

Long-term population dynamics of a sawfly show strong bottom-up effects

PETER W. PRICE and MARK D. HUNTER*

Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011-5640, USA; and *Institute of Ecology, University of Georgia, Athens, GA 30602-2202, USA

Summary

1. Population dynamics of the arroyo willow stem-galling sawfly *Euura lasiolepis* Smith (Hymenoptera: Tenthredinidae) on its host plant, *Salix lasiolepis* Benthham (Salicaceae), was studied for 22 years in the vicinity of Flagstaff, Arizona, USA.
2. Comparatively low levels of population change in drier and wetter sites ranged over two orders of magnitude.
3. Time-series analysis revealed best fit models of population change that included total winter precipitation from October to May and/or cumulative Pearson Drought Severity Index (PDSI) for the same period, plus a 1-year delay in precipitation or PDSI in some cases.
4. For populations on willow clones in drier sites, the model accounted for 73% of sawfly population change, and in wetter sites, with high mean populations, the model predicted 67% of the variation in gall density.
5. The mechanistic link between predictors of water availability to host plants and sawfly populations was better growth of willow after high winter precipitation, producing more and longer shoots. Also, willow clones with younger ramets, with more vigorous growth, were more favourable to sawflies than clones with older ramets.
6. Strong female preference for longer shoots resulted in more eggs laid, and this was coupled with higher larval survival on longer shoots. The major component of loss in a cohort was aborted ovipositions, with significant and negative influence on survival through the immature stages. Survival in one generation was correlated with gall density in the following generation.
7. Dynamics were entirely driven through resource supply.
8. Combining the evolutionary Phylogenetic Constraints Hypothesis with detailed mechanistic studies reveals an explanation of population dynamics which is more broadly applicable than purely ecological studies.

Key-words: bottom-up effects, phylogenetic constraints hypothesis, plant vigour hypothesis, precipitation effects on resources, preference-performance linkage.

Journal of Animal Ecology (2005) **74**, 917–925
doi: 10.1111/j.1365-2656.2005.00989.x

Introduction

What causes populations of plants or animals to fluctuate through time; to flourish or to decline to extinction? Hundreds of studies on population dynamics have reached a multitude of conclusions, but many have been unable to account for the majority of the variation

in populations. Diverse methods of study and the resulting explanations of dynamics provide little opportunity for synthesis, or detection of broad patterns, and therefore little basis for broad theory derived from empirical studies (Price 2003). We suggest that the lack of synthesis results from insufficient emphasis on species' evolutionary constraints, and the influence of adaptive traits on the dynamics resulting there from. Evolved traits are likely to influence the probability that species are eruptive or latent in their dynamics, for example, and which factors, bottom-up or top-down, are important in determining annual fluctuations.

Correspondence: Peter W. Price, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011-5640, USA, Tel.: (928)779 3547; Fax: (928)523 7500; E-mail: peter.price@nau.edu

This evolutionary point of view was encapsulated in the Phylogenetic Constraints Hypothesis, based on a group of gall-inducing sawfly species (Hymenoptera: Tenthredinidae) that shared herbivore and host plant relationships in common (Price 2003). Briefly, the argument is that the saw-like ovipositor acts as a phylogenetic constraint because oviposition is limited to young, rapidly growing willow shoots, and the shortage of high-quality shoots sets a low carrying capacity for the population. Females are strongly philopatric on favourable willow clones. Because of the ovipositor and associated female behaviours, strong bottom-up effects through plant quality dominate the population dynamics of this group of species.

We tested the Phylogenetic Constraints Hypothesis using 16 years of population data on the arroyo willow stem-galling sawfly *Euura lasiolepis* Smith, and on its host, the arroyo willow *Salix lasiolepis* Bentham (Salicaceae) (Hunter & Price 1998). We supported the hypothesis by showing that winter precipitation during sawfly generation t , which was critical to willow growth in the following spring, accounted for much of the population variance in sawfly generation $t + 1$ ($r^2 = 0.52$ in wetter sites, and $r^2 = 0.43$ in drier sites, $P < 0.01$). An additional delayed effect of precipitation was documented in sawfly generation $t + 2$ in the drier site clones ($r^2 = 0.38$, $P < 0.02$). In aggregate, delayed effects of precipitation on willow growth and sawfly populations in generation $t + 1$, and $t + 2$, accounted for 69.4% of the variance in gall density among years in drier sites and 52% of the variance in wetter sites. In this study neither parasitism nor predation provided any explanatory power of sawfly dynamics.

Now we employ 22 years of population census data on the sawfly to test effects of precipitation in more detail. We have added a drought index as an independent variable, which evaluates a combination of temperature and precipitation. Also, we have added mechanistic studies on why precipitation affects sawfly populations, including evaluation of willow ramet age, shoot length, and genotype, gall weight, larval weight, gall abortion, larval death, and adult sex ratio. We also used an improved time-series analysis to model the population dynamics. No new data on parasitism or predation were collected. We develop a mechanistic understanding of the population dynamics of *Euura lasiolepis*, based on evolved traits explained in the Phylogenetic Constraints Hypothesis.

