Release of phylogenetic constraints through low resource heterogeneity: the case of gall-inducing sawflies

PETER W. PRICE[1], TAKAYUKI OHGUSHI[2], HEIKKI ROININEN[3], MICHIHIRO ISHIHARA[4], TIMOTHY P. CRAIG[5], JORMA TAHVANAINEN[6] and SHARON M. FERRIER[1]   [1]Department of Biological Sciences, Northern Arizona University, U.S.A., [2]Center for Ecological Research, Kyoto University, Kamitanakami, Japan, [3]Finnish Forest Research Institute, Vantaa Research Centre, Vantaa, Finland, [4]Department of Environmental Sciences, Osaka Women's University, Sakai, Japan, [5]Department of Biology, University of Minnesota, Duluth, U.S.A. and [6]Department of Biology, University of Joensuu, Finland.

Abstract. 1. A group of six unusual sawfly species, which do not conform to the phylogenetic constraints hypothesis as it has been applied to sawflies, was examined in natural populations. All species were in the genus *Pontania* (Hymenoptera: Tenthredinidae), which induce galls on leaves of willow species (Salicaceae). An understanding of these non-conformist species was important as a test of the validity of the general hypothesis.

2. The six species of sawfly, *Pontania mandshurica*, *P.* cf. *arcticornis*, *P. aestiva*, *P. arcticornis*, *P. pacifica*, and *P.* nr. *pacifica*, showed no oviposition preference for long, vigorous shoots, in contrast to 37 documented tenthredinid species that have demonstrated such a preference. Rather, the non-conformist species attacked the shortest shoot length classes more frequently and larval establishment in galls was successful.

3. The evident escape from the phylogenetic constraint, which commonly limits sawfly attack to the most vigorous shoots in a willow population, resulted from low apparent heterogeneity of the resources exploited by these *Pontania* species. At the time of female oviposition, shoots and leaves were too uniform to allow discrimination by females among shoot length classes, resulting in random, or near random attack of shoots.

4. The unusual relative uniformity of resources to which sawflies were exposed resulted from several characteristics. (1) Females emerged early relative to shoot growth phenology, making discrimination among shoot length and vigour difficult or impossible. (2) Low heterogeneity in leaf length resulted in resource similarity independent of shoot length. (3) Abscission of leaves occurred after emergence of larvae from leaf galls so that differential abscission of leaves in relation to shoot length became irrelevant. (4) In some cases, low variance in shoot lengths was evident in old ramets lacking long, vigorous shoots. Probably as a result of low resource heterogeneity, larvae survived well across all shoot length classes, revealing no ovipositional preference and larval performance linkage related to the exploitation of the longest shoot length classes in a population of willows, as in the conformist species. Therefore, larval survival did not provide positive feedback on female preferential behaviour for long shoots, as in the conformist species studied.

Correspondence: Peter W. Price, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011-5640, U.S.A. E-mail: peter.price@nau.edu

Introduction

The field of study concerning the distribution, abundance, and population dynamics of species is central to ecology and has benefited from close and energetic attention for over 100 years. Studies of individual species have dominated research efforts; an approach that can be characterised as the Idiographic or Idiosyncratic Descriptive Paradigm (Price, 2003). This characterisation is apt because population size and distribution was described from year to year, loss of cohorts was often described in a life table format and, frequently, little or no experimental study was undertaken to elucidate the mechanisms causing population change (cf. Krebs, 1995). However, in a little more than the last two decades, comparative studies have become more common, with the detection of pattern as a central theme, for example, searching for common characters among pest or outbreak species (e.g. Southwood & Comins, 1976; Nothnagle & Schultz, 1987; Wallner, 1987; Haack & Mattson, 1993; Larsson *et al.*, 1993; Hunter, A.F., 1991, 1995; Hunter, M.D., 1994).

Comparative studies can reveal empirical patterns in nature on which theory can be developed, an approach illustrated by this research group's study of gall-inducing sawflies (Hymenoptera: Tenthredinidae) (Price, 2003). A general pattern has emerged that females show an ovipositional preference for rapidly growing long shoots of their host plants on which their larvae survive well. There is a strong ovipositional preference and larval performance linkage (e.g. Craig *et al.*, 1989), apparently the strongest described to date for insect herbivores. Hence, there is a mechanistic explanation for the pattern, with larval survival feeding back positively to beneficial female choice of oviposition sites. These studies resulted in the proposal of the phylogenetic constraints hypothesis in which, for sawflies, the phylogenetic constraint is the saw-like ovipositor (Price *et al.*, 1990; Price, 1994, 2003; Price & Carr, 2000). With such an ovipositor, females are constrained to oviposit into soft tissue, to have a phenology to match availability of young host-plant growth, and to attack vigorous shoots providing the best substrate for oviposition. Therefore, the constraint results in the utilisation of low-density resources because most shoots in a population of hosts are short. Resource heterogeneity in terms of shoot lengths is high, with many unsuitable short shoots and few favourable long shoots available for sawfly oviposition.

Some exceptions to the general trend have been found, however, and these are the subject of this paper. It is asked why such exceptions exist when the general trend among these sawflies favours the preference–performance linkage associated with rapidly growing shoots. So far 37 species of

sawfly that show a preference for vigorous shoots, and only four species that do not fit this pattern, have been recorded (Price, 2003). How do non-conformist species escape what appears to be strong selection for utilising long and vigorous host plant modules?

The search for, and study of, exceptions to a general pattern is not undertaken commonly by ecologists: they generally favour the search for support of a general pattern or hypothesis. However, exceptions to pattern may reveal important insights on why a strong pattern exists and the conditions under which it may break down. Darwin (1859) himself was most interested in cases that seemed to contravene the process of natural selection, devoting two chapters to their inspection, and in so doing he strengthened his case for the general role of natural selection in evolutionary change. The present study is justified using similar logic.

In the family of common sawflies, Tenthredinidae, data have been collected showing a general preference for long, vigorous shoots, in the stem- and bud-galling species (*Euura*), leaf gallers (*Pontania*), leaf folders and rollers (*Phyllocolpa*), stem borers (*Ardis*), and free-feeding sawflies (*Nematus* and other genera) (summarised in Price, 2003). Only four exceptions observed at the time of writing were noted, most in the genus *Pontania*, and since then other species have been searched for that show no ovipositional preference for long, vigorous shoots, and they are reported on them in this paper.

The working hypothesis on the non-conforming species of sawfly was that females attack at random, on the leaves and shoots that are available at the time of attack. Beyond this the interest lay in the reasons for the exceptions which may include: (1) shortage of adequate cues for selecting longer, more vigorous shoots; (2) weak or no advantage to strong female preference for long shoots because larval survival is independent of shoot length or correlated traits. Many alternative hypotheses have been proposed on the sub-optimal decisions by female insects when evaluated with reference to larval performance. Some examples follow, using our own labels for the hypotheses. (1) The adult performance optimisation hypothesis (Schiers *et al.*, 2000; Schiers & De Bruyn, 2002), in which adult performance is optimised rather than larval performance. (2) The ovipositional non-discrimination hypothesis (Larsson & Ekbom, 1995), when short-lived, highly host specific species seldom experience non-host plants. (3) The misleading vigorous growth hypothesis (Kokkonen, 2000), in which females evolve to exploit vigorous shoots on the typical host plant, but the cues are inappropriate on hybrids. (4) The hierarchical ovipositional preference hypothesis (Wiklund, 1974, 1981), which argues for retention of a broad spectrum of

hosts for wide-ranging species, but hosts do not provide equal suitability for larval performance. (5) The plant-stress continuum hypothesis (English-Loeb, 1989; Larsson, 1989; Koricheva *et al.*, 1998), in which a domed response curve to a stress gradient occurs perhaps because of opposite effects of stress on different life stages (Björkman, 1998). (6) The architectural compromise hypothesis (Fay & Whitham, 1990; McKinnon *et al.*, 1999), in which the most vigorous shoots develop growth that is too strong for successful herbivore utilisation. The relevance of these hypotheses will be evaluated in the discussion and in relation to our own hypothesis: the low resource heterogeneity hypothesis. Low heterogeneity would account for more or less random oviposition by females and even distribution of larval performance across shoot length classes.

