = 9$, $r^2 = 0.93$, $P < 0.01$. Points derived from combination of size classes are located at the mid point of the size classes represented which are bracketed



**Fig. 2.** Relationships between shoot length classes and number of buds per shoot (*dashed lines*), and number of galls per 100 shoots (*solid lines*). Regression lines are given for the three sites studied, Linnunlahti, Koita River, and Enonkoski. Regression equations for shoot length and number of buds are given in Table 2, and for shoot length and number of galls in Table 1. The regression lines for number of buds per shoot have been scaled, as indicated, to intersect the appropriate regression line for number of galls, for easier comparison

Note that browsing on 1984 shoots left the full 1985 season for shoot growth and sawfly attack.

All analyses were based on grouping data into shoot length classes, 0–19, 20–39 mm, etc. in 20 mm increments. When fewer than five shoots occurred in any class it was grouped with an adjacent class or classes to form a composite class with five or more shoots. Least squares linear regression was performed using the midpoint of each of the shoot length classes as the independent variable.

## Results

In all sites there was a significant positive relationship between shoot length class and probability of attack by *E. mucronata*, and number of galls per 100 shoots (Table 1). In each case the most heavily attacked shoots belonged to the rarest shoot length classes. Data from Linnunlahti

Forest are given as an example (Fig. 1). These relationships were remarkably uniform across the three habitats studied and on browsed and unbrowsed willows, accounting for 62 to 95 percent of the variance in levels of attack. We therefore addressed the question of why this pattern should be so strong.

The first prediction was that long shoots have more buds on them and are therefore more likely to be attacked (Table 2). This argument is untenable because, while the preponderance of buds in a shoot population is on shoots less than 80 mm, few galls are formed on them (Fig. 1). In Linnunlahti forest 56 percent of shoots were less than 80 mm, and accounted for 54 percent of buds, but only two galls (3.8%) were formed on these shoots. If attack were in response to resource availability, 43 percent of attacks would be expected on shoots of less than 80 mm. Discounting relative abundance of shoots in shoot length classes, there is still a stronger response to shoot length by gallers than expected from the number of buds per shoot (Fig. 2). Sawflies attack longer shoots more frequently than resource availability predicts.

**Table 2.** Relationships between *S. cinerea* shoot length classes (mm) (X), and the mean number of buds per shoot (Y)

| Location and habitat | Correlation equation | Sample sizes shoots/buds | Number of classes[a] | $r^2$ | Probability |
|---|---|---|---|---|---|
| Linnunlahti Forest | $Y = 0.03X + 2.11$ | 113/577 | 11 | 0.97 | $< 0.01$ |
| Koita River Watermeadow | $Y = 0.03X + 2.13$ | 186/937 | 10 | 0.95 | $< 0.01$ |
| Enonkoski Lakeside | $Y = 0.05X + 2.58$ | 93/838 | 9 | 0.95 | $< 0.01$ |

[a] Number of shoot length classes used in correlation

**Table 3.** Relationships between shoot length (X) and failure to establish larva in a gall (Y) estimated as the proportion of eggs and early larvae dying in the cohort of eggs deposited in each shoot length class

| Location and habitat | Regression equation | Sample sizes shoots/galls | Number of classes[a] | $r^2$ | Probability |
|---|---|---|---|---|---|
| Linnunlahti Forest | Y = 0.83 − 0.00017X | 84/126 | 15 | 0.05 | N.S. |
| Koita River Watermeadow | Y = 0.91 − 0.0027X | 112/166 | 10 | 0.77 | <0.01 |
| Enonkoski Lakeside | Y = 0.75 − 0.0024X | 55/ 99 | 8 | 0.76 | <0.01 |
| Ylämylly Forest | Y = 0.65 − 0.0018X | 97/104 | 10 | 0.57 | <0.05 |

[a] Number of shoot length classes used in correlation

**Table 4.** Relationships between shoot length, shoot diameter and gall diameter in three habitats

| Location and habitat | Correlation equation | Sample size | $r^2$ | Probability |
|---|---|---|---|---|
| Shoot length (X) shoot diameter (Y) | | | | |
| Linnunlahti Forest | Y = 0.98 + 0.01X | 30 | 0.97 | <0.01 |
| Koita River Watermeadow | Y = 1.18 + 0.01X | 30 | 0.81 | <0.01 |
| Enonkoski Lakeside | Y = 1.43 + 0.01X | 30 | 0.89 | <0.01 |
| Shoot diameter (X) gall diameter (Y) | | | | |
| Linnunlahti Forest | Y = 2.10 + 0.07X | 36 | 0.02 | N.S. |
| Koita River Watermeadow | Y = 2.19 + 0.65X | 63 | 0.30 | <0.01 |
| Enonkoski Lakeside | Y = 2.03 + 0.14X | 53 | 0.03 | N.S. |

The second prediction was that long shoots enable more successful attack because target size is larger which facilitates more accurate oviposition. To test this possibility we estimated the proportion of eggs and early larvae dying in a cohort of eggs deposited in each shoot length class. This estimated the success in establishing larvae in galls. Eggs and early larvae were grouped together because both stages occur before feeding in the gall is progressing well, and distinction between a dead egg and a dead larva emerging from the chorion of the egg was not always possible. In many cases establishment of larvae failed because gall initiation was incomplete. This evidence suggests an inaccurate oviposition attempt. In fact in every habitat there was a negative relationship between shoot length class and proportion of failures to establish larvae (Table 3), and three of four regressions were significant, accounting for 57 to 77 percent of the variance in failures to establish larvae. Establishment of larvae in galls improves as shoot length increases.

