Interactions between insect herbivores and a plant architectural dimorphism

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Summary

1 Plants possess many traits that influence their resistance to insect herbivores and thus can shape the structure of herbivore assemblages. While plant chemistry and structural defences have received the most attention, plant architecture may also be important. We examined patterns and consequences of insect herbivory for two distinct architectural morphs (prostrate or erect) of the perennial shrub, *Baccharis pilularis* (Asteraceae, coyote bush) in coastal California, USA.

2 For *B. pilularis*, differences in plant height, branch architecture and leaf size persisted in a common garden, consistent with previous evidence suggesting a genetic basis for dimorphism in plant architecture.

3 In both naturally occurring plants and in a common garden experiment, the composition of the herbivore assemblage varied strongly with plant architectural morph. Prostrate plants attracted higher densities of a gall-forming midge (*Rhopalomyia californica*, Diptera), whereas erect plants supported more moth galls (*Gnorimoschema baccharisella*, Lepidoptera) and experienced greater folivory. Furthermore, architectural traits were correlated with herbivory levels both across and within architectural morphs.

4 Prostrate plants had greater reproductive output (flowers or seeds) than erect plants in the presence of herbivores. However, under experimental reductions of herbivory spanning 40 months, the morphs had similar reproductive output, demonstrating that herbivores have the potential to act as agents of selection on the dimorphism in plant architecture.

5 These results confirm that intraspecific variation in plant traits can shape the composition of herbivore assemblages. Furthermore, in this system, herbivores alter the performance of the architectural morphs, suggesting a dynamic system of feedbacks between the population genetic and community levels.

Key-words: *Baccharis pilularis*, community genetics, genetic polymorphism, intraspecific genetic diversity, natural selection, parasitoid, tri-trophic interaction

Introduction

A recent area of emphasis within ecology attempts to link genetic variation at the population level with community dynamics (Neuhauser *et al.* 2003; Whitham *et al.* 2003). In this 'community genetics' framework, a number of studies have shown that genetic variation in plants can have strong structuring effects on higher trophic levels and entire communities. For example, different genotypic classes of hybridizing cottonwoods (*Populus fremontii* × *P. angustifolia*) support distinct arthropod assemblages (Wimp *et al.* 2005). Furthermore, the genetic effects reverberate to higher trophic levels, e.g. insectivorous birds (Bailey *et al.* 2006). However, the majority of this work has been carried out in interspecific hybrid systems (see also *Eucalyptus*, Dungey *et al.* 2000; *Salix*, Hochwender & Fritz 2004), where we might expect the merging of diverged genomes to produce particularly large phenotypic effects; in turn, large community-level effects could arise. A fair question is whether, and by what mechanisms, intraspecific genetic

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variation in plants has community-level effects of similar magnitude.

The emerging evidence suggests that intraspecific genetic variation in plants can also have strong community-level impacts (e.g. Fritz & Price 1988; Maddox & Root 1990; Cronin & Abrahamson 1999; Whitham *et al.* 2003, Johnson & Agrawal 2005). In *Oenothera biennis*, for example, plant genotypes differ by as much as twofold in arthropod diversity and threefold in arthropod abundance (Johnson & Agrawal 2005). However, it remains unclear how widely these patterns hold across different systems, and whether there are particular types of plant traits (e.g. chemical, phenological or morphological) that most frequently form the link between plant genotype and community structure. In addition, further information on how ecological communities can shape plant genetic variation, e.g. via natural selection on particular plant traits, is needed.

Here, we examine two potential effects of variation in plant traits, with an emphasis on architectural traits that may affect herbivores. From an ecological perspective, we ask whether intraspecific variation in plant traits affects the composition and abundance of insect herbivores. From an evolutionary perspective, we examine whether herbivores may be agents of selection on these same traits, with effects that feed back to influence plant fitness. We focus on architectural traits because, compared with secondary chemistry and structural defences (e.g. thorns, trichomes), they have received less attention for their roles in resistance to herbivory (Lawton 1983; Marquis 1992, 1996; Marquis & Whelan 1996; Casas & Djemai 2002; Hare 2002). Encouragingly, some studies do suggest strong effects of architecture on herbivore abundance (e.g. Price *et al.* 1995; Alonso & Herrera 1996; Haysom & Coulson 1998) or herbivore diversity (e.g. Fernandes *et al.* 2004; Price *et al.* 2004). For example, less overlap between leaves of white oak reduced the abundance of caterpillars that tie leaves together to construct shelters (Marquis *et al.* 2002). Plant architecture may also impact herbivores indirectly, via architectural effects on densities of predators or parasitoids (Price *et al.* 1980; Andow & Prokrym 1990; Grevstad & Klepetka 1992; Clark & Messina 1998; Cloyd & Sadof 2000; Whelan 2001; Kaitaniemi *et al.* 2004; Langellotto & Denno 2004). For example, a simple mutation conferring leaflessness in peas increased ladybird beetle control over aphid population growth compared with that on wild-type peas (Kareiva & Sahakian 1990).

The dioecious perennial shrub, *Baccharis pilularis* De Candolle (Asteraceae, coyote brush), grows sympatrically as two distinct architectural forms in coastal California: an erect morph (*c.* 1–4 m tall, formerly classified as subspecies *B. p. consanguinea*) and a prostrate morph (*c.* 0.1–0.2 m tall, formerly *B. p. pilularis* (Munz & Keck 1973), Figure S1 in Supplementary Material). The conspicuous variation in architecture of *B. pilularis* provides a tractable system for examining how intraspecific variation in plant traits affects the composition of

the herbivore assemblage and whether these effects feed back to influence plant fitness. Both architectural morphs are attacked by a gall-forming midge, *Rhopalomyia californica*, a gall-forming moth, *Gnorimoschema baccharisella*, and several folivores (see Fig. S1). Differences in morphology could affect herbivores directly or indirect effects may occur, for example if traits alter competitive interactions among the herbivore species. In addition, one of these herbivores (*R. californica*) is commonly parasitized by wasps (Force 1970, 1974; Hopper 1984; Briggs 1993), suggesting the possibility that plant traits could enhance wasp attack on midges and indirectly reduce midge success. To examine these issues, we addressed the following questions. (i) Which architectural traits differ between the two morphs? (ii) Do morphs experience differential attack by herbivores? (iii) Do correlations exist between specific morphological traits and levels of herbivory, and are these consistent both within and across the two morphs? (iv) Does parasitism of the midge differ between architectural morphs? (v) Do herbivores alter the relative performance of architectural morphs?

Methods

STUDY SYSTEM

The two architectural morphs of *Baccharis pilularis* grow sympatrically in coastal California, USA. Architectural traits are commonly heritable in plants (Kareiva & Sahakian 1990; Teixeira *et al.* 1999; Okogbenin & Fregene 2003; Bailey *et al.* 2004), and several lines of prior evidence support the hypothesis that architectural variation in *B. pilularis* has a genetic basis. First, hybridization of the prostrate morph of *B. pilularis* with the strictly erect species, *B. sarothroides*, produced both upright and prostrate F1 progeny (Thompson *et al.* 1995). Secondly, the prostrate morph of *B. pilularis* is widely used in landscaping and retains its short stature across diverse environments (Ehler 1982). Finally, progeny of a single architectural morph segregated into both erect and prostrate morphs when grown in a glasshouse. Seeds from erect parents produced on average 83% erect and 17% prostrate progeny, while seeds from prostrate parents produced on average 54% prostrate and 46% erect progeny (using 15–20 parents per morph with an average of four progeny per parent, J. A. Rudgers & K. D. Whitney, unpublished data).

