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Adaptation of coyote brush to the abiotic environment and its effects on susceptibility to a gall-making midge

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Many plant traits that affect susceptibility to insect attack may have other functions important to the plant. If so, susceptibility could evolve as a correlated response to selection imposed through these other functions. We studied two populations of coyote brush, Baccharis pilularis, from contrasting habitats to see if plant adaptations to local abiotic environments altered susceptibility to the specific gall-making midge Rhopalomyia californica. Further we tested if genetically based differences in susceptibility are better explained by changes in adapted traits per se, or if susceptibility changes due to increased general vigor of adapted plants. Plant genotypes were cloned from an inland population at Irvine in southern California and from a coastal population surrounding Bodega Bay, 800 km to the north. Clones were reciprocally transplanted into experimental gardens near the collection sites. Several morphological differences between populations were stable across environments, but the phenotypic expression of several other genetically controlled differences, including height, was seen only in the southern, inland garden. The northern coastal plants tend to be shorter, which may be an adaptation to wind pruning. Infestation rates by gallmakers differed between the two plant populations when grown in the southern garden, where genetic differences in plant height were most strongly expressed but not in the northern garden, where wind pruning kept plants from both populations to the same height. In a neutral greenhouse environment plants from the two populations did not differ in attractiveness to ovipositing females or in suitability for gall-induction. Thus, Irvine and Bodega plants are equally susceptible to the gallmaker in some environments, but not others. The results suggest that in some cases plant genotypes dispersing into novel habitats can have lower susceptibility to enemies than in their native habitats.

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Traits that adapt plants for life in particular abiotic environments can also influence susceptibility to enemies. For instance, leaf surface resins of creosote brush (*Larrea* sp.) serve antidesiccant, and UV screening functions, but also deter herbivory (Rhoades 1977). Leaf pubescence provides a reflecting surface for intense light, and acts as a diffusion barrier to retard water loss (Ehleringer and Clark 1988), but also acts as a structural defense against phytophages (Gilbert 1971, Levin 1973, Becerra and Ezcurra 1986).

Over the long run plant populations will adapt to their local abiotic environment. Since herbivorous insects respond to a variety of plant stimuli, we would expect to find some instances where adaptive changes in a plant population to meet new challenges from climate or soil will also change susceptibility. Although it has been recognized in principle that plant susceptibility can evolve as a correlated response to selection on plant physiology and life history traits (Fritz and Simms 1992), ecological-genetic studies exploring its impor-

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tance are few (Daday 1954a, b, Dirzo and Harper 1982). This lack of attention is surprising, given an important alternative hypothesis to coevolution posed by Jermy (1976, 1993) – that insects track plant adaptations to environmental factors (i.e. sequential evolution). This study tests whether genetic adaptations of coyote brush, Baccharis pilularis De Candolle (Asteraceae), to its local abiotic environment alter attack rate by a host specific gall making midge, Rhopalomyia californica Felt (Diptera: Ceccidomyiidae).

One consequence of increased adaptation to local environments can be an increase in plant growth vigor. However, increased growth vigor can increase susceptibility to many insect herbivores, including gallmakers (Price 1991, Vieira et al. 1996; Woods et al. 1996) and other kinds of plant feeding insects (Preszler and Price 1995, Price et al. 1995a). Price (1991) has argued that vigorous plants present superior resources to insect herbivores, which precipitates the evolution of insect preference for them. Should herbivores be particularly abundant, they may even select against vigor (Craig et al. 1988). However, in many habitats, the competition for resources may oppose selection by insects, and compromise the potential for plants to evolve slower growth in response to herbivory (Craig et al. 1988, Weis 1994).

As the mean vigor of the population genetically responds to selection imposed by abiotic conditions, susceptibility to herbivores could also increase as a genetically correlated trait (Abrahamson and Weis 1997). Herbivores may not key in on traits directly involved in meeting the challenges of the abiotic environment, but because those adaptations increase growth vigor, susceptibility increases through a less direct causal link. Conversely, one would also expect that plant genotypes *not* adapted to local conditions would enjoy a reprieve from herbivory, by virtue of lowered vigor. This leads to the testable prediction that when vigor is a major determinant of susceptibility, plant genotypes will show higher vulnerability to attack in their native habitat than in alien habitats.