Methods

STUDY ORGANISMS AND AREAS

Euura lasiolepis has an annual life cycle. Adults emerge in early May to June in the study area, females oviposit into young shoots of the host plant and stimulate gall growth (Price & Craig 1984). Larvae feed in galls until October and spin cocoons in which they overwinter within the gall. Females show a strong preference for longer shoot-length classes during oviposition and

larvae survive better in longer shoots. There exists a strong ovipositional preference and larval performance linkage, as strong as any described (Craig, Itami & Price 1989). In addition, female sawflies are highly philopatric to favourable clones. The host plant for *E. lasiolepis* is the willow, *S. lasiolepis*. In the study area willows grow as shrubs, up to 4 m tall, forming distinct clones by layering of low branches, with subsequent growth of new rootstocks. The most rapid growth of arroyo willow occurs in May and June during the driest months of the year, such that plants depend on soil moisture developed from winter precipitation (Price & Clancy 1986). After winters of high precipitation, mostly as snow, willows grow well, as they do in high-water treatment experiments, and low-water availability results in poor growth (Price & Clancy 1986; Price 2003; references therein). Willows and sawflies were studied in the vicinity of Flagstaff, Arizona (35°14'N, 111°39'W) along the main drainage composed of Schultz Creek and the Rio de Flag. The full distribution of willow clones ranged from 2438 m above sea level (36°17'N, 111°38'W) down to 2084 m (35°11'N, 111°39'W).

Densities of *E. lasiolepis* were estimated from 1981 to 2002 on 15 willow clones representing the full range of gall densities of *E. lasiolepis* per clone in the drainage, on the property of the Museum of Northern Arizona at about 2100 m above sea level (35°14'N, 111°39'W). Clone location was provided in Price (2003), and original clonal designations have been retained for direct comparison with earlier reports. To explore how well the selected clones represented dynamics in the watershed at large, 73 clones spread throughout the drainage were sampled for galls produced in the 1999, 2000 and 2002 generations. Because samples were intended for a spatial analysis of *Euura* distribution, clones were spread more or less evenly over the full 10.5 km of their local distribution in the Flagstaff area (McGeoch & Price 2004).

ANNUAL POPULATION CENSUS AND HOST PLANT PHENOTYPIC VARIATION

We conducted an annual population census of galls on 1000 shoots per clone as described in Hunter & Price (1998), with gall density expressed as number of galls per 100 or per 1000 shoots. Sampling was nondestructive. For the extended census on 73 clones, 200 shoots per clone were sampled.

To investigate variation in gall density among clones within years, we estimated two phenotypic variables per clone: mean age of ramets and mean shoot length. Both variables are critical in female preference and larval performance (Craig, Price & Itami 1986; Craig *et al.* 1989). As ramets age shoot length declines, showing a negative correlation in these growth characteristics. Ramets and shoots were sampled in January 1987 on all 15 willow clones used in the annual population census. At each clone, a ring (diameter of 35–68 cm, area 1000 cm²) was thrown over the sampler's shoulder on

to the clone five times, and at each location ramet age and length of five ungalled shoots were measured. Age of ramets was estimated nondestructively as described in Craig *et al.* (1986, 1989).

GALL DISSECTION AND REARING

Galls were collected at random from clones for 10 years, from 1981 to 1990, and dissected to reveal contents in 1981–85, and reared in Petri dishes to estimate sawfly sex ratio in 1986–90 as described in Hunter & Price (1998). The stage at which death occurred (early, mid or late larva), and the cause of death were recorded. Galls that were fully developed but contained no larvae were classified as aborted oviposition attempts, resulting either from a female's decision not to lay an egg, or very early death, as soon as the larva started emerging from the egg (Price & Clancy 1986; Price 2003). Galls were weighed to the nearest milligram wet weight and larvae were weighed to the nearest microgram wet weight.

HOST PLANT GENOTYPIC VARIATION

We tested the hypothesis in 1986 that female preference and larval performance depended on largely genotypic characteristics of host clones. We used 10 cuttings from each clone and treated them identically, to provide experimental host plants expressing largely genotypic differences among clones, employing methods of culture described in Fritz & Price (1988). Potted plants were displayed at canopy height in willow clones with high sawfly populations and attack occurred by wild sawflies in the field. Gall number on each plant was counted, and the number of sawfly emergence holes was recorded in late June 1987. Thus, female attack preferences and larval performance (survivorship) were recorded among the 15 experimental clone types. To assess differences in clonal growth, the length of five shoots in the upper part of each potted plant was measured to provide an estimate of mean shoot length per plant. All other experiments relevant to *Euura* population dynamics have been reported elsewhere and are summarized in Price (2003). We have repeatedly shown positive relationships among water supply to potted plants, willow shoot growth, sawfly ovipositional preference and larval performance.