To understand the magnitude of divergence from the general pattern, among the non-conformist sawfly species, a general description of a conformist species is required. The arroyo willow stem-galling sawfly, *Euura lasiolepis* (Hymenoptera: Tenthredinidae), that attacks the arroyo willow, *Salix lasiolepis* (Salicaceae) was chosen as an example. This species has received much research attention for over 20 years (cf. Price, 2003). The oviposition preference is for long shoots that are poorly represented in a population of stems on a willow clone; clearly, attack is non-random (Fig. 1). There is a strong linkage between ovipositional preference and larval performance; larvae survive better in longer shoot length classes. In certain studies ramet age results in a better predictor of larval establishment and survival than shoot length (e.g. Craig *et al.*, 1989), but the two variables are highly but negatively correlated (Craig *et al.*, 1986). As ramets age, shoot vigour declines (Price *et al.*, 1990). As shoot lengths increase there is also a strong decline in the probability of shoot abscission: abscission results in 100% death of larvae in the stem galls (Craig *et al.*, 1989). The combination of higher survival on more vigorous shoots and higher abscission of shorter shoots provides strong positive feedback on female preference for safe oviposition sites for larval establishment and survival – on the longest shoots available on the youngest ramets in a population. Indeed, linkage between the female ovipositional preference and larval performance is the strongest detected to date (cf. Craig *et al.*, 1989; Price, 2003).

Figure 1, typical of conformist species of sawfly, will be used as the basis for comparison with variables and responses in non-conformist species.

The comparative study of the gall-inducing sawflies necessarily involves an examination of the plant vigour hypothesis (Price, 1991). An assessment of the strength of bottom-up influences from the plant to the herbivore can also be incorporated (e.g. Hunter, 1992a; Price, 1992b; Hunter & Price, 1992a,b). In addition, it is possible to evaluate the extent to which the world is green for herbivores, involving the argument by Hairston *et al.* (1960) that plants remain largely green and unconsumed because of top-down impacts on herbivores by their natural enemies.
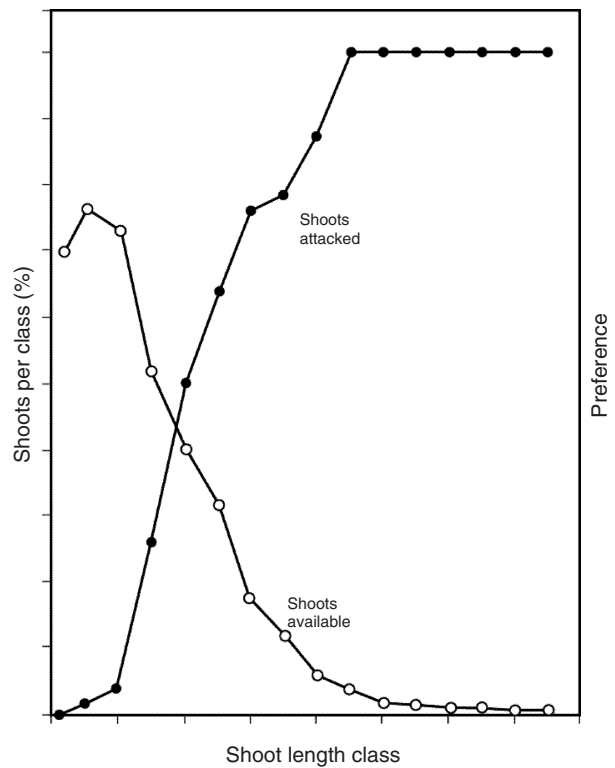

Fig. 1. Patterns observed in conformist species of gall-inducing sawflies, illustrated by *Euura lasiolepis*, a stem-galling species, and its host plant, *Salix lasiolepis*. Many shorter shoots and few longer shoots of willow are available, but attack is concentrated on the longer shoot length classes. Larval survival correlates positively with female preference for longer shoot length classes, and the probability of shoot abscission is negatively correlated with shoot length. (Based on Craig *et al.*, 1986.)

Species studied and localities

Six species of *Pontania*, with two each from Japan, Finland, and the U.S.A., are reported on (Table 1). The systematics of the genus is in a state of flux and the best names available are used. A species without a Latin binomial but systematically very close to a named species is designated as *near* the named species, as in *Pontania* nr. *pacifica* (Clancy *et al.*, 1986). A species that is similar to a named species, but without necessarily a close systematic affinity is referred to as *comparable*, as in *P.* cf. *arcticornis* (Zinovjev, 1993a, 1998). Zinovjev (1985, 1993b) divided the genus *Pontania* into three subgenera, including the subgenus *Eupontania*, to which the species studied belong. *Pontania* (*Eupontania*) species form galls on the underside of willow leaves attached to the midvein or large lateral vein and galls may protrude onto the upper leaf surface (Smith, 1970; Zinovjev, 1993b). Females oviposit into very young leaves in the spring, forming a gall in which a larva feeds during the summer. Larvae chew holes in the gall, emerge and spin a cocoon in the soil in the autumn (e.g. Caltagirone, 1964; Clancy *et al.*, 1986). Sawfly species that induce

Table 1. Species of *Pontania* in the present study, their host plant species, and the study months and years and locations.

Site	Sawfly species	Host plant species	Date	Locality
1	*Pontania mandshurica*	*Salix serissaefolia*	August 2002	Yasu River, south of Lake Biwa, near Kyoto, Japan, 35°03'N, 136°01'E
2	*Pontania mandshurica*	*Salix serissaefolia*	August 2002	Kino River, south of Osaka, Japan, 34°17'N, 135°31'E
3	*Pontania* cf. *arcticornis*	*Salix sachalinensis*	August 2002	Yura River, west of Lake Biwa, Japan, 35°23'N, 135°50'E
4	*Pontania* cf. *arcticornis*	*Salix sachalinensis*	August 1998	Ishikari River, Tobetsu, near Sapporo, Japan, 43°10'N, 141°29'E
5	*Pontania aestiva*	*Salix myrsinifolia*	June 1986	Hasanniemi, Joensuu, Finland, 62°35'N 29°44'E
			July 2001	Höytiäinen Channel near Joensuu, Finland, 62°37'N, 29°38'E
6	*Pontania arcticornis*	*Salix phylicifolia*	August 2001	Matara, near Joensuu, Finland, 62°34'N, 29°49'E
7	*Pontania pacifica*	*Salix lasiolepis*	June 2002	Pigeon Point, California, U.S.A., 37°11'N, 122°24'W
8	*Pontania* nr. *pacifica*	*Salix lasiolepis*	September 1999	Walnut Creek, near Prescott, Arizona, U.S.A., 34°56'N, 112°51'W

galls are usually specific to one willow species. Four species of *Pontania* that are conformist species, with an ovipositional preference for long shoots, have been recorded (Price, 2003). One of these is *Pontania* nr. *pacifica* (Clancy *et al.*, 1986) that is included in the present study for, in some cases, the species shows preference for long shoots and in others no preference is evident.