Experimental work was conducted at the University of California-Davis Bodega Marine Reserve (BMR) in Bodega Bay, California, USA (38°19′ N, 123°04′ W). In this coastal dune community, *B. pilularis*, *Ammophila arenaria* (Poaceae) and *Lupinus arboreus* (Fabaceae) dominated the plant assemblage (Rudgers & Maron 2003). The two architectural morphs of *B. pilularis* accounted for similar percentage cover at this site (prostrate = 13%, erect = 16%, χ^2 test for goodness of fit = 0.01, $P = 0.9$), as estimated along nine 30-m transects (11–12 July 2001). In addition, plant gender in

this dioecious species was independent of architectural morph (erect: male = 60% of plants, female = 40%; prostrate: male = 44%, female = 56%; χ^2 test of independence between gender and architecture, $\chi^2 = 1.3$; $P = 0.3$, $n = 25$ plants per morph).

Several insect herbivores attack *B. pilularis*. A midge, *Rhopalomyia californica* Felt (Diptera, Cecidomyiidae), typically creates galls on the active, terminal buds (Tilden 1951a, 1951b; Figure S1A). Midge galls may contain from 1 to > 100 larvae (Briggs 1993), and midges complete multiple, overlapping generations with a development time of 30–70 days (Doutt 1961; Briggs & Latto 1996). A moth, *Gnorimoschema baccharisella* Busck (Gelechiidae), forms galls in the mid-sections of stems (one larva per gall), completing only a single generation per year (Tilden 1951b; Figure S1B). Folivores include *Trirhabda flavolimbata* (Coleoptera), slugs and, less commonly, an unidentified caterpillar (Tortricidae: Lepidoptera).

Parasitoid wasps are a major source of midge mortality, parasitizing 40–80% of midges (Force 1970, 1974; Ehler 1982; Hopper 1984; Briggs 1993; Briggs & Latto 1996). Fourteen species of wasp can attack the midge, but six species dominated the parasitoid assemblage at BMR: *Eupelmus inyoensis* Girault (Eupelmidae), *Mesopolobus* sp. (Pteromalidae), *Platygaster californica* Ashmead (Platygasteridae), *Torymus baccharidis* Huber (Torymidae), *Torymus koelbelei* Huber (Torymidae) and *Zatropis capitis* Burks (Pteromalidae).

COMMON GARDEN EXPERIMENT

We established a common garden experiment at BMR to control for effects of environmental variation on plant architecture. The common garden occupied a 45×60 m grid in the dunes. Plots of 1 m² were arranged along 15 60-m-long transects. Plots were spaced a minimum of 3 m apart, with a total of 150 plots. Plots were cleared of above-ground vegetation during 2–3 July 1998. Plants were assigned at random to locations within the common garden.

To obtain plant material, we chose 25 locations at random within the 147-ha reserve using BMR's grid of permanent signposts. At each location, we collected several cuttings (10 cm long) from the nearest prostrate and nearest erect plant (5 April 1998). These plants were designated as the source plants in the experiment, and clones grown from cuttings were replicated across the herbivory treatments (see below). Cuttings were surface sterilized in 5% bleach solution, dipped in rooting hormone, planted in square (10-cm) pots filled with 50 : 50 vermiculite : perlite, and grown on a mist bench for 35 days. On 10 May 1998, rooted cuttings were transplanted individually to tree pots filled with sterilized soil (10 cm × 10 cm × 36 cm deep, Stuewe & Sons, Inc. Corvallis, Oregon, USA). These plants were grown in the glasshouse at BMR (in the absence of herbivory) and watered daily with fertilizer (200 : 100 : 200 p.p.m. NPK) for 60 days. A single individual was planted into

each plot during 10–21 July 1998. Individuals were on average 31.0 cm tall when transplanted to the field. Each plant was watered with 5.7 L tap water immediately following transplantation and once weekly thereafter for 8 weeks.

In the common garden, three treatments were applied to manipulate herbivory: a fine mesh to exclude all herbivores (cage treatment), cages with square holes (40.5×40.5 cm) cut from the middle of two sides to allow access by insects yet control for any microclimatic effects of the cage (permeable cage treatment), or no cage (cage-free treatment). The bottom of each hole in the permeable cages was located *c*. 30 cm above ground. Plants were assigned to herbivory treatments at random. Architectural morph (prostrate or erect) was fully crossed with the herbivory treatment (cage, permeable cage, or cage-free) in a 2×3 factorial design. The sample size for each of the six treatment combinations was 25 individuals, with a single individual planted into each of the 150 plots. Cages were constructed from polyethylene screen fabric (1.8 mm × 1.4 mm holes, Lumite Co., Gainesville, Georgia, USA) secured over a 1-m³ PVC frame that was staked into the ground. The edges of the fabric were buried under sand, and one side of the cage had a 1-m vertical opening sealed with velcro to allow access by researchers.

The common garden design aimed to tease apart the effects of morph from effects of the location in which morphs occurred, thereby controlling environmental variation. However, because plants were propagated from cuttings, plants in the common garden represented the combined effects of plant genotype and maternal environment.

WHICH ARCHITECTURAL TRAITS DIFFER?

During April 2000 (21 months after planting), six architectural traits were assessed on each plant in the common garden: (a) maximum plant height (cm); (b) total number of branches; (c) mean branch length (measured for 14 randomly chosen, gall-free branches per plant); (d) mean leaf density (number of leaves per cm of branch, for three randomly chosen, gall-free branches); (e) mean internode length (for three randomly chosen, gall-free branches); and (f) mean leaf area (maximum length × maximum width for 12 randomly chosen undamaged leaves per plant). At the time of measurement, plants were, on average, 24.3 cm tall and bore 172 branches with an average branch length of 2.3 cm. In addition, a subset of randomly chosen, undamaged leaves was processed with a leaf area meter (LI 3000 A, LI-COR, Lincoln, Nebraska, USA) to confirm that length and width predicted leaf area ($r^2 = 0.79$, $P < 0.0001$, $\ln(\text{leaf area}) = 0.43 \times \ln(\text{length}) \times \ln(\text{width}) - 2.77$, $n = 462$ leaves).

The effects of architectural morph and herbivory treatment on the six architectural traits were analysed with mixed model M/ANOVA, including the effects of architectural morph, herbivory treatment, treatment ×

morph, transect and source plant (a random factor nested within morph; SAS Institute 2000). A significant effect of architectural morph would indicate that plants derived from erect vs. prostrate source plants were phenotypically divergent. A significant effect of the herbivory treatment would suggest that either herbivores or cages affected architectural traits. In addition, we tested two *a priori* contrasts within the herbivory treatment: (i) *cage* vs. *permeable cage* tested for a significant effect of herbivory on architecture; and (ii) *permeable cage* vs. *cage-free* tested for the effect of the cage on architecture. Branch number, mean leaf number per cm and height required log-transformation to satisfy assumptions of normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) (Sokal & Rohlf 1995).

DO MORPHS EXPERIENCE DIFFERENTIAL HERBIVORY?

Differences in herbivory on prostrate vs. erect plants were examined in two ways. First, we compared levels of attack on plants occurring naturally at two locations in California, BMR and San Bruno Mountain State Park (SBM, 37°42′ N, 122°26′ W). Secondly, we examined attack on plants in the common garden at BMR.

In natural populations, pairs of prostrate and erect plants (< 5 m apart) were chosen at random locations along linear transects (BMR, $n = 30$ pairs; SBM, $n = 20$ pairs). At BMR, gall numbers were counted per 150 branches, and gall number per branch was calculated (28 July 2004). Here, a branch is defined as a modular unit of the plant containing a single terminal meristem. Each branch can only support a single gall, regardless of branch length. At SBM, gall numbers were determined per unit area by counting all galls per plant and estimating plant area as an ellipse: (major axis + minor axis) ÷ 2 (19 February 1998). Due to the time-intensive nature of folivory assessments in this system, only galling herbivores were assayed at the natural sites. For each population, differences between morphs in herbivore abundance were evaluated with paired, two-tailed, Student's *t*-tests. In contrast to BMR, which had similar frequencies of the two morphs, the erect morph was significantly more common than the prostrate at SBM (erect = 58% of plants, prostrate = 42%, χ^2 test for goodness of fit = 5.7, $P = 0.008$, from a total of 252 plants chosen at random along transects at 3-m intervals, 18 May 1998).