ANALYSES

Time-series analysis was employed to build models of *E. lasiolepis* population dynamics using precipitation and the Palmer Drought Severity Index (PDSI) as abiotic predictor variables. Because rapid willow growth and sawfly attack occur during the driest months of the year (Price & Clancy 1986) we have employed an index of probable moisture relevant to willow growth in the spring, using the total precipitation over the months of October–May. Precipitation data were from the local weather station at Pulliam Airport, 11 km from the main

study site. The PDSI was employed as an additional predictor variable because drought is cumulative and dependent upon temperature, precipitation, and their interplay – evapotranspiration (Palmer 1965). PDSI values for Arizona District 2 of the National Oceanic and Atmospheric Administration were used, which includes the Flagstaff area, and monthly estimates were obtained from the National Climate Data Center at <http://lwf.ncdc.noaa.gov/oa/ncdc.html>. Cumulative PDSI values for the months of October–May were again used to predict willow growth and sawfly responses in the subsequent sawfly generation starting in May. PDSI values have been used successfully to model tree growth in a nearby locality (Trotter, Cobb & Whitham 2002). Note that high PDSI values indicate low levels of drought. Although precipitation and the drought index are weakly correlated within years ($r^2 = 0.37$), drought in one year is not correlated with precipitation the previous year ($r^2 = 0.09$). In no model did drought and precipitation from the same year enter the same model (Table 1) and so they are independent in the analysis.

Time-series models were developed using the time-series forecasting procedure in SAS 8.2 (SAS Institute 2001), which generates maximum likelihood estimates for autoregressive models. With the standard assumption of log-linear relationships in the data (Stenseth, Bjornstad & Falck 1996), we used the model structure and methods described by Royama (1992) and Forchhammer *et al.* (1998) to develop time-delayed models for gall populations. Log-linear models explained more of the population variation than did previous linear models (Hunter & Price 1998). Models were of the form:

$$X_t = (1 + \alpha_1)X_{t-1} + \alpha_2 X_{t-2} + \dots + \alpha_D X_{t-D} + \beta_1 W_{t-1} + \beta_2 W_{t-2} + \dots + \beta_D W_{t-D},$$

where $X = \log$ of gall density at a given time, t , the α 's are the strength of density dependent effects on various time lags (D), and the β 's are the strength of various climatic effects (W) acting on various time lags. We used the corrected Akaike's Information Criterion (AIC_c) to select among competing models (Forchhammer *et al.* 1998). The AIC_c values provide a measure of parsimony by which to choose models with the maximum information gain for the minimum number of model variables. In all cases, the maximum time-lag investigated in our models was 3 years, the maximum lag for which ecological meaning can be easily inferred (Royama 1992).

Overall, three models were developed. The first model was generated from yearly population averages for the three wet-site clones (1982–2002). The second model was developed from yearly averages of a subset of the dry-site clones (eight of 12) that were undisturbed throughout the entire sampling period (1981–2002). Clones MNA1, MNA5, NP8 and NP9 were cut back or removed between 1996 and 2001 due to pipeline and culvert construction and were therefore not included in

Table 1. Results of time-series analysis of the gall-forming sawfly, *Euura lasiolepis*, on its host, *Salix lasiolepis*. Analyses were run both with (top) and without (bottom) the inclusion of precipitation and drought indices

Time series	AIC _c	r ²	AR1	AR2	P1	P2	D1	D2
Drought and precipitation included in analysis								
Wet-site clones (1982–2002)	–15.54	0.67	NA	NA	0.004 (0.0004)	NA	NA	0.160 (0.011)
Dry-site clones (Undisturbed 1981–2002)	–12.95	0.73	0.626 (0.006)	NA	NA	NA	0.215 (0.003)	0.252 (0.001)
Dry-site clones (1981–95)	–7.29	0.69	NA	NA	NA	NA	0.210 (0.023)	0.238 (0.012)
Drought and precipitation excluded from analysis								
Wet-site clones (1982–2002)	–5.08	0.44	0.806 (0.002)	–0.462 (0.048)				
Dry-site clones (Undisturbed 1981–2002)	1.86	0.49	0.935 (0.001)	–0.508 (0.044)				
Dry-site clones (1981–95)	–2.21	0.51	0.794 (0.005)	–0.569 (0.040)				

AIC_c represents the corrected Akaike's Information Criterion, r² is the variance explained by each model, while AR1 (1 + α₁) and AR2 (α₂) represent autoregressive terms of lag $t - 1$ and $t - 2$, respectively. Models including lags up to $t - 3$ were tested, but none was more parsimonious than models with shorter lags. NA indicates that the term did not add significant explanatory power to the model. P1 and D1 are precipitation and drought, respectively, from October–May prior to gall census in winter. P2 and D2 are precipitation and drought, respectively, from October–May, 2 years prior to gall census. Parameter estimates are provided for autoregressive and weather variables, with the significance of each estimate provided below in brackets. Models were developed using the time-series forecasting tool of SAS version 8.1 for Windows.

this second model. The final model included all 12 dry site clones from 1981 to 1995, before human disturbance.

In Hunter & Price (1998), we suggested that autocorrelation in abiotic (precipitation) variables could generate spurious detection of delayed density dependence in time-series analysis of *E. lasiolepis* populations. We investigated that again here by removing both winter precipitation and PDSI from the three autoregressive models (above). Models with precipitation or drought included were always the most parsimonious using the AIC_c values (Results). We reasoned that, if delayed density dependence appeared significant in models without abiotic variables, but disappeared from models with abiotic variables, the apparent delayed density dependence was spurious (Jiang & Shao 2003).

To study the extent to which populations on all 15 clones correlated over the longer term of decades, we used Pearson's product-moment correlation coefficient (Sokal & Rohlf 1995). Synchronous increases and decreases in the *Euura* population among clones would indicate a driving variable in common. Also, persistent differences among clones in gall density would indicate that the same kinds of factors were working over the long-term, be they innate qualities of the clone or the microhabitat in which clones grew.