No *Pontania* species have been studied for ovipositional cues in the host plant, which may have provided a mechanistic explanation for the kinds of female choices observed. Inference from such studies on stem-galling sawflies suggests that phenolic glucosides act as ovipositional stimulants (Kolehmainen *et al.*, 1994; Roininen *et al.*, 1999). Hence, the possibility exists that females could respond to willow phenolics during ovipositional choices, if the relevant phytochemicals are variable enough to provide information on shoot or leaf lengths.

The host plant species in the genus *Salix* are more stable than *Pontania* taxonomically, but *Salix sachalinensis*, a name generally employed in Japan, has been synonymised with *S. udensis* by Skvortsov (1999). In this study the name more familiar in Japan is used. The willow species studied in Japan were trees about 5–20 m tall and the remainder, studied in other countries, were shrubs up to 3 or 4 m tall. In all willow species shoot growth is indeterminate and leaves are present only on currently growing shoots. As growth each year accumulates on a branch the remains of winter bud scars demark commencement of annual growth in branch length, enabling the ageing of branch samples. Also, shoot length and leaf length are positively correlated in willows (e.g. Price *et al.*, 1987a). Hence, longer shoots have more and larger leaves than shorter shoots.

All localities were situated in habitats with high soil moisture, either in riparian sites (*P. mandshurica*, *P.* cf. *arcticornis*, *P.* nr. *pacifica*), excavated channels (*P. aestiva*), drainage ditches (*P. pacifica*), or a plantation in a low-lying moist field (*P. arcticornis*).

Three study sites were located in the Kyoto–Osaka area of Japan, in August 2002. The Yasu River drained into the south-east section of Lake Biwa, and in the floodplain *Salix serissaefolia* grew at 150 m above sea level, on which *P. mandshurica* occurred. Five trees were sampled and samples were combined because attack patterns were similar on each of the trees, as in the other two sample sites. Another five trees of *S. serissaefolia* with the same sawfly species were sampled in the floodplain of the Kino River at about 60 m above sea level, which drains westward into the sea just south of Osaka. Another species, *P.* cf. *arcticornis* on *S. sachalinensis* was sampled on five trees along a tributary of the Yura River in the Nodabata Valley in the Kyoto University Experimental Forest west of Lake Biwa at about 700 m above sea level. The Yura River drains northward into the Sea of Japan.

A fourth site was used to study *P.* cf. *arcticornis* at Tobetsu, on the Ishikari River near Sapporo, Japan. Sampling of five trees occurred in 1998 in the wide floodplain of this channelised river.

In Finland, *P. aestiva* was found in 2001 along the bank of the Höytiäinen Channel excavated for navigation between parts of Lake Saimaa, running between the Pyhäselkä and Höytiäinen parts of the lake, near Joensuu, North Karelia. In 1986 and 1987, *P. aestiva* was sampled at Hasanniemi in the vicinity of Joensuu. *Pontania arcticornis* was sampled in and around a plantation of mixed willow species at Matara, near Joensuu in 2001. Only six shrubs had galls in an area of about 1 km^2.

In the U.S.A., *P. pacifica* was sampled in 2002 along a drainage ditch at Pigeon Point, California at 20 m above sea level and *P.* nr *pacifica* in 1999 occurred in the floodplain of Walnut Creek at 1545 m above sea level, in the Prescott National Forest north-west of Prescott, Arizona. In each case five distinct clones of this willow shrub were sampled. The two *Pontania* species have adults that are very similar but the galls are clearly distinct. *Pontania pacifica* induces galls that project onto both leaf surfaces (Caltagirone, 1964) while *P.* nr. *pacifica* galls protrude only from the lower leaf surface (Clancy *et al.*, 1986).

Non-conformist species might have had unusual traits, such as small gall size, but no trend has been noted in this direction, nor any other special galling characteristic that would allow escape from the usual constraints. All species develop galls within the common range of *Pontania* species, from 5 to 10 mm in diameter (cf. Caltagirone, 1964; Smith, 1970; Clancy *et al.*, 1986; Price *et al.*, 1999), which includes species with strong preference for long shoot length classes (e.g. Price *et al.*, 1999; Kokkonen, 2000; Hjältén *et al.*, 2003).

In all but site 4 at Tobetsu, the *Pontania* species studied were the only sawfly gallers present, so that 'the ghost of competition past' (Connell, 1980; p.131) was not relevant to explanations about divergence of attack from conformist species. Indeed, the phylogeny within the genus *Pontania* is not sufficiently studied to know whether the non-conformist species evolved as a single clade, or whether multiple origins of non-conformity will become apparent.

Methods

Attack of shoots

The eight sampling locations were identified opportunistically, because gall-inducing sawflies are very patchy in their distribution, and frequently occur at low population densities over the landscape. Low and very local populations involving few trees or shrubs were characteristic of all sites. At all sites trees or shrubs were at least 10 m apart. They were located haphazardly as an area was searched through for host plants with a relatively high number of galls present. Even then, gall numbers in aggregate were low at several sites, precluding meaningful comparison among trees or shrubs if less than 100 galls per plant were present. Therefore, emphasis is on general patterns evident when data are pooled, but tree-to-tree variation is illustrated at one site (site 3), as an example, where galls were most abun-dant and relatively evenly distributed across the five trees sampled.

To address the hypothesis that sawfly attack was random, at each site except site 6 branches representing 2–4 years of annual growth on which galls occurred were collected. All shoot lengths were measured and shoots with galls were recorded. In all these sites less than 50% of shoots had a gall present (range of 12–45% of shoots attacked). The numbers of shoots and galls per site will be provided in relevant figure captions. For each branch sampled, representing the scale at which females make decisions to accept or reject a shoot for oviposition, there were ample shoots on which preference could be expressed. For example, each stem grown in year 2000 would, itself, produce a range in length of new shoots in 2001, usually with shorter shoots at the stem base and longer shoots towards the apex. Hence, branches of 2–4 years growth represented the correct scale on which to examine female preference among shoot lengths. At least five branches per host plant were collected from around the entire canopy of each tree or shrub. The distribution of galls among hosts illustrated strong philopatry to the natal host plant, indicating low adult female dispersal, although actual documentation of this pattern has been described for only one species of *Euura* (Stein *et al.*, 1994). Thus, the 10 m distance among host plants ensured the sampling of independent genotypes, and taking branch samples, with many unattacked shoots, provided an unbiased sample with which to assess female preference.

Shoot lengths were ordered into shoot length classes of 1 cm or 5 cm and distributions were compared using the non-parametric χ^2 one-sample test (Siegel & Castellan, 1988): the distribution of all shoots represented the expected distribution of attacks and the shoots with galls represented the observed distribution. Less well represented shoot length classes were aggregated to form classes containing at least five shoots per class, in the expected distribution. This had the effect of reducing the degrees of freedom, resulting in two to five classes, even though 7–12 shoot length classes were represented in samples. At site 6 a very small population of *P. arcticornis* was discovered in and around an experimental plantation of willows, so sampling was non-destructive. When galls were discovered, shoot lengths were measured on the attacked shoot and five adjacent unattacked shoots. The mean length of the attack-free shoots and the shoot with a gall were compared using the non-parametric Wilcoxon matched-pairs signed ranks one-tailed test (Siegel & Castellan, 1988). It was predicted that shoots attacked would be shorter than the mean of adjacent shoots. This prediction resulted because buds on a shoot develop earlier from positions proximal to the ramet axis, although their ultimate length is shorter than shoots resulting from more dominant distal buds near the shoot tip.