In the common garden, we counted the number of active galls per plant repeatedly during the experiment. Midge galls were counted during September 1998, February 1999, April 1999, April 2000, April 2001 and October 2001, and moth galls were counted during April 1999, April 2000, April 2001 and October 2001. Repeated measures analyses did not identify significant treatment and morph interactions with time; therefore, for each plant, we determined the total number of galls experienced over the duration of the 40-month experi-

ment by summing the counts across dates. We also visually estimated folivory to the nearest 25% during February 1999, April 1999, April 2000 and October 2001, and determined the mean percentage folivory across all dates for each plant. Visual estimates of folivory were positively correlated with values determined using a transparent grid (12 randomly selected leaves per plant; April 2000; Spearman $r = 0.66$, $P < 0.0001$, $n = 133$ leaves).

The responses of midge gall number, moth gall number and percentage folivory were evaluated using MANOVA, including the fixed effects of treatment, morph, treatment × morph, and the random effect of source plant (nested within morph). As total herbivore numbers accumulating over 40 months were used as response variables, only plants surviving the duration of the experiment were included in the analysis. (Few plants died (11.33% of the total), and these included similar numbers of each morph (prostrate $n = 8$, erect $n = 9$).) Qualitatively identical results were obtained using repeated measures analysis on data across all dates; totals are used here for simplicity of presentation. Assumptions of homogeneity of variances and normality of residuals were satisfied following square-root transformation of gall numbers and angular transformation of percentage folivory (Sokal & Rohlf 1995). As the permeable cage treatment did not significantly differ from the cage-free treatment in its effects on herbivores (MANOVA, $F_{3,72} = 1.1$, $P > 0.3$, Table 2), these treatments were combined as an 'herbivore-exposed' treatment in the analysis. In addition, the location of holes in the walls of the permeable cages did not appear to bias herbivores against detection of the prostrate morph, because differences between the morphs in herbivory were consistent between the permeable cage and cage-free treatments (test for interaction between morph and treatment, including only the permeable cage and cage-free treatments: MANOVA $F_{3,30} = 2.07$, $P = 0.13$). Furthermore, herbivory differences between morphs observed in the natural populations resembled differences observed in the common garden experiment (see Results). Individual responses were examined with protected, mixed model ANOVA, including Tukey HSD (honestly significantly different) tests to evaluate differences among treatment combinations. Combining herbivory treatments did not violate the assumption of homogeneity of variances for any response variable (Levene's tests for homogeneity of variance, all $P > 0.05$).

Gall number is not sufficient to estimate midge abundance because, unlike moth galls, midge galls can contain more than one larva. The number of midge larvae per gall was significantly correlated with gall volume (length × width × height, $r = 0.81$, $P < 0.0001$, $n = 92$ galls). Therefore, to estimate midge abundance per gall, in the common garden we determined volume for up to 10 randomly chosen midge galls per plant during March 1999 and for three midge galls per plant during March 2000. For gall volume, repeated measures ANOVA included architectural morph, herbivory treatment, year, and all

interactions. Gall volume was log-transformed to meet model assumptions.

DO CORRELATIONS EXIST BETWEEN MORPHOLOGICAL TRAITS AND HERBIVORY?

For the subset of plants exposed to herbivores (cage-free and permeable cage treatments), we used multiple regression analysis to examine relationships among architectural traits and herbivory levels (Proc Reg, SAS Institute 2000). Regressions utilized data from April 2000 when both architectural traits and herbivory were assessed on the same date ($n = 85$ plants). All variables were log-transformed with the exception of percentage folivory, which was angular-transformed. No multicollinearity problems were detected. In addition to examining relationships across both morphs, we also conducted multiple regression analysis to evaluate patterns within each morph (prostrate $n = 45$, erect $n = 40$). Consistency in correlations both across and within architectural morphs would lend greater support to the hypothesis that architectural traits are important factors influencing herbivory.

DOES PARASITISM OF THE MIDGE DIFFER BETWEEN ARCHITECTURAL MORPHS?

Parasitism of midges was assessed for naturally occurring plants chosen at random at BMR (25 February 1999, $n = 20$ erect plants, $n = 20$ prostrate plants; 14 March 2000, $n = 38$ erect plants, $n = 32$ prostrate plants) and for all plants with galls in the common garden experiment (14 March 2000, $n = 12$ erect, $n = 21$ prostrate; 14 April 2001, $n = 25$ erect, $n = 37$ prostrate). On each date, a single gall was randomly chosen and collected from each plant. The number of exit holes created by midges or parasitoids and gall volume (described above) were recorded prior to collection. Exit holes were few, and midge holes are distinguished by the presence of a white pupal case, which adults pull partially out of the hole as they emerge (Latto & Briggs 1995). Galls were reared singly in 20-mL scintillation vials plugged with cotton balls. A total of 95 galls were reared from erect plants, and 110 from prostrate plants. Emerged midges and parasitoids were removed and identified weekly for 3 months, at which time galls were dissected, and gall chambers counted. To estimate total parasitism, the proportion of midges parasitized per gall was determined as: (number of emerged parasitoids + pre-collection parasitoid exit holes) ÷ total number of chambers. Data for naturally occurring plants and for plants in the common garden were analysed separately. ANOVA was used to examine the effects of morph, year, and morph × year on total parasitism rates (all wasp species combined). The power of these tests was then evaluated using PASS power analysis software (Hintze 2002). Finally, MANOVA examined the effects of architectural morph, year, and morph × year on the proportion of total parasitism due to each of the five most common wasp species (proportions were angular-transformed).

DO HERBIVORES ALTER THE RELATIVE PERFORMANCE OF ARCHITECTURAL MORPHS?

Differences in fitness between architectural morphs in the presence, but not in the absence, of herbivores would be consistent with the hypothesis that herbivores alter the relative performance of architectural morphs. A herbivore-mediated difference in performance between the morphs is key to determining whether herbivores can act as agents of selection on the dimorphism (see Marquis 1992; Marquis & Whelan 1996). Because *B. pilularis* plants are dioecious, reproductive fitness was estimated by multiplying the number of inflorescences produced each year (from 1998 to 2001) by the number of flowers (male plants) or seeds (female plants) produced per inflorescence (determined from a random sample of five inflorescences per plant). For female plants, a single seed is produced per flower. Reproduction estimates were summed across years to obtain the total number of seeds (female) or flowers (male) produced by each plant over the course of the experiment and evaluated using mixed model ANOVA as described above for herbivores. Permeable cage and cage-free plants were combined into a herbivore-exposed treatment because they did not significantly differ in reproduction ($F_{1,93} = 2.2$, $P = 0.14$), and combining treatments did not violate the assumption of homogeneity of variance (Levene's test, $F = 1.7$, $P = 0.17$). Too few plants died during the 40-month experiment (prostrate $n = 8$, erect $n = 9$) to examine effects on survival separately; therefore, all plants were included in the analysis of total reproductive output.

Results

WHICH ARCHITECTURAL TRAITS DIFFER?