To analyse sawfly performance factors contributing to differences in *E. lasiolepis* densities among clones within years, we used Pearson's product-moment correlation and simple linear regression (Sokal & Rohlf 1995). Different variables (e.g. sex ratio, gall abortion) were often estimated in different years, and different subsets of clones provided adequate data for analysis in some years, making multiple regression unfeasible.

Results

LATENT POPULATION DYNAMICS AND SYNCHRONY AMONG CLONES

The population dynamics of *E. lasiolepis* has shown low amplitude fluctuations over the course of 22 years (Fig. 1). Mean gall density in dry sites has remained in the 10 s and 100 s per 1000 shoots, varying over only two orders of magnitude, except in the last year, 2002, when the population decreased to a mean of only three galls per 1000 shoots. In wet sites mean gall densities remained in the 100 s and 1000 s until 1996 when a '100-year drought' (predicted to occur only once per century) seriously impacted willows and sawflies. Except for 1996, populations fluctuated only over two orders of magnitude in wet sites. In general, then, the populations met our initial criterion, and prediction, of varying over only two orders of magnitude, and deviations from this pattern were in response to serious drought.

Total winter precipitation immediately before the initiation of each new sawfly generation varied around the 100-year mean for the Flagstaff area until 1995, with high precipitation generally associated with subsequent increases in gall density, and low precipitation associated with decreases in gall density (Fig. 1). The most prominent example of this trend is the increased precipitation in the winters marked as 1990–93, paralleled by increasing populations over those years, with an additional increase in 1994, after a winter that received above average precipitation.

In contrast, an atypical trend in the weather began in the winter of 1996, with very low precipitation followed

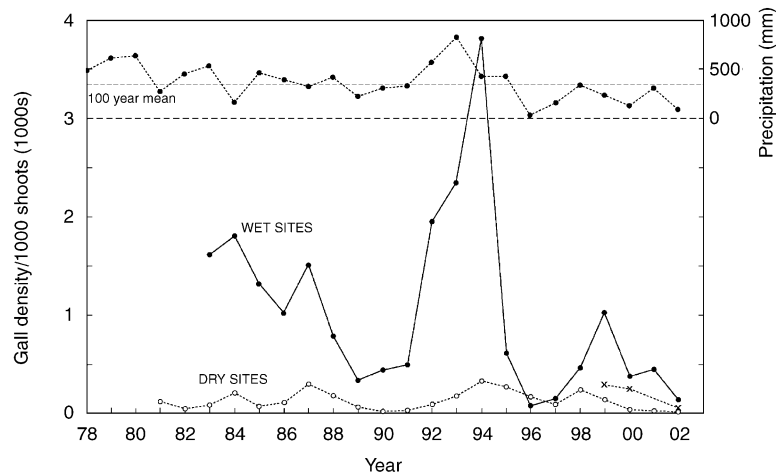


Fig. 1. Mean gall densities (in thousands) per 1000 shoots of *Euura lasiolepis* for three clones in wetter sites (1983–2002) and 12 clones in drier sites (1981–2002) in the Flagstaff area. The density relates to the sawfly generation initiated in May–June that year. Total precipitation from October to May, before peak willow growth, is plotted above, with precipitation relevant to the following sawfly generation plotted in the same year. The 100-year, October–May mean precipitation for the locality is provided showing that six of the last 7 years have received below the mean 100-year average (1996–2002). In the years 1999, 2000 and 2002, mean gall density estimates are provided for 73 willow clones distributed throughout the drainage (\times with dotted line). Winter precipitation is provided relevant to sawfly generations in 1978–80 to show conditions before sampling in the current study.

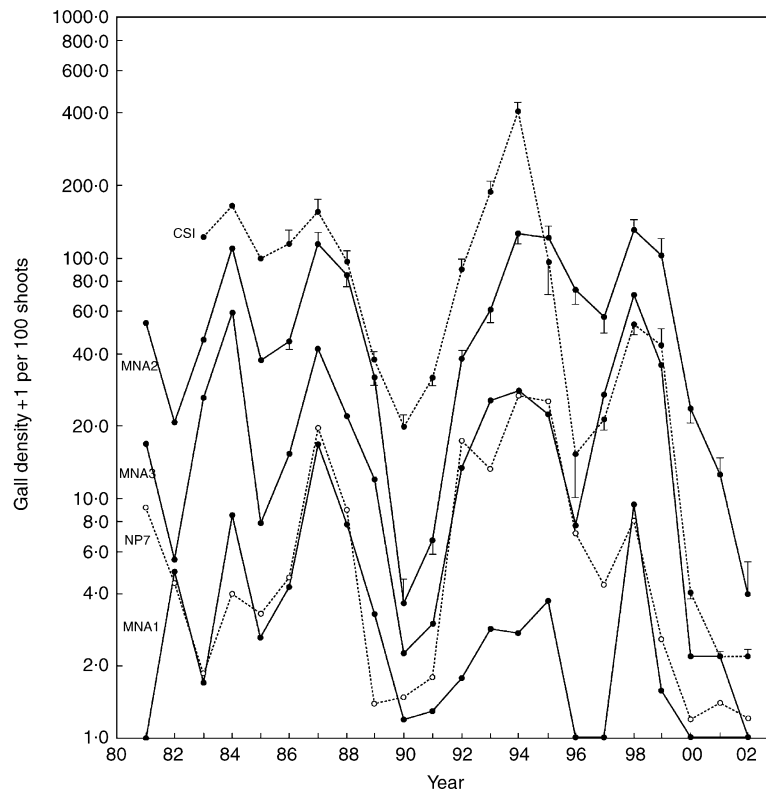


Fig. 2. Gall density +1 per 100 shoots (on a logarithmic scale) for selected clones illustrate a general pattern of synchrony among clones. MNA1, 2 and 3 are typical of others at the MNA site, NP7 represents clones at the NP site and CSI is characteristic of the wet site clones.