Reciprocal transplant experiments (Clausen et al. 1958) were used to examine a hierarchy of questions concerning how coyote brush adaptation to abiotic environments may affect its susceptibility to gall midges. First, do local populations of the plant show differential adaptation in morphology or growth to highly contrasting abiotic environment? Second, if differences are found, do they directly alter susceptibility to the gallmaker? Third, is genetic expression of susceptibility associated with plant vigor, and if so, are vigor and vulnerability higher in native or alien habitats?

If plant susceptibility changes through selection on correlated characters, local midge populations could also be under selection to adapt to their evolving host plant (Jermy 1976, Abrahamson 1989, Mopper and Strauss 1997). Thus, to adequately interpret results of

our primary reciprocal transplant experiment, we performed several smaller greenhouse experiments that test for local differentiation of midge populations.

Experimental system

Coyote brush, B. pilularis is an evergreen dioecious perennial shrub, one to four meters in height, which is common in coastal strand, coastal sage scrub and a range of inland habitats from Oregon to southern California (Munz and Keck 1959). Coastal populations are exposed to a maritime climate typified by moderate temperatures, summer fog, sea spray and frequently heavy on-shore winds. In contrast, inland populations generally experience hot, dry summers, and more severe winters (Doutt 1961). Thus, coyote brush occurs in a variety of climates throughout its range, giving ample opportunity for adaptation to local abiotic conditions.

For instance, one formerly recognized B. pilularis subspecies associated with dunes and headlands along the northern California coast, B. p. pilularis, has an extremely prostrate matted growth form, 0.1–0.15 m in height (Munz and Keck 1959). Several California plant species exhibit short-stature maritime sub-species (Clausen et al. 1958). This reduction in height is thought to be an adaptation to avoid pruning by strong on-shore winds. A second subspecies, B. p. consanguinea, has a more erect, rounded morphology, ranging from 1–4 m in height, and a widespread distribution. When viewed over its entire range, this species shows a cline in stature between these extreme growth forms. Possibly due to the large degree of morphological variability within populations, the most recent treatment of the genus has dropped subspecific designations (Sundberg 1993). Plants used in this experiment generally fit the description of B. pilularis consanguinea (Munz and Keck 1959).

We studied coyote brush from two contrasting climatic areas. One was a coastal population that extended from the coastal bluffs at Bodega Marine Laboratory to Bay Hill (ca 0.7 km inland), in Sonoma County, north of San Francisco (approx. 37° N, 123° W). The other population occurred at the ecological preserve at the University of California-Irvine campus in Orange County, south of Los Angeles (approx. 34° N, 117° W). We will refer to these as the "Bodega" and "Irvine" populations throughout. Part of the Bodega population occurs in a grassland community that is exposed to strong, persistent, northwesterly winds. Baccharis from this windy area is always densely branched, prostrate and seldom reaches 1 m in height. In less windy areas, such as Bay Hill, it can reach 1.5 m. In contrast, the Irvine population occurred in a warmer, drier environment approximately 8 km inland. Coastal hills block on-shore winds, and so Irvine plants are

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more arborescent, with open crowns that consistently grow to over 2 m.

The gall midge *R. californica* is a *B. pilularis* specialist that occurs throughout much of the plant's range. Female midges lay clusters of eggs in bud crevices, usually on terminal buds. Eggs hatch in 3–4 d and neonate larvae move deeply into the crevices of the bud to initiate gall formation (Ehler and Kinsey 1993). Gall formation is apparent after 2–3 weeks. Galls are multi-chambered with each chamber housing a single midge. The number of midges per gall can range from 1 to in excess of 50. Pupation occurs within the galls, and adults emerge from the galls at around 40 d. Females can mate and begin oviposition within three hours of eclosion. Adults live for 3 d or less.

