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Mites attack males of the sexually polymorphic tree *Acer opalus* more harmfully and more often

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Summary

1. Theory predicts that plants that achieve fitness more through male function may be less tolerant of herbivory than those that achieve fitness through the female function. We tested this hypothesis by measuring the degree of infection and damage inflicted by the gall-forming eriophyid mite *Aceria macrorhynchus* on three different sexual morphs (males, protandrous bisexuals and protogynous bisexuals) of the Mediterranean tree *Acer opalus*.

2. The dependence of each morph on male function, estimated by registering gender changes over 5 years and quantifying male function, decreased in the order males, protandrous, protogynous.

3. The same decreasing order was found in the degree of gall infection produced by the mite, and in the reduction of photosynthetic rates and shoot growth, but not in the carbon-isotope discrimination caused by the mites.

4. Mites attack the morphs of *A. opalus* that rely more on the male function more often and more harmfully than they do other morphs. Male-biased herbivory is a selective force that could have been driving the separation of sexes in the genus *Acer*.

Key-words: *Acer*, herbivory, maleness, photosynthesis

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Introduction

It is well known that male plants are preferred to female plants by herbivores (Boecklen & Hoffman 1993; Ågren *et al*. 1999; Ashman 2002). A recent review of sexual differences in herbivory showed that male plants were more heavily utilized than females by different herbivores in 17 out of 21dioecious species (Ågren *et al*. 1999). Male-biased herbivory may be the result of differential resource investment because females allocate more energy to reproduction and defence, whereas males invest more in vegetative growth (Putwain & Harper 1972; Boecklen *et al*. 1990). Gender-specific differences in growth, survival, reproductive output, resource allocation and physiology have been described for some dioecious plant species, although the evidence is still too scarce to reach general conclusions about sexual dimorphism in physiology and morphology (Dawson & Geber 1999; Obeso 2002). The only general conclusion, although still weak, is that males are usually more resource-use efficient than females (Dawson & Geber 1999). These intersexual differences, whether positive or negative, may influence the outcome of the interaction between herbivores and plants.

Although plant–herbivore interactions become more complex when host species have more than two sexual morphs, male-biased herbivory also seems to be common in sexually polymorphic plants, where herbivores attack more often and cause more harm to the pollen-bearing morphs (Ashman 2002). Because the risk of herbivore damage appears to increase with increasing allocation to male function, Ashman (2002) has proposed that plants that increase fitness via male function may be less tolerant than those that increase fitness via female function. The gender continuum of the morphs of sexually polymorphic species provides a way to test Ashman's hypothesis of increasing herbivory with increasing plant maleness.

The among-year consistency of male-biased herbivory on sexually dimorphic or polymorphic plants has rarely been studied (but see Ågren 1987), although temporal variation in damage may be caused by among-year fluctuations in the herbivore and plant populations (fluctuations in herbivore population size and phenology, leaf concentrations of nutrient and chemical defences, etc.; Ågren *et al*. 1999). Similarly, temporal fluctuations in gender may also occur in sexually polymorphic species (Barker *et al*. 1982; Dommée *et al*. 1990) and therefore alter the plant–herbivore interaction.

To test for male-biased herbivory and its interannual consistency in a sexually polymorphic species, we investigated the tree species *Acer opalus* Boiss. (Aceraceae)

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which has three different sexual morphs: males, bisexuals with a male-first flowering sequence (protandrous), and bisexuals with a female-first flowering sequence (protogynous) (de Jong 1976). These three morphs are expected to form a decreasing continuum in maleness, from males to protandrous to protogynous individuals, as in the case of the close relative *Acer japonicum* (Sato 2002).