by additional years at, or below, mean precipitation (Fig. 1). Since 1998 in dry sites and 1999 in wet sites, sawfly populations have declined to the lowest levels recorded. The extent to which the 15 clones were representative of the drainage at large was tested on 73 clones distributed over the whole drainage, with the

evidence supporting their representative status (Fig. 1).

Gall density fluctuations on individual clones showed generally synchronous change (Fig. 2). Examples illustrated show synchrony between adjacent clones MNA1, 2 and 3, and Clone NP7, about 800 m downstream from the MNA clones, all in drier sites. Note that MNA1, 2

and 3 retain their relative gall densities throughout the 22 years with MNA2 having the highest densities, MNA3 with intermediate and MNA1 with the lowest densities. A clone at Coyote Spring, CS1, is also illustrated and was largely synchronous with the other clones. The same patterns were observed for clones not illustrated.

Correlations of gall density across all 15 clones in 1983 with gall densities in 1992 and 1993 were highly significant, accounting for 87% and 99% of the variance, respectively ($P < 0.01$). The correlation remained significant for the 1983–94 comparison ($r^2 = 0.86$, $P < 0.01$) suggesting that, over a 12-year period from 1983 to 1994, gall densities per clone on all clones tended to vary synchronously as shown in Fig. 2. (Were the clones further apart such that each supported a discrete population of sawflies, the Moran effect would be relevant here.) After peak populations in 1994, correlation coefficients declined as the relative magnitude of gall densities became more erratic with the drought, and as some clones were cut back or removed from 1996 to 2001.

TIME-SERIES ANALYSIS

In all cases, the most parsimonious (lowest AIC_c) models for *E. lasiolepis* populations included terms for recent and delayed effects of winter precipitation and/or drought (top of Table 1). High precipitation and low drought were associated with high densities of galls, with the effects of precipitation and drought persisting over 2 years (time-lag = 2, Table 1). These weather-based population models explained between 67 and 73% of population variance (Table 1). There was no evidence of delayed density dependence (lag = 2 or 3) in any of the best-fit models. For those gall populations on dry-site clones unaffected by human disturbance, there was evidence of rapid ($t - 1$) density dependence. This rapid feedback was not detected on either wet site clones, or on the shorter time-series for all dry-site clones (top of Table 1). The lack of delayed density dependence does not mean that sawflies are unaffected by resource abundance. Rather, it suggests that sawflies do not influence resource renewal which is driven primarily by water availability.

After removing the effects of precipitation and drought from the time-series models (bottom of Table 1), AIC_c values increased and r^2 values decreased, indicating poorer model fits. In each case, apparent delayed density dependence was now detected. Given that this apparent delayed density dependence disappeared with the inclusion of precipitation and drought data (top of Table 1), we consider it to be the spurious product of autocorrelation in the abiotic data (Jiang & Shao 2003).

Figure 3 illustrates the predictions of the time series models using parameters from Table 1 and real precipitation and drought data. Graphs show for: (Fig. 3a) the wet site clones; (Fig. 3b) the dry site clones that were unaffected by human disturbance; and (Fig. 3c) all dry site clones prior to human disturbance. Given