Shoot length has been employed as a synoptic character for many years because length is correlated positively with other traits such as leaf length and internode length, stem diameter, and phytochemical concentrations of phenolic

glucosides (e.g. Craig *et al.*, 1986, 1989; Price *et al.*, 1987a,b, 1989; Price, 1991). Therefore, while the specific trait to which sawflies respond may not be known, shoot length provides a general character for comparing responses both within the sawflies and among other groups of herbivores (cf. Price, 2003). Use of shoot length permits broad comparisons to be undertaken.

Because leaf size is a variable of interest when studying leaf-galling sawflies, the relationship between shoot length and leaf length on two willow species, *S. sachalinensis* at site 4 and *S. lasiolepis* at site 8, was studied. For each shoot haphazardly identified, the longest leaf per shoot was measured. Pearson's product moment correlation coefficient estimated the variance in leaf length accounted for by shoot length (Sokal & Rohlf, 1995). These studies enabled a broadening of the view in the literature that shoot and leaf lengths are correlated in willows [*S. cinerea*, $r^2 = 0.88$ (Price *et al.*, 1987a), *S. exigua*, $r^2 = 0.66$ (Woods *et al.*, 1996)].

Position of galls on shoots

Another test of the pattern of galls utilised the position of galls on shoots. This test was applied at sites 1–4. At sites 1–3 all nodes were counted on a shoot by including axillary buds at the base of the shoot which had leaves abscised, plus the nodes with leaves present. The node position of galled leaves was noted. At site 4 only leaves were counted and the node position of attacked leaves was recorded. When these data were ordered into 1 cm shoot length classes, if attacks were random, the expected distribution of galls should be described by the pattern of availability of leaves on shoots. The pattern of attack provided a view of the phenology of shoot growth and attack by sawflies, and the presence or absence of any preference in female oviposition in relation to shoot length and leaf position. Least squares linear regression (Sokal & Rohlf, 1995) was employed to evaluate the significance of shoot length class as the predictor variable and number of nodes per shoot and nodes attacked as response variables.

Larval establishment in galls

The conformist species, represented in Fig. 1, show in many cases that performance of larvae is positively linked to female ovipositional preference (Price, 2003). The selective advantage to females ovipositing into longer shoots is that their progeny survive better. Mother knows best. The alternative hypothesis for non-conformist species may well be therefore *Mother doesn't know best*, the title of Courtney and Kibota's (1990) review of preference and performance relationships in insect herbivores.

To study larval performance the criterion of larval establishment in the gall was used. This criterion was used for several reasons. (1) Generally, in a cohort of insect herbivore individuals, there is a high risk of mortality between the egg and larval establishment in a secure feeding site (e.g. Cornell & Hawkins, 1995; Price, 1997). (2) In particular, this is evident in gall-inducing sawflies (Price & Craig, 1984; Clancy *et al.*, 1986; Preszler & Price, 1988). In some years, failure of larvae to establish in galls was the highest mortality factor observed (Clancy *et al.*, 1986; Price, 1992a,b), with mortality between egg and established larva being highly variable in some species from year to year, clone to clone, and across shoot length classes. (3) In later larval instars mortality factors such as predation and parasitism became unpredictable and probably a weaker selective influence on female ovipositional decisions than any direct link between female choices and larval establishment. (4) In some samples only early instar larvae were present (sites 1 and 7) so, for comparative purposes, early instar establishment in a gall, before mortality caused by natural enemies, was the most general criterion available. These data enabled an evaluation of any advantage to the female choice observed in relation to shoot length or leaf position.

Phenology of shoots and oviposition

As a direct measure of time of oviposition, new gall initiation and egg deposition of *P. aestiva* females were recorded during June in Hasanniemi, Joensuu, Finland, in 1986 and 1987. At frequent intervals of 1–5 days approximately 100 shoots on 25 ramets were checked for new galls and eggs. Elongation of shoots was also recorded to reveal the phenology of leaf production that could be coupled with phenology of oviposition. In addition, in 1986 at the same site, 100 or more shoots (mean 159, range 100–308) attacked by *P. aestiva* were sampled every few days (range 4–7) and the mean shoot length, mean number of leaves per shoot, the mean position of leaves attacked, and gall content were estimated: egg, larva, parasite or inquiline and failure of larval establishment, probably attributable to plant resistance. Sampling started on 10 June and ended on 30 September. Clones sampled were not equally represented on each sampling date, adding to the variation from week to week, but patterns through time were clear.

Evaluation of resource heterogeneity

Lack of a positive response to shoot length among non-conformist species may result from weak or absent cues that enable discrimination. Shoots may be too similar in growth phenology and/or length at time of attack, for discrimination by females to be possible or for a strong response to be quantified. Therefore, the interest lay in the relative variation of shoot lengths in the sampled sites. Variation was compared using the coefficient of variation (CV): the standard deviation of a sample expressed as a percentage of the mean of that sample (Sokal & Rohlf, 1995). The CV of shoot and leaf lengths was also estimated, for although *Pontania* females oviposit into very young leaves, cues may be available that predictably vary with ultimate leaf

length on which the galls grow and on which galls act as sinks for plant metabolites, water, and inorganic nutrients. In the conforming galling species, represented in Fig. 1, females are evidently able to discriminate among shoot and/or leaf lengths (Price *et al.*, 1999; Price, 2003).

Within the latitudes studied willows generally grow rapidly in the spring and complete growth around the end of July, with leaves falling in October. Hence, samples taken from late June into September, as in Table 1, span a period in which most growth has occurred. For example, the earliest sampling, in late June at site 7, was in the long growing season climate of coastal California and shoots had grown up to 60 cm long before sampling.

Results

Attack of shoots, position of galls, and larval establishment

Pontania mandshurica at sites 1 and 2 showed similar patterns. The distribution of shoots available and shoots attacked were significantly different (site 1: $\chi^2_3 = 9.64$, $P < 0.01$; site 2: $\chi^2_4 = 14.32$, $P = 0.01$; Fig. 2); however, attacks were concentrated on the shortest shoot length classes and diminished as shoot availability decreased and shoot length classes increased. This pattern of attack was diametrically divergent from the pattern observed in conformist species represented in Fig. 1. In both sites, patterns of establishment of larvae in the gall were very different from conformist species: 100% of galls had larvae established across all shoot length categories at site 1 (Fig. 2), a remarkable survival compared to published records on other species (e.g. Clancy *et al.*, 1986; Price *et al.*, 1999) and at site 2, the per cent of larvae established averaged 72%, ranging from 57 to 92%, but without a linear trend.