Architectural classification of the source plant (representing both plant genotype and, potentially, maternal environment) strongly influenced the morphology of cloned plants in the common garden (MANOVA, $P < 0.0001$, Table 1). Clones from erect source plants were 54% taller, possessed 61% larger leaves, had 72% fewer branches, and had 54% longer branches than clones from prostrate source plants (Fig. 1). Leaf density and internode length did not significantly differ between morphs (Fig 1; $P > 0.05$). In addition to morph classification, the identity of the source plant explained substantial variation in architecture for several traits (MANOVA, $P = 0.0004$, Table 1). The architectural traits of both prostrate and erect plants responded similarly to the presence of cages (treatment × morph, $P > 0.5$; Table 1), and only two traits were significantly affected by caging (permeable cage vs. cage-free contrast, $P > 0.09$ for all other traits). Plants without cages were on average 44% shorter (mean ± SE, permeable cage = 27.8 ± 1.9 cm, cage-free = 15.6 ± 1.4 cm) and possessed 31% shorter branches than plants in cages (permeable cage = 2.37 ± 0.20 cm, cage-free = 1.63 ± 0.10 cm). No

Table 1 MANOVA results for the effects of morph, source plant and herbivory treatment on six plant architectural traits: plant height (cm), mean branch length (cm), mean internode length (cm), branch number, leaf number per cm, and leaf area (cm^2). ANOVA results are given in the text and in Fig. 1. Significant *P*-values (< 0.05) are indicated in bold face

| Effect	d.f.	Pillai's trace	F	P
Transect	72,402	0.80	0.9	0.7870
Source plant (morph)	288,402	3.05	1.4	**0.0004**
Herbivory treatment	12,126	0.70	5.6	**< 0.0001**
Morph	6,43	0.70	16.5	**< 0.0001**
Herbivory treatment × morph	12,126	0.16	0.9	0.5259
A priori contrasts				
Cage vs. permeable cage	6,43	0.19	1.7	0.1479
Permeable cage vs. cage-free	6,43	0.35	3.9	**0.0032**
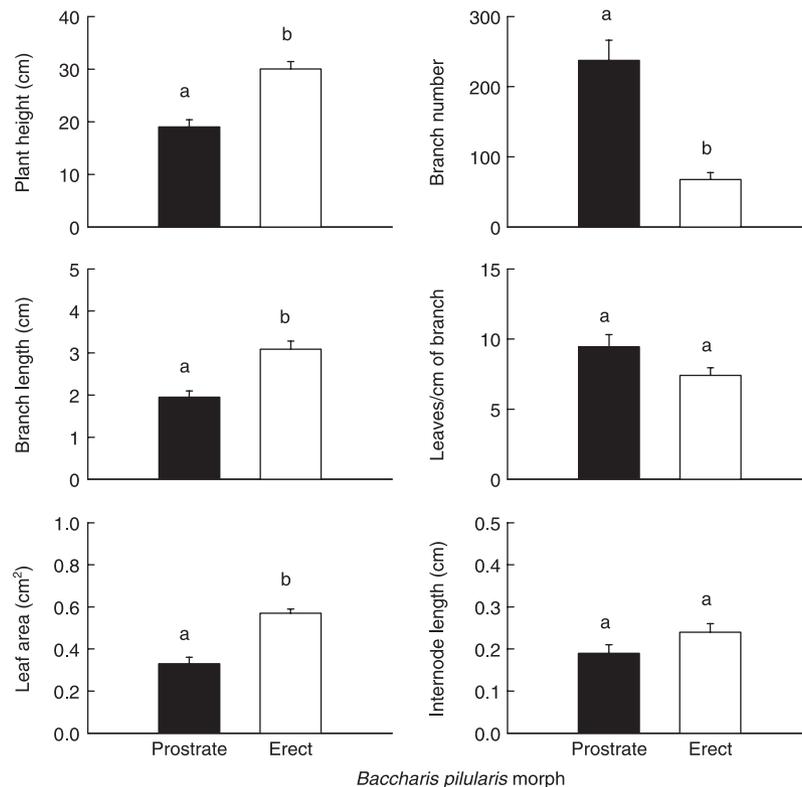
Fig. 1 Architectural traits of *Baccharis pilularis* plants derived from cuttings of prostrate or erect source plants and grown in a common garden (*n* = 25 source plants morph^{-1}). Bars are means + 1 SE. Different letters indicate a significant effect of the architectural morph of the source plant in univariate analysis of variance (see also MANOVA results, Table 1).

architectural traits were significantly altered by herbivory (cage vs. permeable cage, *P* > 0.14, Table 1).

DO MORPHS EXPERIENCE DIFFERENTIAL HERBIVORY?

Prostrate and erect morphs diverged for all types of herbivory measured. In surveys of naturally occurring *B. pilularis*, prostrate plants had *c*. 290% more midge galls than erect plants at BMR (Paired *t* = 4.9, *P* < 0.0001, *n* = 30 plants/morph; Fig. 2a) and *c*. 90% more midge galls at SBM (*t* = 3.0, *P* = 0.005, *n* = 20; Fig. 2b). In contrast, erect plants experienced *c*. 580% more moth galls at BMR (*t* = 6.4, *P* < 0.0001, *n* = 30; Fig. 2a) and *c*. 350% more at SBM (*t* = 2.8, *P* = 0.01; Fig. 2b).

Similar patterns were apparent in the BMR common garden. Over the 40-month study, prostrate morphs experienced *c*. 250% more midge galls than erect morphs (Fig. 3a; mean ± SE, prostrate = 47.1 ± 6.4 galls, erect = 13.4 ± 2.5 galls). Despite effects on gall number, architectural morph did not affect the number of midge larvae per gall as estimated by gall volume (prostrate = 141.8 ± 20.2 mm^3 (*n* = 60); erect = 130.8 ± 16.1 mm^3 (*n* = 46); morph $F_{1,94}$ = 0.1, *P* = 0.8, morph × year $F_{1,94}$ = 0.9, *P* = 0.3). Erect morphs received *c*. 100% more moth galls (Fig. 3b; prostrate = 3.9 ± 0.8 galls, erect = 7.7 ± 1.4 galls) and *c*. 60% more folivory (Fig. 3c, prostrate = 3.3 ± 0.4%, erect = 5.4 ± 0.7%); as expected, these differences were stronger in treatments exposed to herbivores than when plants were protected in cages (treatment ×
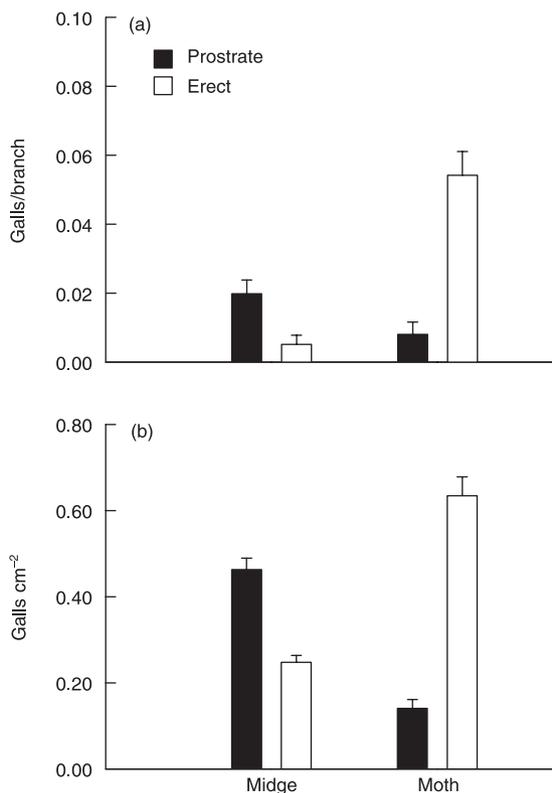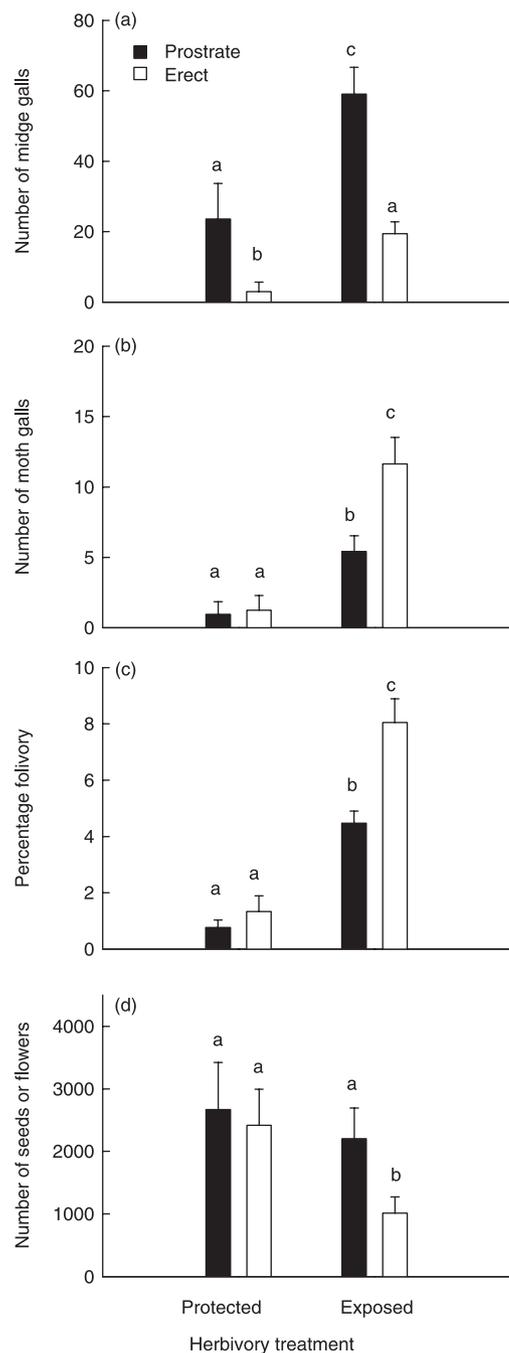
Fig. 2 Gall densities on naturally occurring prostrate vs. erect morphs of *Baccharis pilularis* at (a) Bodega Marine Reserve, CA ($n = 30$ plants morph^{-1}), and (b) San Bruno Mountain, CA ($n = 20$ plants morph^{-1}).