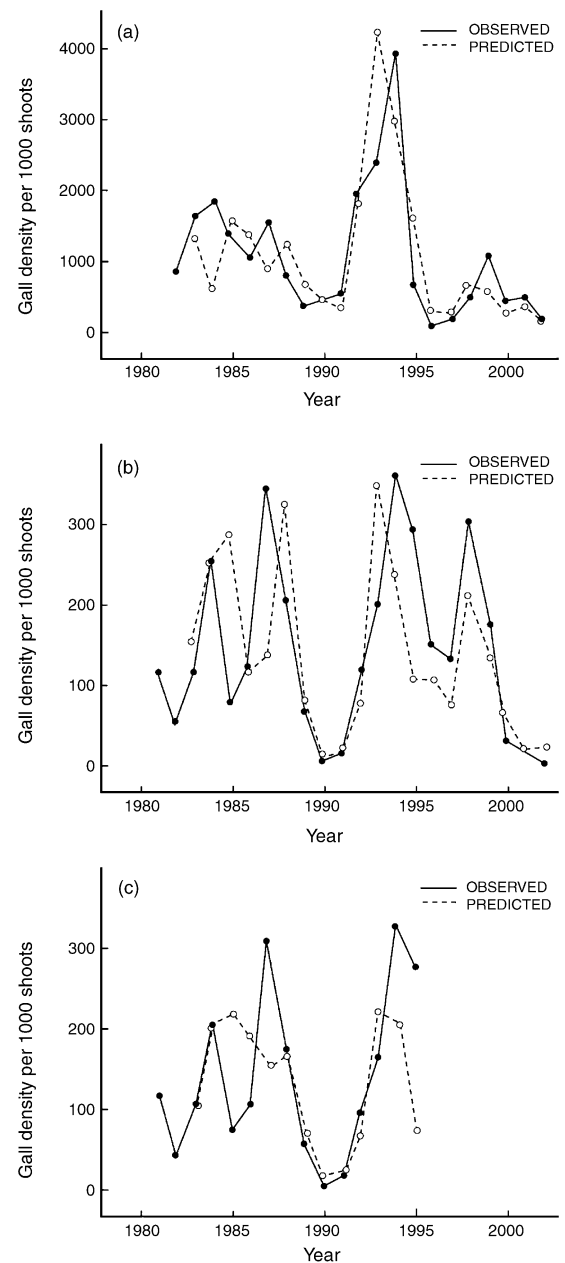


Fig. 3. Average gall densities of *Euura* observed (solid line) and predicted (dashed line) on (a) three wet-site clones from 1982 to 2002, (b) eight dry-site clones unaffected by human disturbance from 1981 to 2002, and (c) all 12 dry-site clones from 1981 to 1995.

that the models were derived from sampling data, it is not surprising that the predictions fit the sampling data quite well. Predicted population peaks sometimes occur before and sometimes after peak gall densities in the real data (e.g. Fig. 3b), suggesting that there exist unrecognized factors that influence gall dynamics. However, the analyses presented in Table 1 suggest that delayed density dependence does not contribute to unexplained population variance. We conclude that precipitation and drought, by influencing the soil moisture available for willow growth, have the greatest impact on sawfly populations from the bottom up.

Table 2. Regression equations for variables used in the analysis of within and between generations of sawflies across 15 willow clones. Numbers (*n*) below 15 clones indicate inadequate sample sizes on some clones

Generation	<i>n</i> ¹	<i>r</i>	<i>P</i>	<i>r</i> ²	Intercept	Slope
% Aborted (<i>X</i>) vs. % survival within generations (<i>Y</i>)						
1983	15	-0.86	< 0.01	0.75	83.73	-0.99
1984	15	-0.65	< 0.01	0.42	46.92	-0.53
1985	15	-0.71	< 0.01	0.50	51.74	-0.50
% Aborted + larval death (<i>X</i>) vs. % survival (<i>Y</i>)						
1983	15	-0.94	< 0.01	0.88	91.37	-0.98
1984	15	-0.90	< 0.01	0.80	63.66	-0.66
1985	15	-0.89	< 0.01	0.79	76.53	-0.79
% Survival (<i>X</i>) vs. gall density in next generation (<i>Y</i>). Significant regressions only						
1983	15	0.74	< 0.01	0.54	-568.41	26.74
1984	15	0.62	< 0.05	0.39	-50.81	19.97
1986	12	0.83	< 0.01	0.69	-205.35	15.59
1988	14	0.85	< 0.01	0.73	28.97	7.75
1989	7	0.87	< 0.01	0.76	-138.70	31.19

DIFFERENCES IN POPULATION DENSITY AMONG CLONES WITHIN YEARS

Clones in wetter sites generally supported higher densities of *Euura* than did clones in drier sites (Figs 1 and 2). The availability of water to clones is therefore capable of generating major differences in gall densities among clones. Part of these differences was explained by the mean age of ramets per clone, and the mean shoot length per clone. Higher water availability resulted in a higher density of younger ramets, producing in general a younger mean age of ramets per clone and longer mean shoot lengths than in dry-site clones. In 1986, mean ramet age accounted for 61% of the variance in gall density per clone across all wild clones ($n = 15$, $r = -0.78$, $P < 0.01$, $Y_{(\text{galls}/1000 \text{ shoots})} = 1623.91 - 148.68X_{(\text{clone age in years})}$). When NP8 (which had most galls removed by grasshopper damage in 1981) was excluded from the regression, the regression accounted for 69% of the variance ($n = 14$, $r = 0.83$, $P < 0.01$, $Y = 1789.58 - 163.29X$). Mean shoot length was also a good predictor of gall density ($n = 15$, $r = 0.84$, $P < 0.01$, $r^2 = 0.76$, $Y_{(\text{galls}/1000 \text{ shoots})} = -343.93 + 3.71X_{(\text{mean shoot length in mm})}$). When NP8 was excluded from the regression, 91% of the variance was accounted for ($n = 14$, $r = 0.95$, $P < 0.01$, $Y = 3.71X - 343.93$). Mean ramet age and mean shoot length were negatively correlated, as explained above ($n = 15$, $r = -0.87$, $P < 0.01$, $r^2 = 0.76$, $Y_{(\text{mean shoot length, mm})} = 600.31 - 46.35X_{(\text{mean ramet age in years})}$). Thus, most of the differences in gall density among clones were accounted for by clonal phenotypic variation in the form of ramet age and shoot growth.