Acer opalus is attacked by the eriophyid mite *Aceria macrorhynchus* Nalepa, which produces galls on the leaves. Eriophyid mites are a diverse group of host-specific plant-feeders, and their interaction with plants is so ancient and species-specific that an evolutionary arms race may have occurred in which plants have evolved defences, and mites adaptations in response to those defences (Oldfield 1996; Sabelis & Bruin 1996). To study such an old and strong interaction it is important to obtain greater temporal information than is possible in a 1-year study. Therefore we followed gender constancy and sexual morph-biased herbivory over 5 years. We estimated the investment of each morph in male function by assessing maleness and checking interannual gender constancy. Based on this classification, we tested if mite herbivory is more frequent in the genders that invest more in the male function, and if this pattern is consistent across several years. We also tested, under the hypothesis that males invest less in defence (Putwain & Harper 1972; Boecklen *et al*. 1990), if the impact of the mite galls in vegetative traits (shoot growth and leaf size) and physiological traits (photosynthetic rates and carbon isotope discrimination as a long-term integrator of ecophysiological processes) is greater in the morphs that have a larger investment in male function.

Methods

STUDY SITE AND ORGANISMS

The study was carried out in La Font Roja Natural Park (Alcoi, eastern Spain) at 1350 m a.s.l. The climate is mediterranean with mean annual rainfall 825 mm and mean annual temperature 11·6 °C. Vegetation comprised a mixed wood of evergreen oaks (*Quercus ilex*) and deciduous trees such as *Acer opalus*, *Fraxinus ornus*, *Quercus faginea* and *Sorbus aria*. More details are given by Laguna & García (1988).

Aceria macrorhynchus is an eriophyid mite that causes gall formation, which hibernates in bark crevices or the surrounding vegetation. In the spring founder females move to expanding leaves, pierce them and start to suck the sap. As a reaction, the injured cells multiply intensively forming a red, pouch gall (Rohfritsch 1992). Females oviposit within the gall and the subsequent development of juveniles stimulates gall maturation. In June and July the galls are full of mites, and in August mites exit the galls to locate a place to hibernate until the next spring (Castagnoli 1996; Vaneckova-Skuhrava 1996a; J. L. Nieves, personal communication).

Acer opalus (Aceraceae) is a deciduous, small tree (up to 5 m tall in the study area) with monopodic growth and opposite foliage. The leaves are five-lobed and the inflorescences have eight to 22 drooping, yellow, functionally unisexual flowers (Gleiser *et al*. 2004). Fruits are samaras with divergent wings (Van Gelderen *et al*. 1994). Three different sexual morphs (males, protandrous bisexuals and protogynous bisexuals) have been described by de Jong (1976).

MORPH-BIASED HERBIVORY

We marked all the trees (44 individuals) along a 2000 m linear transect on April 1999, and morph type was determined in spring by direct observation of flowers. The same trees were also visited in the spring of each of the following 4 years to estimate gender constancy among years.

To estimate the maleness of each morph, we used the equation provided by Sato (2002), which consists of a weighted proportion of the staminate to the total number (staminate plus pistillate) of flowers in which the weight is the mean dry mass of a pistillate or staminate flower. We quantified the average proportion of staminate flowers on each gender over 2 years in two to five marked inflorescences per tree. To reproduce the maleness continuum necessary to test the hypothesis relating herbivory to maleness, sexual morphs were coded with three integers 1–3 (morph coded 1 had greater maleness than morphs coded 2 or 3). Thus morph was considered an ordered factor to which a linear polynomial contrast (–1, 0, +1) was fitted to test the hypothesis of the existence of a linear trend among the three morphs.

A semiquantitative leaf gall index was estimated for the same trees in May–June of each year. Galls on leaves from the entire canopy were located and given a 0–3 index (0, no galled leaves; 1, 0–1% of leaves galled; 2, 1–10% of leaves galled; 3, >10% of leaves galled). The maximum number of galled leaves on a tree was usually ≤30%. This index reflected the real percentage of the galled leaves in the tree (Spearman's $r = 0{\cdot}95$; df = 44; $P < 0{\cdot}001$ for 2001; $r = 0{\cdot}96$; df = 44; $P < 0{\cdot}001$ for 2002) and followed a Poisson distribution as indicated by the Kolmogorov–Smirnov test ($Z = 0{\cdot}94$; $P = 0{\cdot}36$; $n = 220$) and the increase in variance with the mean of the groups (morphs).