If plant genes influencing gall development are also associated with normal growth and development processes (Weis et al. 1988, Price 1991), then genetic differences which underlie morphological differences between the two *Baccharis* populations could also affect their suitability as host plants. The gall forms from tissues normally destined to become leaf and stem, and so genetically influenced differences in these structures could lead to differences in gall structure (Weis et al. 1988). Additionally, plant architectural differences, such as tendency toward tree vs shrub-like growth form, could lead to differences in the number of buds or their availability for oviposition, which in turn could influence vulnerability to attack, as has been seen with gall midges attacking *Salix lutea* and *S. exigua* (Price et al. 1995b).

Materials and methods

We used reciprocal transplant and common garden experiments to determine if the apparent differences between the Bodega and Irvine populations were due to direct environmental effects on growth and development, or if they reflected genetic divergence. In addition, we determined if the reactivity and susceptibility of plants from the two sites arose directly from midge response to adaptive traits, or indirectly through midge response to increased plant vigor brought on by increased adaptation.

Plant propagation

Most experiments used plants cloned by vegetative propagation from mature individuals in the two populations. Cuttings were collected from both populations in the spring of 1992. Actively growing shoots were cut from 10 plants at each site, treated with rooting hormone (Rootone® F), and rooted in a greenhouse misting bench. After roots developed, cuttings were transplanted to 10-cm pots containing a 3:2 mixture of potting soil and sand. Plants were then grown under common greenhouse conditions, with their bench positions randomized. During the spring of 1993, additional copies of each genotype were produced from the greenhouse plants by the same methods. One experiment used greenhouse plants started from wild-collected seed.

Population differences in reactivity to *Rhopalomyia*

Plants from the Bodega and Irvine populations were offered to *R. californica* on a no-choice basis to evaluate differences in reactivity to the midge. The experiment was performed in the greenhouse in January of 1993, using plants propagated directly from cuttings in the spring of 1992 (see above).

The insects were descendants from gall midges collected at Bodega Marine Laboratory (BML). The captive population was reared for one generation on greenhouse plants prior to the experiment. Ventilated plastic vials were attached to galls in situ to capture newly emerged adults for the experiment. Midges were transferred by aspirator to empty vials for mating. We then introduced single mated female midges to plastic oviposition vials affixed to branch tips of either Bodega or Irvine plants. Insects were removed from the plant after one hour.

We collected the resulting galls just after the first adult midges began to emerge (approximately six to ten weeks). Gall diameter was measured and the number of larval chambers per gall was counted. These measures were not significantly different between the different areas within the Bodega population, and so they were pooled for comparison with the Irvine population (Miller 1996). We used a *t*-test for these comparisons; because of unequal variances we used Satterthwaite's approximation to calculate degrees of freedom (Sokal and Rohlf 1981: 408). Larval chamber numbers were square root transformed to correct for scaling of variances to the mean.

Susceptibility in the greenhouse

We tested the susceptibility of the Bodega and Irvine plant populations to oviposition by free-ranging midges in the greenhouse. Two experiments were run in tandem, one utilizing midges collected at Bodega Bay, and one utilizing Irvine-collected midges. Therefore, two isolated greenhouse rooms were used, each with similar arrays of Bodega and Irvine plants, but employing different source populations of *R. californica*. In these experiments, plants from the BML and Bay Hill areas of the Bodega population were treated as if separate populations. For each of the experiments we used eight seed-reared plants from each of the three

populations, for a total of 24 plants. Ovipositing midges emerged from gall-laden plants dispersed throughout each greenhouse room. Thus midges had free choice of host plants.

Susceptibility was measured by counting the total number of galls per plant. Differences among plant populations were compared by ANOVA. For the experiment that used the Bodega midges, we also compared plant populations for the proportion of potential oviposition sites (i.e. branch nodes and developing branches) per branch that were occupied by galls. Gall numbers per plant were logarithmically transformed, and the proportion of oviposition sites occupied was arcsin(square root)-transformed.