Pontania mandshurica also showed similar utilisation of leaf node position at sites 1 and 2 (Fig. 3). Attack was concentrated on leaves at nodes 8–14 at both sites while longer shoot length classes typically increased in total node number up to 50 and over. All shoots were evidently attacked early in their growth, independent of characteris-
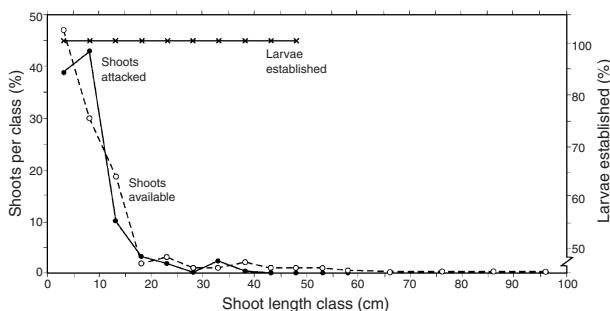

Fig. 3. Utilisation of leaves at nodes, numbered from the shoot base, by *Pontania mandshurica* at site 1. The nodes attacked remained at around node 10 while shoot length increased up to 50 nodes per shoot in some cases. The graph is based on 290 attacked shoots (total nodes: $Y = 8.14 + 1.28X$, $n = 17$, $r^2 = 0.96$, $P < 0.01$; attacked nodes: $Y = 12.80 - 0.09X$, $n = 17$, $r^2 = 0.07$, NS, where X is shoot length, Y is node position, and n is the number of shoot length classes).

tics that would eventually result in very different shoot lengths at the end of the growing season.

Pontania cf. *arcticonis* patterns at sites 3 and 4 were similar to patterns in *P. mandshurica*. The distributions of shoots available and shoots attacked were similar, but with a significant difference at site 3 ($\chi^2_3 = 11.87$, $P < 0.01$; Fig. 4) and no significant difference at site 4 ($\chi^2_4 = 4.08$, NS). Again, establishment of larvae in galls was very high in all shoot length classes at site 3, ranging from 98 to 100% establishment (Fig. 4). As an illustration of variation

Fig. 2. Willow shoots available and shoots attacked by *Pontania mandshurica* at site 1, and the per cent establishment of larvae in safe feeding sites in the galls. The graph is based on 739 shoots and 290 galls.
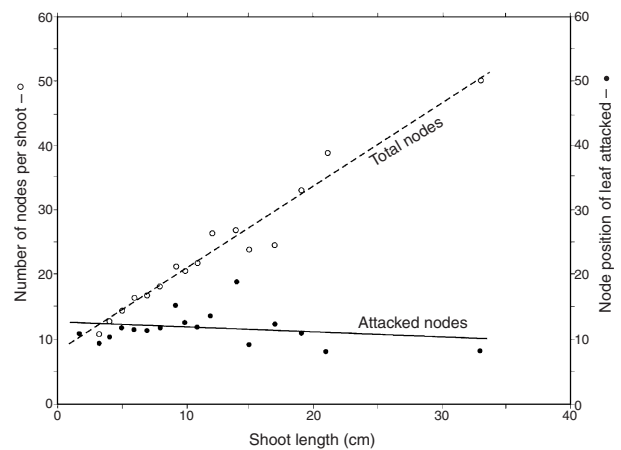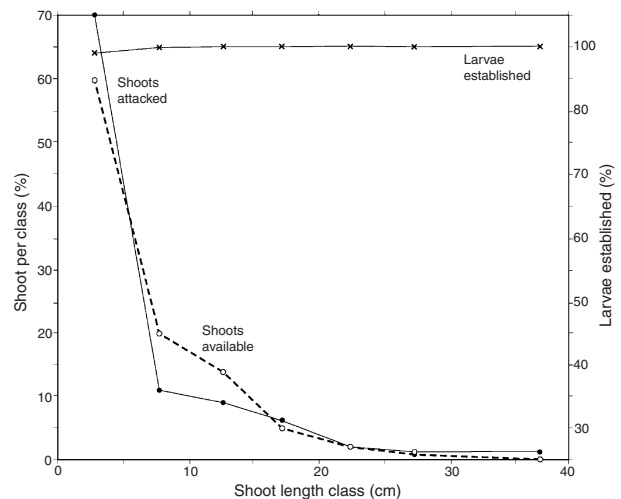

Fig. 4. Willow shoots available and shoots attacked by *Pontania* cf. *arcticornis* at site 3, and the per cent establishment of larvae in safe feeding sites in the galls. The graph is based on 956 shoots and 426 galls.

Table 2. Comparison of shoot distributions on five trees at site 3 and the standard errors in each shoot length class.

Shoot length class (cm)	All shoots combined	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	1 SE
1–5	60%	57%	58%	67%	53%	55%	2.41
6–10	20%	25%	18%	21%	26%	13%	2.39
11–15	14%	14%	11%	8%	18%	14%	1.68
16–20	5%	4%	6%	2%	3%	7%	0.93
21–25	2%	1%	4%	2%	0	6%	1.08
26–30	1%	0	3%	0	0	3%	0.74
31–35	0	0	0	0	0	1%	0.20
36–40	0	0	0	0	0	1%	0.20
Total shoots	956	166	159	225	260	146	

among trees, distributions of shoot lengths for five trees at site 3 are provided in Table 2. Standard errors were generally low for well-represented shoot length classes as a per cent of the mean, but inevitably increasing as sample sizes declined. At site 4, establishment reached 94% at the lowest shoot length class and trended downwards to about 75%.

Pontania cf. *arcticornis* also showed very similar patterns to *P. mandshurica* in leaves attacked. At site 3 leaves at nodes 5–8 were attacked – a very narrow range of leaf positions (Fig. 5). At site 4, in which nodes without leaves were not recorded, there was a flat pattern of attack similar to those seen at sites 1–3, with available leaves 1–3 attacked while up to 25 leaves were present on the longest shoots at the end of the season.

Pontania aestiva illustrated patterns similar to the other species discussed and very different from those depicted in Fig. 1. The distributions of shoots available and shoots attacked were not significantly different ($\chi^2_4 = 4.08$, NS; Fig. 6), and larval establishment was high in 2001 across all shoot length classes, ranging from 82% to mostly 100%.
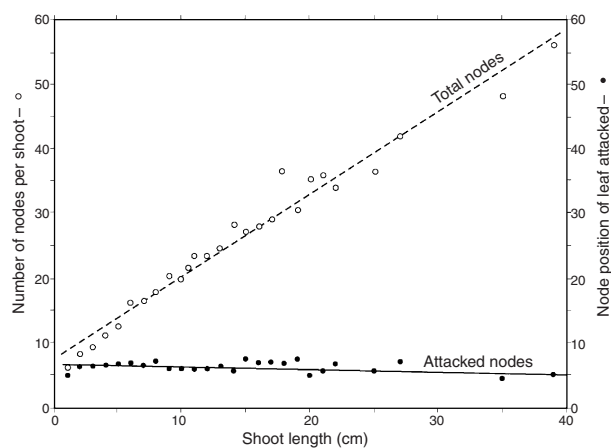
Pontania arcticornis was rare at site 6, the only site at which this species was known to occur in 2001. Only six galls on six shoots were discovered in 3 h of searching; however, in every case the pairwise comparison of the shoot length attacked was shorter than the mean of the adjacent unattacked shoots, giving a significant difference in the expected direction (Wilcoxon matched-pairs signed ranks one-tailed test, $T = 0$, $P < 0.025$).