The third prediction tested involved the possibility that on longer shoots buds are larger and so larger galls develop, providing more resources for a sawfly larva per gall. Shoot length correlated positively with shoot diameter (Table 4) but a relationship between shoot diameter and gall diameter was significant only in the Koita River sample, and only 30 percent of the variance was accounted for. The explanatory power of this prediction is local and weak relative to the second prediction.

The fourth prediction was tested for better survival on longer shoots because plant resistance is less, and/or natural enemy attack is less. In the term plant resistance we group all factors which caused failure of the larvae to thrive which may have included water relations in the gall, other nu-

trients, or allelochemicals. Any larva that died without attack by natural enemies was assumed to have died from plant-related causes. We did not test for pathogens, but these would be transovarially transmitted in order to reach a larva concealed in a gall, and we would not expect any relationship to shoot length.

At each site for each shoot length class an index of survivorship was calculated. The five categories 1, 2, 3a, 4a and 5 as described in the methods were used to weight the proportion of a cohort in each category, and the total score across all categories provided an index of survivorship. One hundred percent survival of a cohort yielded a score of 5. Fifty percent egg death (0.5 × 1) plus 50 percent early larval death (0.5 × 2) would yield a score of 1.5. No enemy attack was included in this analysis, so survivorship related to plant resistance only. In three of the four habitats there was a significant and positive relationship between shoot length class and index of survivorship, accounting for 40 to 54 percent of the variance in survivorship (Table 5). This estimate includes death of eggs and early larvae tested in prediction 2. When the effect of poor establishment of larvae was removed, there remained an additional positive effect on survival after establishment, in all except the Linnunlahti Forest habitat (Table 5). Thus, the results of predictions 2 and 4 (without enemies) were additive, with failure to establish decreasing with shoot length, and survivorship after establishment increasing with shoot length.

We also tested relationships between shoot length classes and enemy attack (Table 6). Only at the Koita River site were relationships significant at the 5 percent level or less, and the positive response of bird predation to shoot length was the only factor leading to the significant response in the "all enemies" category. Thus, if natural enemies had any impact on patterns of attack by the sawfly, shorter shoots would be selected. This is not the case, so natural enemy attack has no explanatory power.

The index of survivorship provided an estimate of the relative length of life for a cohort on a particular shoot length class. A better estimate of survival would be the proportion of a cohort emerging from the gall. However, emergence was low, so large samples per shoot length class are needed for reliable analysis, and as sample sizes decline, detection of pattern becomes more difficult. With these reservations in mind the analysis of shoot length class and proportion of emergence per cohort was undertaken for all sites and then all data were grouped to obtain a larger sample size. For individual sites only Ylämylly Forest showed a significant relationship, and this was positive (Y = 0.13 + 0.0016X, $n = 10$, $r^2 = 0.56$, $P < 0.05$). Proportion of sawfly emerging (Y) increased as shoot length class (X) increased. When data from all habitats were grouped, the

**Table 5.** Relationships between shoot length (X) and index of survivorship (Y) with enemy attack excluded, and with enemies and failure to establish in gall excluded

| Location and habitat | Regression equation | Sample sizes shoots/galls | Number of classes[a] | $r^2$ | Probability |
|---|---|---|---|---|---|
| **Enemy attack excluded** | | | | | |
| Linnunlahti Forest | $Y = 2.34 - 0.0011X$ | 84/126 | 15 | 0.19 | N.S. |
| Koita River Watermeadow | $Y = 1.92 + 0.0031X$ | 112/129 | 10 | 0.40 | <0.05 |
| Enonkoski Lakeside | $Y = 2.61 + 0.01X$ | 55/ 99 | 8 | 0.54 | <0.05 |
| Ylämylly Forest | $Y = 2.04 + 0.01X$ | 97/104 | 10 | 0.54 | <0.05 |
| **Enemy attack and failure to establish in gall excluded** | | | | | |
| Linnunlahti Forest | $Y = 0.00020X + 0.43$ | 84/126 | 15 | 0.01 | N.S. |
| Koita River Watermeadow | $Y = 0.01X - 0.49$ | 112/129 | 10 | 0.77 | <0.01 |
| Enonkoski Lakeside | $Y = 0.01X + 0.16$ | 55/ 99 | 8 | 0.83 | <0.01 |
| Ylämylly Forest | $Y = 0.01X + 0.64$ | 97/104 | 10 | 0.57 | <0.05 |