morph, $P < 0.05$ Table 2). In addition, although the combined analysis of herbivory (MANOVA) revealed only marginal differences between the cage-free and permeable cage treatments (see Methods, $P = 0.13$), moth galls alone were more abundant on plants in permeable cages than plants in the open (mean ± SE, permeable cage = 45 ± 7.6, cage-free = 29 ± 5.4, $P = 0.02$), which may indicate a response by the moths to cage-induced changes in plant height or branch length.

DO CORRELATIONS EXIST BETWEEN MORPHOLOGICAL TRAITS AND HERBIVORY?

Multiple regression analysis identified a number of key plant traits that correlated with herbivory. Across both architectural morphs, midge galls were more abundant on plants with more branches (partial regression coefficient $b = 0.47$, $P < 0.0001$), plants with longer branches ($b = 0.55$, $P = 0.02$) and plants with smaller leaves ($b = -0.66$, $P = 0.04$). In contrast, only branch length affected numbers of moth galls, which were more abundant on longer branches ($b = 0.92$, $P = 0.0008$). Folivory was marginally greater on taller plants ($b = 0.01$, $P = 0.052$). All other partial regression coefficients did not differ significantly from zero ($P > 0.15$).

Similar patterns were obtained for multiple regression analyses conducted within each architectural morph. Within morphs, midge gall abundance remained positively correlated with branch number (prostrate,

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Fig. 3 Responses of *Baccharis pilularis* plants derived from cuttings of prostrate or erect plants and exposed to herbivory treatments (exposed or protected from herbivores) in a common garden for 40 months. The permeable cage and cage-free treatments were combined into the 'exposed' herbivory treatment ($n = 25$ source plants morph^{-1}). (a) Number of midge galls (*Rhopalomyia californica*) plant^{-1}. (b) Number of moth galls (*Gnorimoschema baccharisella*) plant^{-1}. (c) Percentage folivory plant^{-1}. (d) Total number of seeds (female plants) or flowers (male plants) produced plant^{-1}. Bars show means + 1 SE and letters indicate significant differences among treatments and morphs via a Tukey HSD test.

partial regression coefficient $b = 0.55$, $P = 0.006$; erect, $b = 0.27$, $P = 0.04$) and branch length (erect morph only, $b = 0.57$, $P = 0.04$). In addition, within the erect morph, plant height was negatively correlated with midge

Table 2 Results of M/ANOVA testing the effects of architectural morph (prostrate vs. erect) and herbivory treatment (protected vs. exposed) on herbivory. Because the *a priori* contrasts between the permeable cage and cage-free plants were non-significant (see contrasts, bottom of table), these two treatments were combined in the MANOVA as an 'herbivore exposed' treatment. Significant *P*-values (< 0.05) are indicated in bold face

Effect	MANOVA			ANOVA	Number of midge galls		Number of moth galls		Percentage folivory	
	d.f.	*F*	*P*	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Source plant (morph)	147,231	1.3	0.0532	49,77	1.0	0.3548	1.4	0.0793	0.9	0.6742
Treatment	3,75	45.1	**< 0.0001**	1,77	39.1	**< 0.0001**	42.1	**< 0.0001**	100.8	**< 0.0001**
Morph	3,47	14.2	**< 0.0001**	1,63	36.6	**< 0.0001**	2.9	0.0944	5.5	**0.0224**
Treatment × morph	3,75	4.8	**0.0042**	1,77	0.4	0.5192	5.3	**0.0235**	4.2	**0.0448**
A priori contrasts within herbivory treatment										
Protected: prostrate vs. erect	3,75	4.2	**0.0088**	1,77	12.4	**0.0007**	0.1	0.8298	0.1	0.9197
Exposed: prostrate vs. erect	3,75	25.4	**< 0.0001**	1,77	33.2	**< 0.0001**	12.6	**0.0007**	12.3	**0.0008**
A priori contrasts (3 herbivory treatments)										
Cage vs. permeable cage	3,72	50.2	**< 0.0001**	1,74	35.8	**< 0.0001**	27.2	**< 0.0001**	133.5	**< 0.0001**
Permeable cage vs. cage-free	3,72	1.1	0.3472	1,74	2.3	0.1376	1.7	0.2026	0.8	0.3875

Table 3 Means ± SE for the total percentage (%) parasitism of the midge *Rhopalomyia californica* by all parasitoid wasp species, and for parasitized midges the relative contributions of the five most common parasitoid species. Different letters indicate a significant difference for architectural morph as demonstrated by ANOVA