Pontania pacifica and its host plant, *Salix lasiolepis*, at site 7 diverged from the patterns noted above and from patterns in Fig. 1 (Fig. 7). There were uncharacteristically few short shoots, with most shoots in the 10–20 cm shoot length classes. Samples were taken in late June well before any senescence and abscission of short shoots. Ramets were large and relatively old, at 12–20 years, so a low frequency of long, vigorous shoots should be expected. The distribution of attacks was significantly different from shoots available ($\chi^2_5 = 79.38$, $P < 0.001$), the least concordant pattern observed in the six species and eight sites. Larval establishment ranged from 60 to 100% across the shoot length classes with no strong trend evident (Fig. 7).

Pontania nr. *pacifica* had most attacks on the shortest shoots, with declining attacks as availability of shoots declined, but the distributions were significantly different ($\chi^2_2 = 14.54$, $P < 0.001$; Fig. 8). Larval establishment was high across all shoot length classes, ranging from 91 to 50%,
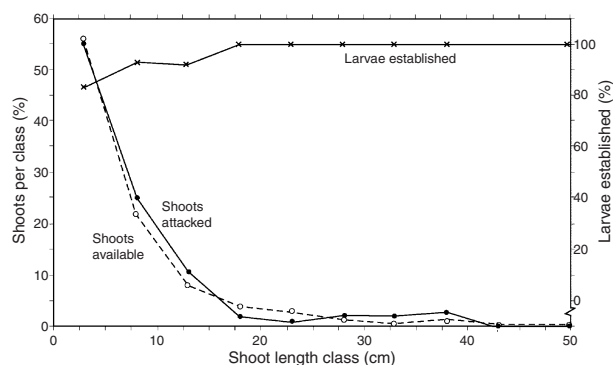

Fig. 5. Utilisation of leaves and nodes, numbered from the shoot base, by *Pontania* cf. *arcticornis* at site 3. The pattern is similar to that in Fig. 3 with attacked node positions at around 5–8. The graph is based on 426 attacked shoots (total nodes: $Y = 7.66 + 1.26X$, $n = 26$, $r^2 = 0.97$, $P < 0.01$; attacked nodes: $Y = 7.04 - 0.03X$, $n = 26$, $r^2 = 0.23$, NS).

Fig. 6. Willow shoots available and shoots attacked by *Pontania aestiva* at site 5, and the per cent establishment of larvae in galls, based on 995 shoots and 119 galls.
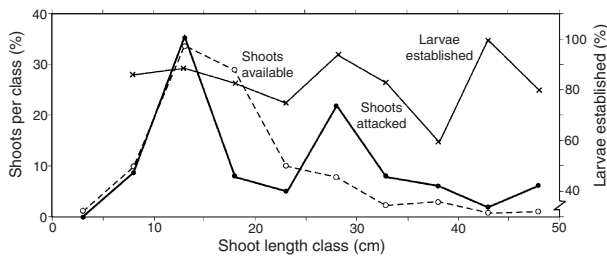
Fig. 7. Willow shoots available and shoots attacked by *Pontania pacifica* at site 7, and the per cent of larvae established in galls, based on 177 shoots and 79 galls.

although a negative and significant trend was evident ($Y = 93.41 - 1.44X$, $n = 7$, $r^2 = 0.77$, $P < 0.01$). Such a trend was opposite to that seen in the conformist species.

In both the willow species studied to test shoot length as a predictor of maximum leaf length, the correlations were significant and positive (*S. lasiolepis*: $n = 87$, $r^2 = 0.59$, $P < 0.01$; *S. sachalinensis*: $n = 100$, $r^2 = 0.69$, $P < 0.01$). This confirmed that shoot length is an adequate correlate of leaf length as found in two other willow species (Price *et al.*, 1987a; Woods *et al.*, 1996); however, in all *Pontania* species studied no evidence was found that large leaves were preferred oviposition sites.

Phenology of shoots and oviposition

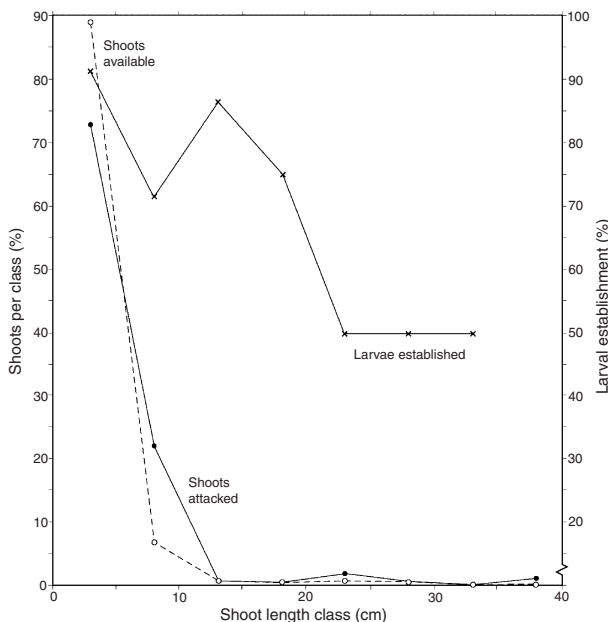*Pontania aestiva* appeared to have a brief and early oviposition period in Joensuu, Finland. The first eggs and

Fig. 8. Willow shoots available and shoots attacked by *Pontania* nr. *pacifica* at site 8, and the per cent of larvae established in galls, based on 1193 shoots and 417 galls.

galls observed occurred on 6 June 1986, when 31% of galls ($n = 123$) contained eggs. By 14 June, only 3% of galls ($n = 99$) contained eggs and no more eggs were found that season. No eggs were present in a sample on 19 June of 161 galls. That spring leaves started to appear on about 20 May, meaning that oviposition was into young shoots. In 1987 a similar pattern was observed with oviposition recorded from 5 to 8 June (unpublished data from Oyafuru, within 2 km of site 4, showed that oviposition lasted no more than 14 days in *P.* cf. *arcticornis*).

Following *P. aestiva* shoot and leaf attack through the growing season in 1986 revealed a pattern similar to those for other *Pontania* species in which node position of galls was recorded at one sample date (cf. Figs 3 and 5). As mean shoot length increased, the mean of nodes attacked remained almost constant over a very narrow range, between nodes 4 and 6 except for the last sample in the year (Fig. 9). This result reinforces the conclusion that attack is early in the growing season while shoots were young and short (means of 6–8 cm in 1986, when shoots had a mean of seven or eight leaves).

Examination of gall content through the season in 1986 revealed that *P. aestiva* females were effective in inducing galls with established larvae present, on average 86% of the time (range 79–96%). These results were similar to the 2001
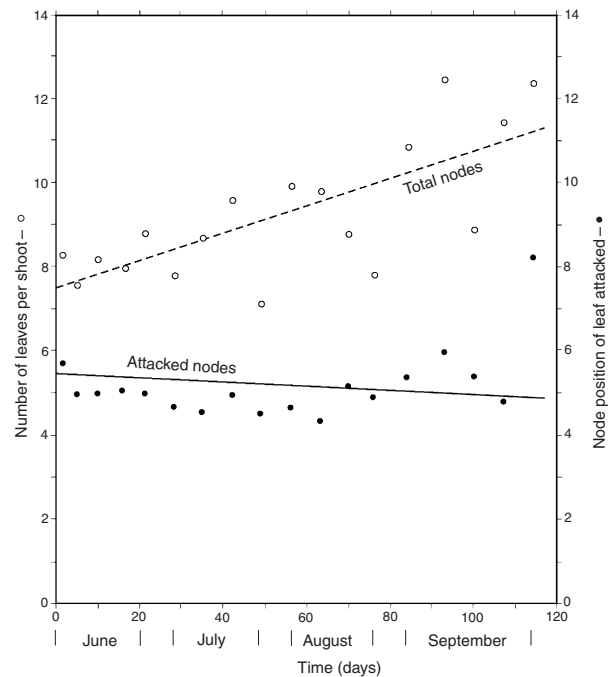

Fig. 9. Utilisation of leaves and nodes, numbered from the shoot base, through the season, by *Pontania aestiva* at site 5, at Hasanniemi in 1986. Days are numbered from 1 at the start of sampling on 10 June, through the last sample on 30 September. The period during which samples were taken each month is indicated by bars between months. The graph is based on 2182 attacked shoots (total nodes: $Y = 7.54 + 0.032X$, $n = 18$, $r^2 = 0.52$, $P < 0.01$; attacked nodes: $Y = 5.43 + 0.0046X$, $n = 18$, $r^2 = 0.033$, NS).

results (Fig. 6), although the latter showed even higher establishment from 84 to 100%.