Tree selection by mites was first analysed by contrasting the frequencies of galled *vs* ungalled trees of each sexual morph during the 5 years using a log-linear model under the null hypothesis of random tree selection. Subsequently we tested for differences in the leaf-gall index across the sexual morphs during the 5 years using a repeated-measures analysis by means of a generalized estimation equation (GEE) with an autoregressive of order 1 covariance structure and a Poisson distribution of errors. Generalized estimation equations are methods of parameter estimation for correlated data, as in the present case, in which data have been collected successively on the same individuals (Liang & Zeger 1986). The GEEPACK package of the R statistical software was used to fit these models (Ihaka & Gentleman 1996).

MORPH-BIASED DAMAGE

Vegetative traits

The shoot length of the current year's growth was measured with a digital calliper for all galled individuals (19 males, nine protandrous and seven protogynous) in midsummer 2000. We measured the length of three to five shoots with galled leaves, and that of three to five shoots with ungalled leaves. To determine if shoot growth differed among morphs and with galling, a generalized linear mixed model via penalized quasi-likelihood with Gaussian distribution was constructed with shoot length (log-transformed for normality) as the dependent variable, galling and gender as fixed factors, and individual as random factor. As this study mainly focused on galling and gender effects we did not consider covariance parameter estimates and significance tests associated with random effects in these models, although it must be noted that significant individual variation usually exists (see Herrera 2000 for a similar procedure). These models were run in the glmmPQL procedure of the MASS library on the R statistical package (Ihaka & Gentleman 1996; Venables & Ripley 2002).

Mean leaf size was measured in all galled individuals (17 males, nine protandrous and nine protogynous) in midsummer 2002. Ten ungalled leaves and 2–10 galled leaves for each tree were collected from the whole perimeter of the canopy in June 2002 and the leaf area was estimated using the Matrox Inspector 2·1 imaging software (Matrox Electronic Systems Ltd, Canada). Sample size of galled leaves varied among trees because depended on the amount of galling on each tree (i.e. by definition, few galled leaves were available on trees with a galling index of 1). Leaf size was analysed statistically in the same way as shoot length.

Physiological traits

Leaf photosynthetic rates were measured in midsummer 2000 using a portable infrared gas-exchange system (HCM-1000, Walz, Germany) in 13 galled trees (five males, four protandrous and four protogynous). In each tree photosynthesis was measured in a galled leaf from a galled shoot, and in an ungalled leaf from an ungalled shoot. Two to four measurements were taken for each leaf, and the mean used in subsequent analyses. Each galled leaf that was measured had about 10 galls. We could not get similar photosynthetically active radiation (PAR) fluxes across trees (Kruskall–Wallis test, $\chi^2 = 33{\cdot}7$, df = 12, $P = 0{\cdot}01$), but it was possible within trees (Friedman's test, $\chi^2 = 0{\cdot}15$, df = 2, $P = 0{\cdot}93$). Consequently, to avoid confounding effects of PAR and sexual morph in photosynthesis, we did not compare absolute photosynthetic rates among individuals or morphs, but the variation in photosynthetic rate that mite galls produce in each individual. The variation in photosynthetic rate produced by galls was calculated as (photosynthetic rate of galled leaves from galled shoots/photosynthetic rate of ungalled leaves from ungalled shoots) × 100. Morph differences in this ratio were analysed using a generalized linear model following the Poisson distribution and the canonical link. The dispersion parameter was included in the model to account for overdispersion.

Leaf carbon isotope ($^{13}C/^{12}C$) discrimination (Δ) was used as a time-integrated measure of potential water use per unit C assimilated under the expectation that stressed leaves discriminate less against the heavy isotope (Rundel *et al.* 1988). Galled and ungalled leaves were collected at midsummer 2002 from 16 individuals (seven males, three protandrous and six protogynous). Samples were analysed by isotope ratio mass spectrometry (Carlo Erba 1108-Micromass CF-ISOCHROM, Micromass Ltd, Manchester, UK) in the Laboratorio de Isótopos Estables (Universidad Autónoma de Madrid, Spain). Analytical precision was ± 0·1‰. Δ was analysed statistically using the same models as for shoot length and leaf size.

Means and standard errors are shown throughout the text unless stated otherwise.