The contribution to phenotypic variation made by largely genotypic effects, as estimated by the common-garden experiment, were not significant in the majority of cases tested. None of the variables measured on experimental plants helped to explain the variation in gall density on wild clones. Mean shoot length on experimental plants did not help to explain gall densities on experimental plants ($n = 15$, $r = -0.17$, NS), or on wild plants ($n = 15$, $r = -0.09$, NS). Nor did mean

shoot length account for survival on experimental plants ($n = 15$, $r = 0.30$, NS), or on wild clones ($n = 13$, $r = -0.11$, NS). At the genotypic level, all plants were attractive to *Euura* females, and all plants allowed sufficient survival for rapid population growth.

The current study supports results in Craig *et al.* (1989) that an ovipositional preference for long shoots correlated with higher larval survival on such shoots. In 1986, mean shoot length on wild clones accounted for 36% of survival on those clones ($n = 13$, $r = 0.60$, $P < 0.05$, $Y_{(\% \text{ survival})} = 23.09 + 0.16X_{(\text{mean shoot length in mm})}$). The data available from dissection of galls in 1983, 1984 and 1985 showed consistent and negative, significant relationships between percentage of galls with aborted oviposition and percentage survival (Table 2). Aborted oviposition attempts were the highest cause of lost potentials in a cohort in every year in which data were sufficient for study. This plant-resistance effect was compounded by subsequent larval death, also attributed to plant resistance, with aborted ovipositions plus larval death accounting for most variation in survival across clones within the years 1983–85 (Table 2). Survival in one generation was a significant predictor of population density in the following generation in five of 8 years for which adequate data were available, from the 1983 to the 1990 generations (Table 2).

Alternative mechanistic explanations for gall density variation across clones within years included differences in gall weight and larval survival, larval weight, adult sawfly sex ratio, and concentrations of the ovipositional stimulant, tremulacin. None provided significant explanatory power in any of the years tested.

Discussion

The nature of population dynamics of this species was predicted based on an evolutionary hypothesis. The Phylogenetic Constraints Hypothesis was developed based on detailed studies of evolved traits such as life history and behaviour. After observing 8 years of gall population data in dry-site clones (1980–87), in

conjunction with comparative studies on related species (Price 2003), we predicted relatively low levels of population change, and the population has retained its latent characteristics for the subsequent 15 years (1988–2002). Populations have not erupted beyond two orders of magnitude in density, while outbreak species frequently reach densities three to five orders of magnitude above their lowest levels.

We noted positive responses of *Euura* sawflies to vigorous plants after high winter precipitation (Price & Clancy 1986) enabling the prediction that plant vigour, stimulated by winter precipitation, favoured sawfly populations. Therefore, precipitation from October–May, before maximum growth rate of willows, would act as a good predictor variable for modelling purposes. This prediction has been substantiated in this study. We are also able to predict the onset of population increases or declines based on previous precipitation history. Studies of this and related sawflies prompted the proposal of the Plant Vigor Hypothesis, which argued that many herbivore species exploited vigorous plants or modules more frequently than stressed plants, and immatures survived better on or in vigorous plants (Price 1991).

Earlier studies also showed a delayed effect of precipitation in one sawfly generation on the next generation (Price & Clancy 1986). The immediate effect of low winter precipitation was a decline in number and length of new shoots, so oviposition was reduced. The delayed effect operated through increased aborted ovipositions, reduced survival, and consequently a lower population density in the next generation, even though willow growth may have recovered. The evaluation of plant quality and quantity traits is crucial in the understanding of population variation of this sawfly and should promote more concern for, and documentation of, resource variation in studies that would otherwise concentrate only on top-down effects on herbivores.

Results of time-series analysis show that changes in gall density are driven primarily by an exogenous variable (precipitation) that has both immediate and delayed effects upon gall populations. In the absence of climate data, time-series models detect spurious delayed density dependence (Table 1) that disappears when effects of climate are incorporated. This supports previous work in this system and others, which suggests that abiotic variables can generate such spurious patterns of delayed density dependence (Hunter & Price 1998, 2000; Jiang & Shao 2003).

We only detected rapid density dependence operating upon gall populations on the dry-site clones that were unaffected by human disturbance (Table 1). We suggest that, given the close association between gall density and precipitation/drought documented above, gall densities in most cases are more closely related to current and previous weather than to previous population density. The strong effects of precipitation on gall density may generally decouple current population density from that in the following year. The detection

of rapid density dependence from the longest dry-site time-series suggests that it has a weak effect that is only detected with many years of observation on clones with low resource availability.

We showed in earlier analyses, coupled with field observations and experiments, that natural enemies were unimportant in *E. lasiolepis* population dynamics (Hunter & Price 1998). Top-down effects on *Euura* were weak while bottom-up effects were very strong. Teasing apart the mechanisms of population change requires experiments (e.g. Krebs 1995), which in the case of *Euura*, have supported bottom-up dominance in the system. Experiments relevant to these arguments on *Euura* are listed in Price (2003).