Response variable	Morph	Naturally occurring plants		Common garden plants	
		1999	2000	2000	2001
Total percentage parasitism	Prostrate	41.5 ± 6.8	36.4 ± 7.9	58.9 ± 9.7	42.0 ± 7.0
	Erect	42.5 ± 7.4	30.8 ± 6.0	44.7 ± 12.1	49.8 ± 8.3
% *Mesopolobus* sp.	Prostrate	11.1 ± 7.6	16.9 ± 9.1	24.9 ± 9.5	14.0 ± 7.2
	Erect	16.4 ± 8.6	32.1 ± 8.7	27.9 ± 13.9	19.8 ± 8.2
% *Platygaster californica*	Prostrate	23.1 ± 8.5	26.9 ± 10.0	1.3 ± 1.3	34.2 ± 9.7
	Erect	16.7 ± 8.0	24.2 ± 8.3	7.1 ± 7.1	40.1 ± 11.1
% *Torymus baccharidis*	Prostrate	11.1 ± 7.6	28.2 ± 10.5	53.6 ± 10.5	17.8 ± 7.9
	Erect	45.0 ± 10.3	22.0 ± 8.8	54.1 ± 17.5	15.7 ± 7.6
% *Torymus koelbelei*	Prostrate	22.2 ± 9.2	8.0 ± 6.7	14.7 ± 7.3	17.2 ± 7.7
	Erect	19.3 ± 7.7	19.3 ± 7.9	10.9 ± 7.1	15.1 ± 7.6
% *Zatropis capitis*	Prostrate	32.4 ± 9.9[a]	20.0 ± 10.7[a]	5.6 ± 5.6	11.9 ± 6.8
	Erect	2.6 ± 1.9[b]	2.4 ± 2.4[b]	0 ± 0	9.3 ± 6.5

gall abundance ($b = -0.65$, $P = 0.01$), a relationship that was not detected across morphs. The positive relationship between branch length and the number of moth galls also persisted within each morph (prostrate $b = 0.80$, $P = 0.01$; erect morph, $b = 0.97$, $P = 0.03$); thus, branch length was the only trait measured that was important to moth galls. No other partial regression coefficients for midge or moth galls significantly differed from zero ($P > 0.16$). For folivory, neither multiple regression model was significant within a morph (prostrate $F_{4,35} = 2.4$, $P = 0.072$; erect, $F_{4,40} = 0.8$, $P = 0.5$), suggesting that effects of height seen in the across-morph analysis were largely driven by differences between morphs rather than variation within morphs.

DOES PARASITISM OF THE MIDGE DIFFER BETWEEN ARCHITECTURAL MORPHS?

In both common garden and natural plants, architectural morph did not affect total parasitism rates on midges (Table 3; ANOVA, $F_{1,91} = 0.2$, $P = 0.64$ and $F_{1,106} = 0.1$, $P = 0.76$, respectively). These tests were only moderately powerful, reflecting the high plant-to-plant variance in parasitism rates; at $\beta < 0.2$, they were capable of detecting differences in morph means of 51% and 54% for common garden and natural plants, respectively. With respect to parasitoid species composition, there were no differences among the morphs in the common garden (Table 3; MANOVA, morph $F_{5,53} = 0.4$, $P = 0.88$; morph × year $F_{5,53} = 0.0$, $P = 0.99$). The only detectable effect on parasitoids was a shift in the composition of wasps on natural plants: prostrate forms had *c.* 1150% more *Zatropis capitis* than did erect forms in 1999 and *c.* 730% more in 2000 (Table 3; MANOVA morph $F_{5,65} = 2.7$, $P = 0.03$; morph × year $F_{5,65} = 1.0$, $P = 0.41$). Because this effect was not found in the common garden, it is not possible to distinguish whether differences in *Zatropis* attack were caused by architectural morph or resulted from differences in the local environments in which the morphs occurred.

DO HERBIVORES ALTER THE RELATIVE PERFORMANCE OF ARCHITECTURAL MORPHS?

The cages effectively reduced herbivory (MANOVA, herbivory treatment, $P < 0.0001$, Table 2). Over the 40-month experiment, plants protected in cages experienced c. 70% fewer midge galls (Fig. 3a, mean ± SE, protected = 12.8 ± 5.2 galls, exposed = 39.8 ± 4.7 galls), c. 90% fewer moth galls (Fig. 3b, protected = 1.1 ± 0.7 galls, exposed = 8.4 ± 1.1 galls), and c. 80% less folivory (Fig. 3c, protected = 1.2 ± 0.3%, exposed = 6.1 ± 0.5%) than plants exposed to herbivores. The herbivory treatment did not affect midge gall volume (treatment $F_{2,94} = 0.8$, $P = 0.5$, treatment × year $F_{2,94} = 0.9$, $P = 0.4$; treatment × morph $F_{2,94} = 0.5$, $P = 0.6$, treatment × morph × year $F_{2,94} = 3.0$, $P = 0.1$), suggesting that any midges breaching the cage formed galls of similar size to those on herbivore-exposed plants.

Herbivores significantly reduced *B. pilularis* reproductive success (Fig. 3d, herbivory treatment, $F_{1,95} = 17.8$, $P < 0.0001$). Over the 40-month experiment, plants protected by cages produced c. 60% more seeds (female plants) or flowers (male plants) (mean ± SE, 2540.7 ± 467.2 seeds or flowers) than plants exposed to herbivores (1603.1 ± 280.4). Similar numbers of seeds and flowers were produced per inflorescence (mean ± SE, seeds (female plants) = 23.99 ± 0.67, flowers (male plants) = 23.77 ± 0.56, $F_{1,115} = 0.07$, $P = 0.80$).

Importantly, herbivores altered the relative performance of prostrate vs. erect morphs. When exposed to herbivores, prostrate plants outperformed erect plants, producing c. 120% more seeds or flowers (Fig. 3d, exposed treatment: prostrate vs. erect contrast, $F_{1,95} = 7.7$, $P < 0.007$). In contrast, prostrate and erect plants did not significantly differ in reproduction when plants were protected from herbivores (Fig. 3d, protected treatment: prostrate vs. erect contrast, $F_{1,95} = 0.6$, $P = 0.4$).

Discussion

ARCHITECTURAL VARIATION IN *BACCHARIS PILULARIS*

In the common garden, four architectural traits differed between plants cloned from prostrate vs. erect parents. Plants cloned from prostrate morphs were shorter, had shorter branches, more branches, and smaller leaves than plants originating from erect morphs. Significant effects of architectural morph and source plant in the common garden as well as prior hybridization experiments (Thompson *et al*. 1995) suggest that these architectural traits are genetically based. However, genotype × environment effects have also been documented for *B. pilularis* architecture, including plasticity in responses to shading and/or wind reduction by cages (this study) and exposure to strong wind (Miller & Weis 1999). In this study, the common garden design may have been limited in its ability to examine genetic variation because

source plant effects reflected a combination of plant genotype and maternal environment. However, the effects of source plant architectural morph (a 52% difference between prostrate and erect across all traits measured) were substantially greater than effects of caging (a 22% difference between permeable cage and cage-free), consistent with the hypothesis of greater genetic than environmental control of architectural variation. Finally, segregation of plants grown from seeds collected from each morph (erect = 83% erect progeny, 17% prostrate; prostrate = 45% erect progeny, 54% prostrate) provides additional support for the existence of a genetic basis underlying the architectural dimorphism (J. A. Rudgers & K. D. Whitney, unpublished data).

PLANT MORPHOLOGY AND THE HERBIVORE ASSEMBLAGE

The herbivore assemblage on prostrate plants differed strikingly from the assemblage on erect plants. In both natural and common garden environments, midge galls dominated the prostrate morph, whereas the erect morph experienced more moth galls and, in the common garden, greater folivory. Furthermore, several plant traits were correlated with variation in herbivory. Plants with more branches, longer branches and smaller leaves had more midge galls. Plants with longer branches had more moth galls, and taller plants experienced marginally greater folivory. Correlations involving branch number and branch length persisted even when variation was examined within morphs.

Although correlations between herbivory levels and morphological traits were strong, the traits targeted here could simply be highly correlated with other traits important to herbivory (e.g. plant secondary chemistry or physiology; Abrahamson *et al*. 2003). Manipulations of morphological traits combined with herbivore preference and performance assays would be highly useful for teasing apart potentially correlated traits. In addition, future work in the system would benefit from direct tests of mechanisms driving herbivore resistance. For example, the plant vigour hypothesis predicts that herbivores prefer or perform better on plants with the most vigorously growing shoots (Price 1991). This hypothesis is typically tested by assuming that the longest shoots have the most vigorous growth (Price 1991; Price *et al*. 1995; Price *et al*. 2004). In *B. pilularis*, branch length was positively correlated with the abundance of both gall-forming species, suggesting that these herbivores may prefer more vigorous shoots; thus, direct comparisons of growth rates between the morphs combined with laboratory choice tests for the herbivores could be informative.