Results

MORPH-BIASED HERBIVORY

The study population comprised 45% males, 32% protogynous individuals and 23% protandrous individuals. This composition was marginally biased towards the two bisexual morphs ($\chi^2 = 3{\cdot}63$, df = 1, $P = 0{\cdot}057$).

Males and protogynous individuals did not change their gender during the 5 years, but most of the protandrous trees (seven out of 10) produced only male structures in some years. Maleness followed the expected decreasing trend from true males (1·00 ± 0·00) to protandrous (0·93 ± 0·03) to protogynous trees (0·48 ± 0·02) in 2002 (GLM polynomial contrast, –0·50 ± 0·03, $z = -15{\cdot}25$, $P << 0{\cdot}001$). Similar results were obtained in 2003 (1·00 ± 0·00 for males; 0·93 ± 0·04 for protandrous trees and 0·53 ± 0·02 for protogynous trees; GLM polynomial contrast –0·43 ± 0·03; $z = -11{\cdot}59$, $P << 0{\cdot}001$).

The log-linear model showed a significant association between galling and sexual morph ($\chi^2 = 10{\cdot}9$, df = 2, $P < 0{\cdot}01$) that was consistent across the 5 years (galling × morph × year interaction, $\chi^2 = 12{\cdot}9$, df = 8, $P > 0{\cdot}05$). This indicates that mites choose trees based on the sexual morph of the tree. Leaf galling significantly decreased among morphs, from males to protandrous to protogynous trees (GEE polynomial contrast 0·45 ± 0·09, Wald statistics = 24·29, $P << 0{\cdot}001$). This pattern was consistent across the 5 years (Fig. 1).

MORPH-BIASED DAMAGE

Vegetative traits

Shoots with galled leaves grew similarly to the control (ungalled) shoots (non-significant galling contrast, Table 1). The non-significant interaction shows that

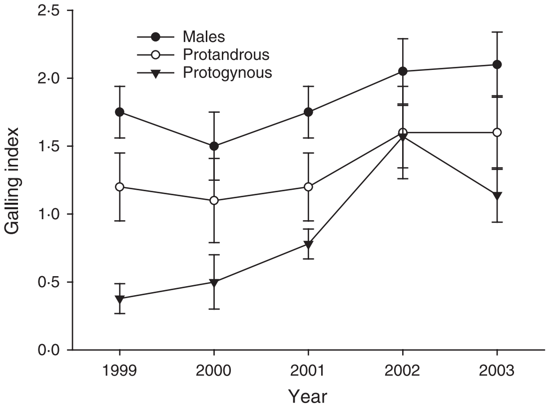

Fig. 1. Leaf-gall index (mean ± 1 SE) in the three different morphs of *Acer opalus* during the 5 years of the study. The index ranged from 0–3 (0, no galled leaves; 1, 0–1% of leaves galled; 2, 1–10% of leaves galled; 3, >10% of leaves galled).

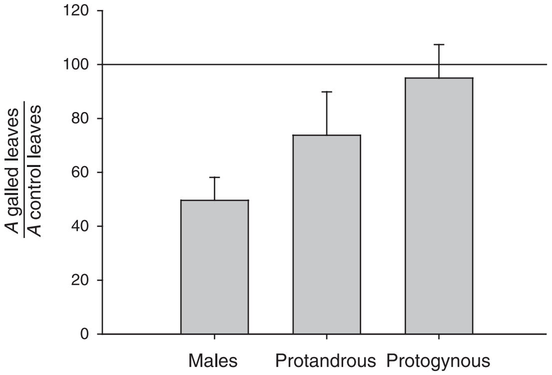

Fig. 2. Percentage of photosynthetic rate (mean ± 1 SE) from galled leaves on galled shoots relative to that in control leaves (ungalled leaves on ungalled shoots) in different morphs of *Acer opalus*. Percentages <100% indicate that galling reduced the photosynthetic rate, whereas values >100% show a positive effect of galling on photosynthetic rate.

this pattern was consistent across the morphs. However, the significant polynomial contrast indicates that shoot growth increased from males (15·7 ± 0·8 cm) to protandrous (21·0 ± 1·9 cm) to protogynous (25·4 ± 3·1 cm) individuals. Thus the galling effect is not detected when comparing galled *vs* control shoots within trees, but the most galled morph (males) have the least shoot growth. This effect at the tree level is supported by the negative association between galling and shoot growth: the larger the galling index of the tree, the smaller the shoot growth (linear contrast of galling −0·17 ± 0·07, $t = -2{\cdot}22$, $P < 0{\cdot}05$). This analysis at tree level also shows the trend of increasing shoot growth from males to protandrous to protogynous trees (polynomial contrast of morph 0·17 ± 0·04, $t = 4{\cdot}15$, $P < 0{\cdot}001$).