[a] Number of shoot length classes used in correlation

**Table 6.** Relationships between shoot length (X) and proportion of larvae killed by natural enemies (Y). In the two forest sites only parasitoids caused mortality. In the other two sites both parasitoids and birds attacked galls, so equations for total enemy-induced mortality, mortality from parasitoids, and mortality from birds are provided

| Location and habitat | Regression equation | Sample sizes shoots/galls | Number of classes[a] | $r^2$ | Probability |
|---|---|---|---|---|---|
| **Linnunlahti Forest** | | | | | |
| Parasitoids | $Y = 0.22 - 0.00034X$ | 84/146 | 15 | 0.26 | $0.05 < p < 0.10$ |
| **Koita River Watermeadow** | | | | | |
| All enemies | $Y = 0.17 + 0.0013X$ | 112/205 | 10 | 0.76 | <0.01 |
| Parasitoids | $Y = 0.27 - 0.00055X$ | 112/205 | 10 | 0.35 | N.S. |
| Birds | $Y = 0.0019X - 0.10$ | 112/205 | 10 | 0.72 | <0.01 |
| **Enonkoski Lakeside** | | | | | |
| All enemies | $Y = 0.18 - 0.00034X$ | 55/118 | 8 | 0.05 | N.S. |
| Parasitoids | $Y = 0.08 + 0.000039X$ | 55/118 | 8 | 0.0001 | N.S. |
| Birds | $Y = 0.10 - 0.00038X$ | 55/118 | 8 | 0.25 | N.S. |
| **Ylämylly Forest** | | | | | |
| Parasitoids | $Y = 0.04 + 0.00033X$ | 97/121 | 10 | 0.10 | N.S. |

[a] Number of shoot length classes used in correlation

same relationship was highly significant when classes with over 20 galls were used ($Y = 0.11 + 0.00071X$, $n = 10$, $r^2 = 0.78$, $P < 0.01$). Shoot length accounted for 78 percent of the variance in proportion of sawfly emerging from shoots of that class.

In conclusion, there existed a relationship between shoot length, the number of buds per shoot and the number of sawfly attacks per shoot. We established that number of buds per shoot was an inadequate explanation of sawfly attack. The most general correlates whith shoot length were increased success in establishing larvae in galls, and increased survivorship after establishment, which were additive components of sawfly success related to shoot length. Attack by natural enemies had little explanatory power. The net result over all habitats was that more fully grown larvae emerged from longer shoot length classes.

### Discussion

It is a satisfying conclusion that sawflies attack more frequently shoots on which they survive better. Few studies on insect herbivores have shown such an expected consequence of host selection patterns, as discussed in the introduction.

Of course, other factors may also be involved, although they may not account for as much of the variance in success as establishment and survivorship did (57 to 77 percent, and 57 to 83 percent of significant cases respectively). Females may reject short shoots without attempting oviposition. This was the case for *E. lasiolepis*, for in an experiment exposing plants with different shoot lengths to the same population of sawflies, plants with longer shoots were attacked more frequently (Price and Clancy 1986a). Some oviposition attempts may not result in gall formation at all, as in *E. lasiolepis* (Price and Craig 1984), and we would predict that success in gall formation should increase as shoot length increases. Long shoots grow for longer in the season, so resources are produced over a longer period of time (Price et al. 1987), increasing the probability of attack. At the other end of the life cycle there may well be important differences in weight of larvae leaving galls and sex ratio relating to shoot length. Since the sawflies are haplo-

diploid females can adjust the sex of an egg at oviposition in relation to resource quality, and our unpublished studies on *E. lasiolepis* show that on long vigorous shoots the sex ratio may be female biased, and on poor shoots it is male biased. All these factors need further study for a more complete analysis of the selective pressures on long shoot length utilization.

*E. mucronata* attacks longer shoots, because it establishes and survives better, although the actual mechanisms involved are unclear. Do larvae establish better on longer shoots just because target size is larger so a gall can be stimulated more predictably? Or are more active meristems more readily induced to form galls? And what are the factors in galls that influence plant resistance once the larva is established?

It is interesting to note that natural enemy attack did not help to account for the attack pattern by *E. mucronata*, or the success of this sawfly. This situation is similar to others in which natural enemies may play a role in population dynamics subsidiary to the plant-herbivore interaction, as in bark beetles (Berryman 1982) and in *E. lasiolepis* (Price and Clancy 1986b; Price 1987b, 1988).

We have shown that shoot length in *S. cinerea* is a good indicator of many plant traits of potential importance to many herbivores such as leaf size and internode length (Price et al. 1987). For herbivores attracted to vigorous plant growth all traits of long shoots are favorable, and many herbivores are likely to respond positively to long shoots (e.g. Dannell and Huss-Dannell 1985, Dannell et al. 1985), and thus show positive associations with each other, contrary to predictions based on competitive interactions. Shoot length appears to be an excellent index of many plant traits to which herbivores respond. We are now investigating how generally shoot length is a significant predictor of herbivore attack across many insect herbivore taxa.

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