An alternative to the plant vigour hypothesis is the sink competition hypothesis, which predicts that galling insects prefer or perform better on plants with high ratios of sources to sinks (Larson & Whitham 1997). Although correlations suggest a lack of support for the

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sink competition hypothesis (midge gall numbers were positively correlated with sink strength (as estimated by branch number per plant because sinks occur at terminal buds of each branch) and negatively correlated with source strength (as estimated by photosynthetic leaf area because *B. pilularis* branches are rarely photosynthetic); furthermore, moth gall abundance was not significantly correlated with either branch number or leaf area), direct quantification of resource translocation in *B. pilularis* (e.g. via ^{14}C labelling) is needed to test the validity of the sink competition model for this system (see Larson & Whitham 1991; Arnold *et al.* 2004). Results from *B. pilularis* also suggest that traits other than branch length and source to sink ratios (e.g. plant height) may affect herbivores or be highly correlated with other traits important to herbivory. For example, generalist folivores may be more likely to encounter tall plants that rise above surrounding vegetation, resulting in less damage on prostrate individuals.

The patterns observed may reflect a combination of direct effects of plant traits on herbivore preference or performance and indirect effects mediated through other community members. For example, the observed sorting of galling species by architectural morph may reflect competitive interactions among these herbivores (e.g. Denno *et al.* 1995; Cronin & Abrahamson 1999) and may also include plant-mediated interactions that depend on the order and timing of attack. Because both herbivores can be found on the perennial *B. pilularis* all year round, there is no obvious timing to the pattern of attack. With regard to parasitoid-mediated interactions, plant architecture did not appear to indirectly affect herbivores. Rates of parasitoid wasp attack on midge galls were similar between prostrate and erect morphs, although high plant-to-plant variance in attack rates resulted in tests of only moderate power. The only exception was a greater abundance of the parasitoid *Zatropis capitis* on prostrate as compared with erect plants. This effect, seen in naturally occurring plants, was not replicated in the common garden; thus, the difference may reflect an effect of the local environment in which each architectural morph occurs, rather than a real effect of architecture. Further examination of parasitism rates, spanning more time periods and using greater sample sizes, could help confirm the lack of an influence of the plant dimorphism on parasitoids.

HERBIVORES AFFECT THE RELATIVE PERFORMANCE OF ARCHITECTURAL MORPHS

Herbivore exclusion over 40 months significantly enhanced *B. pilularis* reproduction. This result contributes to our understanding of the importance of insect herbivory for long-lived perennial plants, which are typically underrepresented relative to annual plants in studies on the fitness effects of herbivory (Marquis 1992). Additional data could improve the assessment of fitness in this system, including estimates of the germination rate and survival of seedlings, the number of offspring sired by male plants, and reproductive output spanning plants' entire lifetimes.

In addition to reducing average plant reproduction, herbivores also may act as agents of selection on *B. pilularis*. In the common garden experiment, prostrate plants had higher fitness than erect plants in the presence of herbivores, but had similar reproductive success in the absence of herbivores, which demonstrates that the presence of herbivores alters the relative performance of morphs. To confirm that herbivores are currently posing significant selective pressures on the architecture of *B. pilularis*, experiments are required that directly link architectural traits and herbivory levels. In addition, the heritability of specific architectural traits must be demonstrated. The observed benefit of the prostrate habit may indicate that folivores and gall-forming moths (which were more abundant on the erect morph) have a greater impact on plant reproduction than do gall-forming midges (which were more abundant on the prostrate morph). Alternatively, a prostrate growth form may enhance the plants' ability to re-grow following damage, a form of tolerance to herbivory (Marquis 1996). In addition to architecture, other (as yet unmeasured) traits may differ between the morphs and thereby contribute to their differential success. For example, morphs may vary in secondary compounds that enhance resistance to herbivory, as has been found for male vs. female plants of a related species, *Baccharis halimifolia* (Krischik & Denno 1990).

Conclusion

Within the shrub *Baccharis pilularis*, plant architectural dimorphism plays a key role in shaping the distribution and abundance of herbivores, including both dipteran and lepidopteran gall-forming insects. These results confirm the ecological importance of intraspecific variation in plants for structuring dependent communities (e.g. Whitham *et al.* 2003, Johnson & Agrawal 2005). In addition, reciprocal effects of herbivores influenced the relative performance of architectural morphs; prostrate plants produced more flowers and seeds than erect plants in the presence of herbivores, despite equal reproduction of the morphs when herbivory was experimentally reduced. As in other recent studies on other variable plant characters (e.g. flower colour, Irwin *et al.* 2003; fruit colour, Whitney & Stanton 2004), these results highlight the potential for herbivores to act as agents of selection on plant characters other than the obvious traits of secondary chemistry and physical deterrents.

References

Abrahamson, W.G., Hunter, M.D., Melika, G. & Price, P.W. (2003) Cynipid gall-wasp communities correlate with oak chemistry. *Journal of Chemical Ecology*, **29**, 208–223.

Alonso, C. & Herrera, C.M. (1996) Variation in herbivory within and among plants of *Daphne laureola* (Thymelaeaceae): correlation with plant size and architecture. *Journal of Ecology*, **84**, 495–502.

Andow, D.A. & Prokrym, D.R. (1990) Plant structural complexity and host-finding by a parasitoid. *Oecologia*, **82**, 162–165.

Arnold, T., Appel, H., Patel, V., Stocum, E., Kavalier, A. & Schultz, J. (2004) Carbohydrate translocation determines the phenolic content of Populus foliage: a test of the sink-source model of plant defense. *New Phytologist*, **164**, 157–164.

Bailey, J.K., Bangert, R.K., Schweitzer, J.A., Trotter, R.T., Shuster, S.M. & Whitham, T.G. (2004) Fractal geometry is heritable in trees. *Evolution*, **58**, 2100–2102.

Bailey, J.K., Wooley, S.C., Lindroth, R.L. & Whitham, T.G. (2006) Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecology Letters*, **9**, 78–85.

Briggs, C.J. (1993) *The effect of multiple parasitoid species on the gall-forming midge,* Rhopalomyia californica. Dissertation. University of California-Santa Barbara, Santa Barbara, California.

Briggs, C.J. & Latto, J. (1996) The window of vulnerability and its effect on relative parasitoid abundance. *Ecological Entomology*, **21**, 128–140.

Casas, J. & Djemai, I. (2002) Canopy architecture and multitrophic interactions. *Multitrophic Interactions* (eds T. Tscharntke & B.A. Hawkins), pp. 174–196. Cambridge University Press, Cambridge.

Clark, T.L. & Messina, F.J. (1998) Plant architecture and the foraging success of ladybird beetles attacking the Russian wheat aphid. *Entomologia Experimentalis et Applicata*, **86**, 153–161.

Cloyd, R.A. & Sadof, C.S. (2000) Effects of plant architecture on the attack rate of *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), a parasitoid of the citrus mealybug (Homoptera: Pseudococcidae). *Environmental Entomology*, **29**, 535–541.

Cronin, J.T. & Abrahamson, W.G. (1999) Host-plant genotype and other herbivores influence goldenrod stem galler preference and performance. *Oecologia*, **121**, 392–404.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology*, **40**, 297–331.

Doutt, R.L. (1961) The dimensions of endemism. *Annals of the Entomological Society of America*, **54**, 46–53.

Dungey, H.S., Potts, B.M., Whitham, T.G. & Li, H.F. (2000) Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. *Evolution*, **54**, 1938–1946.

Ehler, L.E. (1982) Ecology of *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) and its parasites in an urban environment. *Hilgardia*, **50**, 1–32.