Mean surface area per leaf (12·4 ± 0·2 cm^2) was not affected by galling or morph (Table 1).

Physiological traits

Galling reduced the photosynthetic rates of leaves differently in the three morphs. This was because the photosynthetic rates of galled leaves relative to those of ungalled controls increased linearly across the morphs (GLM polynomial contrast 0·46 ± 0·17, $t = 2{\cdot}64$, $P < 0{\cdot}05$). Photosynthetic rates in galled leaves of male trees were reduced by 50% relative to the rates in ungalled control leaves. Relative photosynthetic rate was reduced slightly in protandrous trees, but was unaffected in protogynous individuals (Fig. 2).

Δ was significantly affected by galling, but in a similar way across morphs (Table 1). Galled leaves discriminated significantly less (18·7 ± 0·18‰) against ^{13}C than did control leaves (19·2 ± 0·19‰).

Discussion

The impact of eriophyid mites on their hosts can range from zero to rapid death (Royalty & Perring 1996). More usually, however, mites are mild ectoparasites that withdraw nutrients, change photosynthetic and growth rates, but leave the plant somatically intact (Welter 1989; Willson & O'Dowd 1990; Sabelis & Bruin 1996; Larson 1998). This study shows that this impact of the eryiophyid mite *A. macrorhynchus* depends on the sexual morph of the host plant, because these mites attack more often, and do more harm to, males of *A. opalus*.

Male-biased herbivory is common in many plants, and might be caused by sexual differences in the quality of plant tissues for herbivore consumption, the different herbivore performance on male and female plants, or both (Ågren *et al.* 1999). In the dioecious species *Acer*

Table 1. Generalized mixed linear models used to test the effects of galling and sexual morphs on shoot length (cm), leaf area (cm^2) and carbon isotope discrimination (Δ, ‰) in *Acer opalus*

	Shoot length			Leaf size			Δ		
Source	Estimate ± SE	df	*t*	Estimate ± SE	df	*t*	Estimate ± SE	df	*t*
Morph	0·12 ± 0·04	32	2·80**	0·02 ± 0·04	32	0·86ns	−0·44 ± 0·27	13	−1·59ns
Galling	0·004 ± 0·027	285	0·16ns	−0·02 ± 0·01	652	−1·53ns	−0·38 ± 0·16	13	−2·39*
Morph × galling	−0·01 ± 0·04	285	−0·25ns	0·04 ± 0·02	652	1·61ns	0·07 ± 0·23	13	0·32ns

ns, non-significant; *$P < 0{\cdot}05$; **$0{\cdot}05 > P > 0{\cdot}001$.
Morph was considered as an ordered factor following a decreasing maleness trend (male, protandrous, protogynous trees), thus the estimate for morph tests if the dependent variable follows that trend. The estimate for galling tests if the dependent variable is greater for galled than for control leaves.

negundo, male-biased herbivory occurs and sexual differences in leaf defence characters, such as phenolic compounds and total nitrogen content, were not detected, but leaves from female trees were tougher than those of males, suggesting that leaf toughness may be an important feature preventing herbivory in this species (Jing & Coley 1990). Alternatively, the male-biased preference of mites can be explained if mites perform better on males, which are usually more efficient in using resources (Dawson & Geber 1999). Mites can also perform better on male hosts because of the lack of fruits that would compete internally for resources (Larson & Whitham 1997).

Short-term data are unreliable if interannual variation in key aspects of plant–animal interactions largely determine the outcomes of those interactions (Herrera 1998). However, although 5 years is a small fraction of a tree's lifespan, the temporal consistency of the herbivory pattern found here suggests that our results are sufficiently reliable to conclude that mites exert a male-biased selective pressure on *A. opalus*.