Evaluation of resource heterogeneity

Coefficients of variation in shoot lengths varied considerably among sites (Table 3) Where values of CV are below 100%, the variation in shoot lengths was low, meaning that discrimination among shoot length classes was predictably more difficult for females, promoting the expectation for little of no ovipositional preference for longer shoots. An extreme case of low shoot length variation was observed at site 7 on *P. pacifica* (CV = 39%, Table 3) which is characteristic of shoots on old ramets in the range of 12–20 years, lacking any vigorous shoots.

Coefficients of variation in shoots and leaves were markedly different, as would be expected. In *Salix lasiolepis*, mean CV for shoots was 128% (10 samples of 100 shoots each) and for leaves the CV was 29%. Variation in shoots was 4.4 times greater than in leaves. In the three willow species sampled, CVs varied between 30 and 43% (Table 3). Therefore, sawfly species attacking leaves, such as in the genus *Pontania*, are exposed to a resource generally much less variable than stems, which are attacked by stem-galling sawflies (an unusual exception was the CV of 39% for shoots on the old ramets of *S. lasiolepis* at site 7). Resource variation for *Pontania* species was relatively low for ovipositing females and for gall development and larval performance.

Discussion

In general, conformist species of gall-inducing sawflies show strong positive responses to shoot length, with higher gall density, larval establishment, and emergence of adults (Fig. 1). None of the species of *Pontania* treated in this paper conformed to the patterns illustrated in Fig. 1. Ovipositional patterns were close to the availability of shoots with only *Pontania pacifica* deviating well away from the pattern of shoots available (Fig. 7). Even then, no similarity to the pattern in Fig. 1 was evident. Also, larval establishment in galls was generally high and was observed across all

shoot length classes, contrary to the patterns in Fig. 1. The six species discussed were, indeed, non-conformist species when compared to the more common pattern observed in tenthredinid sawflies.

This study adds three non-conformist *Pontania* species to the list of three *Pontania* species provided in Price (2003) and provides new data on all six species. In Table 5.4 in Price (2003) the *Pontania* sp. on *Salix sachalinensis* is identified now as *Pontania* cf. *arcticornis* and the data provided was from site 4 in this study. *Pontania arcticornis* was mistakenly named *P. arctica* in Price (2003).

The evidence presented for *P. mandshurica* (Fig. 3) and *P.* cf. *arcticornis* indicated that attack of leaves was early in the spring, because early nodes on a stem were utilised and this was independent of shoot length. This conclusion was reinforced with the oviposition data from *P. aestiva*. Early attack would occur when all shoots were growing vigorously in the spring and shoot length differences were minimised. This made discrimination among shoot length classes unlikely even if a selective advantage were to accrue from such discrimination in the form of larval performance. Further south, in Frankfurt, Germany (at about 50°N compared with 63°N for Joensuu, Finland), emergence times of *P. aestiva* and related sawflies were more prolonged, lasting up to 6 weeks (Kopelke, 1985; J.-P. Kopelke, pers. comm.), so it would be valuable to examine shoot length utilisation by *Pontania* species in more southerly latitudes of Europe; however, at sites 1–4 in Japan, at about 35–43°N, emergence times must have been brief, indicated by the narrow range of nodes per shoot utilised by sawflies. In northern latitudes, such an in Finland, the evolution of early emergence and attack would certainly become increasingly beneficial as warm season length declined as latitude increased.

Larval performance in relation to establishment in safe feeding sites was very high, at 100% across all shoot length classes in some cases. Thus, there was unlikely to be any positive feedback from differential larval performance in relation to shoot length to female preference in any of the species discussed. It should be considered therefore why larvae survive so well and why females should not show ovipositional preference for longer shoots as in the conformist species. There appears to be a strong contrast among most *Pontania* species and *Euura* species in the ease with

Table 3. Coefficients of variation of shoot lengths and leaf lengths at selected study sites.

Site	Sawfly species	Host plant species	Shoots		Leaves	
			n	CV (%)	*n*	CV (%)
1	*Pontania mandshurica*	*Salix serissaefolia*	210	142	167	43
2	*Pontania mandshurica*	*Salix serissaefolia*	201	102	–	–
3	*Pontania* cf. *arcticornis*	*Salix sachalinensis*	205	78	–	–
4	*Pontania* cf. *arcticornis*	*Salix sachalinensis*	201	86	200	30
5	*Pontania aestiva*	*Salix myrsinifolia*	–	–	–	–
6	*Pontania arcticornis*	*Salix phylicifolia*	–	–	–	–
7	*Pontania pacifica*	*Salix lasiolepis*	177	39	–	–
8	*Pontania* nr. *pacifica*	*Salix lasiolepis*	239	125	200	38

which oviposition attempts are converted to successful gall formation and larval establishment. Success was high in all species in the present study (Figs 2, 4, 6, 7, and 8) and in two of the three additional species, *P. amurensis* and *P. pustulator*, examined by Price *et al.* (1999). Earlier papers on *P. nr. pacifica* support the pattern of high establishment probabilities. At one gall per leaf, establishment of larvae was 76% successful in Flagstaff, Arizona (Clancy & Price, 1989), a little higher at 80–84% (Clancy & Price, 1986) but much lower in a later study (Stein & Price, 1995). In contrast to generally high establishment in *Pontania*, establishment in *Euura* is very variable and frequently low. In *E. lasiolepis* establishment averaged 51% over 3 years (Price, 1992a), dipping as low as 20% in one generation. Equivalent values were 10–36% on the shorter shoots for *E. mucronata* (Price *et al.*, 1987b), 34–51% in the stem-galling *E. exiguae* (Price, 1989), and 50–70% in the leaf midrib galler, *Euura* sp. on *S. exigua* (Woods *et al.*, 1996). Evidently, for reasons as yet unknown, probability of successful establishment in sawfly galls is generally much higher for leaf gallers (*Pontania* spp.) than for stem, bud, and midrib gallers (all *Euura* spp.).