We now have a strongly mechanistic, experimentally supported, scenario for the population dynamics of the arroyo willow stem-galling sawfly. High winter precipitation promotes willow growth in the following spring, with more and longer shoots produced (Price & Clancy 1986). Females oviposit into longer shoots preferentially, and larvae survive better in longer shoots. There is a strong ovipositional preference and larval performance linkage (Craig *et al.* 1989). Survival is higher in longer shoots and after higher precipitation because aborted oviposition attempts are reduced. Females lay more eggs per gall on average and withhold fewer, and newly hatched larvae die less frequently. Early larval death is correlated with high osmotic potential in galls, which we assume will reduce the ability of larvae to absorb nutrients from ingested cellular material (cf. data in Price 2003). Thus, high precipitation results in higher numbers of galls and higher survival within galls resulting in higher populations in the next generation. A delayed increase in population density ($t + 1$ generation) results, in addition to the immediate increase in generation t , after high winter precipitation. These effects can be observed across the landscape where soil availability varies and where ramet age and plant vigour vary. Phenotypic variation of living plant resources explains the distribution, abundance and population dynamics of this sawfly. Top-down effects of natural enemies are weak, and members of the third trophic level depend more on sawfly abundance than they influence their dynamics. Bottom-up influences are of paramount importance. We predict that the relationship between plant vigour and sawfly population responses will remain the same throughout the ranges of the host plant and sawfly, even in wetter areas because sawflies will always favour the longest shoots available (Craig *et al.* 1989).

Predictions from the Phylogenetic Constraints Hypothesis have been expanded to other herbivores that rely on high-quality plant modules as resources: rapidly growing large shoots, large leaves, flower heads, fruits and large cones (Price 2003). All are likely to be influenced by weather and local growing conditions such as soil moisture. The more favourable the weather, the better the plant growth and productivity, which favours many kinds of insect herbivores: the Plant Vigor Hypothesis

(Price 1991). Under such conditions natural enemies are likely to have a weak top-down impact on dynamics because plant quality is so important, and large modules offer effective protection. This hypothesis offers a broadly comparative approach with an emphasis on bottom-up host plant effects and the evolved responses of herbivores to plant quality. This unites population dynamics with the evolutionary synthesis and provides a more comprehensive understanding of the field than a purely ecological approach.

Acknowledgements

For sage advice on earlier versions of this paper we are most grateful to Naomi Cappuccino, Jessica Hellmann, Alison Hunter, Judith Myers, Dan Quiring and Christer Solbreck. Research by the Price group was supported financially from NSF grants DEB-7816152, DEB-8021754, BSR-83144594, BSR-8705302, BSR-8715090, BSR-9020317, DEB-9318188, and DEB-9527522. MDH was supported by NSF grants DEB-9906366 and DEB-0342750.

References

- Craig, T.P., Price, P.W. & Itami, J.K. (1986) Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology*, **67**, 419–425.
- Craig, T.P., Itami, J.K. & Price, P.W. (1989) A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. *Ecology*, **70**, 1691–1699.
- Forchhammer, M.C., Stenseth, N.C., Post, E. & Langvatn, R. (1998) Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proceedings of the Royal Society of London, Series B*, **265**, 341–350.
- Fritz, R.S. & Price, P.W. (1988) Genetic variation among plants and insect community structure: willows and sawflies. *Ecology*, **69**, 845–856.
- Hunter, M.D. & Price, P.W. (1998) Cycles in insect populations: Delayed density dependence or exogenous driving variables? *Ecological Entomology*, **23**, 216–222.
- Hunter, M.D. & Price, P.W. (2000) Detecting cycles and delayed density dependence: a reply to Turchin and Berryman. *Ecological Entomology*, **25**, 122–124.
- Jiang, L. & Shao, N. (2003) Autocorrelated exogenous factors and the detection of delayed density dependence. *Ecology*, **84**, 2280–2213.
- Krebs, C.J. (1995) Two paradigms of population regulation. *Wildlife Research*, **22**, 1–10.
- McGeoch, M.A. & Price, P.W. (2004) Spatial abundance structures in an assemblage of gall-forming sawflies. *Journal of Animal Ecology*, **73**, 506–516.
- Morris, R.F. (1955) The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. *Canadian Journal of Zoology*, **33**, 225–294.
- Palmer, W.C. (1965) Meteorological drought. *United States Department of Commerce Weather Bureau Research Paper No.*, **45**, 1–58.
- Price, P.W. (1991) The plant vigor hypothesis and herbivore attack. *Oikos*, **62**, 244–251.
- Price, P.W. (2003) *Macroevolutionary Theory on Macroecological Patterns*. Cambridge University Press, Cambridge.
- Price, P.W. & Clancy, K.M. (1986) Multiple effects of precipitation on *Salix lasiolepis* and populations of the stem-galling sawfly, *Euura lasiolepis*. *Ecological Research*, **1**, 1–14.
- Price, P.W. & Craig, T.P. (1984) Life history, phenology, and survivorship of a stem-galling sawfly, *Euura lasiolepis*, in northern Arizona. *Annals of the Entomological Society of America*, **77**, 712–719.
- Royama, T. (1992) *Analytical Population Dynamics*. Chapman & Hall, London.
- SAS Institute (2001) *SAS Version 8.1 for Windows*. SAS Institute, Cary, NC.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman, San Francisco.
- Stenseth, N.C., Bjornstad, O.N. & Falck, W. (1996) Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. *Proceedings of the Royal Society of London, Series B*, **263**, 1423–1435.
- Trotter, T.R., Cobb, N.S. & Whitham, T.G. (2002) Herbivory, plant resistance, and climate in the tree ring record: Interactions distort climatic reconstructions. *Proceedings of the National Academy of Sciences, USA*, **99**, 10197–10202.

Received 29 October 2004; accepted 15 March 2005