The temporal dimension of our study also allows us to assess the extent to which each gender invests in male function, precluding the possibility of misassigning protandrous trees as males. By registering gender changes across years and quantifying the maleness of each morph, we determined that investment in male function decreases in the order: males, protandrous, protogynous. Thus, according to Ashman's (2002) hypothesis, tolerance of herbivory in *A. opalus* should also decrease in this order. This prediction was upheld for relative photosynthetic rate and shoot growth, but not for other physiological (Δ) or vegetative (leaf area) traits.

Mite galls reduced the photosynthetic rates of galled leaves by 29%. This result agrees qualitatively with studies on three other gall-formers (two aphids and an eriophyid mite on *Rhus glabra*, *Carya illioensi* and *Prunus serotina*, respectively) and contrasts with that found for a cynipid wasp on *Taraxacum officinale* (Andersen & Mizell 1987; Bagatto *et al*. 1996; Larson 1998). The effect of mite galls on *A. opalus* trees was also different across morphs. The reduction in relative photosynthetic rate also corresponded with the maleness continuum, being most severe for males (50%), intermediate (26%) for protandrous trees, and least for protogynous individuals (5%). This suggests that protogynous individuals are more tolerant of mite galls, in accordance with the general pattern of males being less well defended against herbivores (Putwain & Harper 1972; Boecklen *et al*. 1990).

Galling also reduced Δ in galled leaves. Smaller Δ can mean a larger water-use efficiency, other things being equal, but also smaller photosynthetic rates and a greater survival under long-term water shortage (Ehleringer 1993). Our Δ suggests that galled leaves were stressed by the mites that are competing for photoassimilates and nutrients, and altered their physiology as a consequence. However, caution is needed to interpret the results because Δ reduction, although statistically significant, was small (0·5‰), and the biological significance of such a small difference can be assessed only from further studies. The galling effect in Δ was similar across the three morphs. The lack of intersexual differences in Δ contrasts with those found in other species (Dawson & Ehleringer 1993; Retuerto *et al*. 2000; Verdú 2004; Verdú *et al*. 2004).

Leaf size was not affected by galling or morph. This was unexpected, as there is clear evidence of leaf-area reduction associated with attacks of eriophyid mites on two other *Acer* species: *Artacris* (= *Aceria*) *macrorhynchus* on *Acer pseudoplatanus* (Vaneckova-Skuhrava 1996b), and *Vasates quadripedes* on *Acer rubrum* (Mara 1995). However, a significant effect of galling and gender was detected in the other vegetative trait that we measured, shoot growth, which decreased with increasing galling. This effect was detected not at shoot level, but at tree level, suggesting that the negative effect of galling is produced not only in the galled shoot, but in the whole tree (Fay *et al*. 1993; Larson 1998). Because males were more galled, shoots grew less in males than in protogynous trees, with protandrous individuals in between. Alternatively the negative association between galling and shoot growth may be a consequence of mites selecting trees with lower shoot growth. Negative galling effects were also described for the eriophyid mite *Phytopus emarginatae* on its host plant *Prunus americana*, in which leaf galling decreased shoot length by 30–60% (Willson & O'Dowd 1990).

In summary, according to Ashman's hypothesis plants investing more in the male function are attacked more heavily by herbivores. Fossil galls of *A. macrorhynchus* on *Acer* trees have been found on Upper Miocene strata from eastern Spain (Diéguez *et al*. 1996), indicating that the interaction is very ancient, allowing an arms race between mites and plants to occur as Sabelis & Bruin (1996) suggest. If such an arms race has taken place, it has probably been different for each morph of the host. Finally, it should be noted that Ashman's (2002) hypothesis aims to explore male-biased herbivory as a selective pressure in the evolution from hermaphroditism to dioecy via gynodioecy. Male-biased herbivory has been found in the genus *Acer* (Jing & Coley 1990; this study), and the evolutionary path to dioecy is not through gynodioecy but through heterodichogamy (de Jong 1976). It would be valuable to test the role of male-biased herbivory in this evolutionary path as a possible selective force driving the separation of sexes.

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