Several probable reasons for lack of ovipositional preference are apparent. First, larval survival is high and independent of shoot length, providing no feedback on female preference. Second, early oviposition in the spring leaves only weak or absent cues that would guide a female in any discriminatory behaviour. Third, leaves are much less variable in length than stems and probably other factors also, so that oviposition, gall development, and larval survival are exposed to a resource of low heterogeneity across shoot length classes. Predictably, this would result in indiscriminate oviposition on available leaves and uniform performance. Fourth, *Pontania* species all emerge from galls largely before leaf abscission, so limiting or differential abscission of leaves on different shoot lengths is immaterial to these species. This contrasts with some *Euura* species, such as *E. lasiolepis*, that remain in the gall through the winter and die if the shoot carrying the gall abscises. Abscission has a high probability on short shoots and a very low probability on long shoots, acting as a very strong selective agent in relevant species on female ovipositional preference for long shoots (Craig *et al.*, 1989; Nozawa & Ohgushi, 2002). Fifth, emergence phenology of female sawflies in the species studied appears to be very brief and early in willow growth. Early nodes were attacked over a very narrow range of nodes (Figs 3, 5 and 9) and egg laying was brief in *P. aestiva*, lasting only 7–10 days at most. This pattern contrasts with some conformist species that emerge over a period of 30 days or more (e.g. Price & Craig, 1984; Price & Clancy, 1986). As shoot length increases rapidly through a more prolonged oviposition period, detectable cues are likely to strengthen, enabling preferences to be expressed, as was observed for *E. mucronata* by Roininen (1991).

Even though all shoots appear to be available to these *Pontania* species, a large proportion of leaves are not. Early

and brief female emergence results in only a narrow window of attack, with many leaves being developed well after gall initiation is terminated. Even species that emerge later in the season, such as *P. pacifica* and *P. nr. pacifica*, emergence is narrow relative to the phenology of leaf production (cf. Clancy *et al.*, 1986). For example, shoot elongation and leaf production lasted for 3–4 months on *S. lasiolepis* but attack by *P. nr. pacifica* occurred over 5–6 weeks (Clancy *et al.*, 1986). Hence, since only the very youngest leaves are utilised by ovipositing females, over 60% of leaves are not available for oviposition. A much smaller percentage of leaves is available for early emergers when only three or four nodal positions are utilised on shoots with 20–50 nodes available during the course of the growing season. The world is not totally green for any of these sawflies (cf. Hairston *et al.*, 1960); however, apparent underutilisation of resources by these sawflies results mainly from their limited emergence period rather than bottom-up limitation of adequate resources. Therefore, these sawfly species differ from the conformist species which are subjected to severe resource limitation resulting from a low production of long, vigorous shoots in a willow population.

The conformist species respond strongly to the plant vigour observed in young ramets and long shoots. Indeed, *Euura* species provided the motivation for the plant vigour hypothesis (Price, 1991). The non-conformist species of *Pontania* do not prefer vigorous plants or modules. But neither do they show a preference for short shoots or ramets with poor growth.

Concerning the relative strengths of bottom-up influences on herbivores, from the plant, and top-down impact of natural enemies, the results in this report suggest that resources are homogeneous enough to have little effect on distribution and abundance. While data on top-down effects were not presented in this paper, there is evidence that natural enemies in the form of parasitoids, inquilines, and ants can cause much mortality (Caltagirone, 1964; Clancy *et al.*, 1986; Woodman & Price, 1992). What, then, drives the very patchy distribution of non-conformist species over a landscape and their relatively low abundance? Locally benevolent environments are likely to be important but perhaps natural enemies are even more relevant (cf. overviews by Clancy, 1993; Price *et al.*, 1994), and genetic variation in susceptibility and resistance to gall induction may also play a role (cf. Fritz, 1992).

It is concluded that, for non-conformist *Pontania* species, willow host resources are not sufficiently heterogeneous to provide strong cues for the selection of vigorous shoots at the time of oviposition. Therefore, females and larvae do not show an ovipositional preference and larval performance linkage. Females utilise shoots for oviposition in a pattern similar to the availability of shoots. Even though significant differences between shoots available and shoots attacked were evident in some cases, most species utilised a preponderance of shorter shoot length classes which were most abundant in willow clones. Added to this, the low variance in leaf size contributed to low heterogeneity of

resources. The result is that resources, or bottom-up supplies of shoots, appear to be plentiful, representing a high carrying capacity locally, in contrast to the low carrying capacity of resources for the conforming species.

This probable explanation for the patterns observed in non-conformist species reinforces the general thesis on the conformist species. Whereas there is a general pattern of attack on long, vigorous shoots in conformist species, it has been shown here that low heterogeneity of resources during attack results in random utilisation of shoots, or at least greater utilisation of common rather than rare shoot length classes. For the non-conformist species the non-discriminatory pattern of attack results from four major contributors to low resource heterogeneity: (1) early female emergence relative to shoot phenology; (2) low heterogeneity of leaf size; (3) abscission of leaves after emergence of larvae from galls; and (4) low variance of shoot lengths on old ramets because no long, vigorous shoots are developed. An additional feature is a generally high proportion of larvae establishing in galls, probably resulting from low variation in resources at the time of larval eclosion.

So many species of insect herbivore show a strong positive response to vigorous plant modules, including many outside the tenthredinid sawfly taxon (reviewed in Price, 2003), that it is interesting and valuable to explore the mechanisms involving non-conformist species such as the leaf gallers in this paper. These *Pontania* species utilise plants that are growing well, but the plants are exploited at a time when resource heterogeneity is low. A case, equivalent to the species of *Pontania* discussed in this paper, was described by Roininen (1991) in which the bud-galling sawfly, *Euura mucronata*, attacked shoots at random, early in the season when all shoots exhibited similar lengths, but showed a preference for longer shoots when a stronger shoot length gradient was available. Thus, it can be understood why the phylogenetic constraints are relaxed and how predictions could be made about plant and insect herbivore interactions under prevailing low heterogeneity resources. The limiting requirement is that not enough is understood about the details of resource variation at the scale to which small herbivores respond. A growing appreciation of the importance of plant phenology as a resource variable for insect herbivores has been witnessed (e.g. Hunter, 1990, 1992b; Coleman *et al.*, 1994; Auerbach *et al.*, 1995; Yukawa, 2000) in addition to the long-standing interest in phytochemical variation (e.g. Rosenthal & Berenbaum, 1991, 1992), but many other resource variables demand more attention, as illustrated in this paper. Whereas high resource heterogeneity has been emphasised in the past (e.g. Hunter *et al.*, 1992), and has formed the basis for many hypotheses on plant and herbivore interactions (cf. Price, 1997), the mechanisms by which the plant–herbivore interaction minimises heterogeneity would be worthy of more attention.

Alternative hypotheses, for example those discussed in the Introduction, cannot all be discounted by the results in this paper. The adult performance optimisation hypothesis cannot be falsified until it is known exactly what ovipos-itional cues exist for each species. In fact, for some *Pontania* species the same reason has been suggested for lack of a preference–performance linkage (Price *et al.*, 1999). The ovipositional non-discrimination hypothesis was developed for female choices among host plant species, but may be applied to lack of preference within host plants, if the costs are low, as is evident in data on larval establishment in this paper. No data are available relevant to the misleading vigorous growth hypothesis, but any hierarchical ovipositional preference within a host plant species was not evident, as attack was more or less random. Since all shoot types were utilised, and on all shoot length classes larval establishment was relatively high, no results were obtained that were consistent with the plant-stress continuum hypothesis, and for the same reason, the architectural compromise hypothesis was not supported. Fritz *et al.* (2000) argued for a broader view of plant traits that influence female preference and larval performance, including architectural features, physiology including source–sink relations, and the recognition and use of 'multiple causative factors' (p. 562) in the testing of hypotheses. This is sage advice, for there is certainly much more to explore and synthesise in the field of ovipositional preference and nymphal/larval performance in insect herbivores.

Acknowledgements

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