Fernandes, G.W., Castro, F.M.C., Faria, M.L., Marques, E.S.A. & Greco, M.K.B. (2004) Effects of hygrothermal stress, plant richness, and architecture on mining insect diversity. *Biotropica*, **36**, 240–247.

Force, D.C. (1970) Competition among four Hymenopterous parasites of an endemic insect host. *Annals of the Entomological Society of America*, **63**, 1675–1688.

Force, D.C. (1974) Ecology of insect host-parasitoid communities. *Science*, **184**, 624–632.

Fritz, R.S. & Price, P.W. (1988) Genetic variation among plants and insect community structure: willows and sawflies. *Ecology*, **69**, 845–856.

Grevstad, F.S. & Klepetka, B.W. (1992) The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia*, **92**, 399–404.

Hare, J.D. (2002) Plant genetic variation in tritrophic interactions. *Multitrophic Interactions* (eds T. Tscharntke & B.A. Hawkins), pp. 8–43. Cambridge University Press, Cambridge.

Haysom, K.A. & Coulson, J.C. (1998) The Lepidoptera fauna associated with *Calluna vulgaris*: effects of plant architecture on abundance and diversity. *Ecological Entomology*, **23**, 377–385.

Hintze, J. (2002) *PASS*. Number Cruncher Statistical Systems, Kaysville, Utah.

Hochwender, C.G. & Fritz, R.S. (2004) Plant genetic differences influence herbivore community structure: evidence from a hybrid willow system. *Oecologia*, **138**, 547–557.

Hopper, K.R. (1984) The effects of host-finding and colonization rates on abundances of parasitoids of a gall midge. *Ecology*, **65**, 20–27.

Irwin, R.E., Strauss, S.Y., Storz, S., Emerson, A. & Guibert, G. (2003) The role of herbivores in the maintenance of a flower color polymorphism in wild radish. *Ecology*, **84**, 1733–1743.

Johnson, M.T.J. & Agrawal, A.A. (2005) Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology*, **86**, 874–885.

Kaitaniemi, P., Vehvilainen, H. & Ruohomaki, K. (2004) Movement and disappearance of mountain birch defoliators are influenced by the interactive effects of plant architecture and induced resistance. *Ecological Entomology*, **29**, 437–446.

Kareiva, P. & Sahakian, R. (1990) Tritrophic effects of a simple architectural mutation in pea plants. *Nature*, **345**, 433–434.

Krischik, V.A. & Denno, R.F. (1990) Patterns of growth, reproduction, defense, and herbivory in the dioecious shrub *Baccharis halimifolia* (Compositae). *Oecologia*, **83**, 182–190.

Langellotto, G.A. & Denno, R.F. (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1–10.

Larson, K.C. & Whitham, T.G. (1991) Manipulation of food resources by a gall-forming aphid: the physiology of sink–source interactions. *Oecologia*, **88**, 15–21.

Larson, K.C. & Whitham, T.G. (1997) Competition between gall aphids and natural plant sinks: plant architecture affects resistance to galling. *Oecologia*, **109**, 575–582.

Latto, J. & Briggs, C.J. (1995) Factors affecting distribution of the gall forming midge *Rhopalomyia californica* (Diptera, Cecidomyiidae). *Environmental Entomology*, **24**, 679–686.

Lawton, J.H. (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, **28**, 23–39.

Maddox, G.D. & Root, R.B. (1990) Structure of the encounter between goldenrod (*Solidago altissima*) and its diverse insect fauna. *Ecology*, **71**, 2115–2124.

Marquis, R.J. (1992) The selective impact of herbivores. *Plant Resistance to Herbivores and Pathogens: Ecology Evolution and Genetics* (eds R.S. Fritz & E.L. Simms), pp. 301–325. University of Chicago Press, Chicago.

Marquis, R.J. (1996) Plant architecture, sectoriality and plant tolerance to herbivores. *Vegetatio*, **127**, 85–97.

Marquis, R.J., Lill, J.T. & Piccinni, A. (2002) Effect of plant architecture on colonization and damage by leaftying caterpillars of *Quercus alba*. *Oikos*, **99**, 531–537.

Marquis, R.J. & Whelan, C. (1996) Plant morphology and recruitment of the third trophic level: subtle and little-recognized defenses? *Oikos*, **75**, 330–334.

Miller, W.B. & Weis, A.E. (1999) Adaptation of coyote brush

to the abiotic environment and its effects on susceptibility to a gall-making midge. *Oikos*, **84**, 199–208.

Munz, P.A. & Keck, D.D. (1973) *A California Flora*. University of California Press, Berkeley, California.

Neuhauser, C., Andow, D.A., Heimpel, G.E., May, G., Shaw, R.G. & Wagenius, S. (2003) Community genetics: expanding the synthesis of ecology and genetics. *Ecology*, **84**, 545–558.

Okogbenin, E. & Fregene, M. (2003) Genetic mapping of QTLs affecting productivity and plant architecture in a full-sib cross from non-inbred parents in Cassava (Manihot esculenta Crantz). *Theoretical and Applied Genetics*, **107**, 1452–1462.

Price, P.W. (1991) The plant vigor hypothesis and herbivore attack. *Oikos*, **62**, 244–251.

Price, P.W., Abrahamson, W.G., Hunter, M.D. & Melika, G. (2004) Using gall wasps on oaks to test broad ecological concepts. *Conservation Biology*, **18**, 1405–1416.

Price, P.W., Andrade, I., Pires, C., Sujii, E. & Vieira, E.M. (1995) Gradient analysis using plant modular structure: pattern in plant architecture and insect herbivore utilization. *Environmental Entomology*, **24**, 497–505.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weis, A.E. (1980) Interaction between three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11**, 41–65.

Rudgers, J.A. & Maron, J.L. (2003) Facilitation between coastal dune shrubs: a non-nitrogen fixing shrub facilitates establishment of a nitrogen-fixer. *Oikos*, **102**, 75–84.

SAS Institute (2000) *SAS Version 8.1*. SAS Institute, Cary, North Carolina.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: the Principles and Practice of Statistics in Biology Research*, 3rd edn. W.H. Freeman, New York.

Teixeira, F.F., Ramalho, M.A.P. & Abreu, A.D.B. (1999) Genetic control of plant architecture in the common bean (*Phaseolus vulgaris* L.). *Genetics and Molecular Biology*, **22**, 577–582.

Thompson, A.E., Lee, C.W. & Gass, R.E. (1995) Development of hybrid Baccharis plants for desert landscaping. *Hortscience*, **30**, 1357–1362.

Tilden, J.W. (1951a) The insect associates of *Baccharis pilularis* DeCandolle. *Microentomology*, **16**, 149–188.

Tilden, J.W. (1951b) Observations on *Rhopalomyia californica* Felt. *Pan-Pacific Entomologist*, **XXVII**, 20–22.

Whelan, C.J. (2001) Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology*, **82**, 219–231.

Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M., Wimp, G.M., Fischer, D.G., Bailey, J.K., Lindroth, R.L., Woolbright, S. & Kuske, C.R. (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, **84**, 559–573.

Whitney, K.D. & Stanton, M.L. (2004) Insect seed predators as novel agents of selection on fruit color. *Ecology*, **18**, 165–186.

Wimp, G.M., Martinsen, G.D., Floate, K.D., Bangert, R.K. & Whitham, T.G. (2005) Plant genetic determinants of arthropod community structure and diversity. *Evolution*, **59**, 61–69.

Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com

Figure S1 Photographs of *Baccharis pilularis* and its galls in coastal California. (A) *Rhopalomyia californica* gall (Diptera: Cecidomyiidae). (B) *Gnorimoschema baccharisella* gall (Lepidoptera: Gelechiidae). (C) Prostrate and erect morphs of *B. pilularis*.