Reciprocal transplant experiment in the field

This field experiment had four purposes. The first was to confirm morphological differences between Bodega and Irvine plant populations seen in previous greenhouse experiments (Miller 1996). These differences included a higher density of nodes per branch, smaller leaves with more strongly serrate margins, and a more prostrate growth form in the Bodega population compared to Irvine. Second, was to see if natural infestation rates differed between the two plant populations, and if such differences could be interpreted as a direct consequence of midge response to the morphological differences. The third purpose was to determine if midges also respond more to general plant growth vigor, which should increase in adapted plants. Fourth, we tested if susceptibility for plant genotypes was greater in the native or alien environment.

In January 1994, vegetatively propagated plants were reciprocally transplanted into experimental gardens close to where plants were collected. One garden was established at the University of California-Irvine Arboretum (hereafter referred to as the UCI location) and the other on the natural reserve at the Bodega Marine Laboratory (hereafter referred to as the BML location). Garden sites were within 3 km of the collection sites for the local populations. Since preliminary greenhouse studies showed no morphological differences between Bay Hill and BML areas (Miller 1996), genotypes from both sites were included in the "Bodega" population.

Each garden consisted of three plots with 24 plants each (144 plants per garden). Seven Bodega and six Irvine genotypes were used. An attempt was made to include 2 replicates of each genotype in each plot, although a shortage of 2 genotypes prevented a completely balanced design (Miller 1996). Positions of each plant clone were randomized within the plots.

Plants from the two populations were of approximately equal size at the start of the experiment (ANOVA not significant for branch length). After plants had grown for six months in the two gardens, we measured total plant height, length, and number of nodes on three secondary branches per plant (that is, woody branches sprouting newly elongating lateral buds). We also measured length, width and number of serrations on three fully expanded leaves on each sampled branch. The means of the several branches and leaves sampled per plant were used as the analysis variables for each trait. The volume of surviving plants was estimated (length × width × height) in the spring of 1995.

Data were analyzed as a two-way mixed model MANOVA using PROC GLM (SAS Institute Inc., 1988). The experimental design consisted of two orthogonal main factors, plant origin (Bodega vs Irvine) and garden location (BML vs UCI), with plant genotype nested within plant origin. An additional level of nesting, that of plots within location, was initially incorporated in the experimental design. This level was dropped from the final analysis because in most cases it was far from significant, and because its inclusion would limit denominator degrees of freedom for testing main effects. Plant origin and garden location were treated as fixed effects, and genotype and the interactions as random effects. Survivorship of plants was also monitored throughout the study, and population differences assessed by separate χ^2 test of homogeneity for the two garden locations.

The same experiment also tested for population differences in susceptibility under field conditions. To assure adequate midge population sizes, we placed potted, gall-laden plants from the greenhouse among the garden plants. Midges used at each garden location (UCI or BML) were native to that site. Some of the experimental plants produced no galls, and these "zero" scores produced a bimodal distribution for the "galls per plant" variable. To eliminate bimodality, and to satisfy parametric assumptions, replicates within genotype were pooled, i.e., the "raw data" for the analysis was the mean number of galls per plant for each genotype. One-way ANOVAs were performed separately on the log + 1 transformed data from the two garden locations.

Results

Reactivity and susceptibility in the greenhouse

In no-choice oviposition trials, the Bodega and Irvine populations of *Baccharis pilularis* were equally susceptible to *Rhopalomyia californica* collected from Bodega Bay. Neither number of larval chambers in terminal galls, the diameter of terminal galls (Fig. 1) nor the total number of larval chambers per plant ($t = 0.188$, d.f. = 44, $P = 0.85$) differed between populations. Thus, Bodega and Irvine plant populations appeared equally reactive to the northern midge population.

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Fig. 1. Gall diameter at terminal buds, and number of larval chambers in terminal galls of Bodega and Irvine plants exposed to Bodega-collected *R. californica* in greenhouse confined oviposition trials.
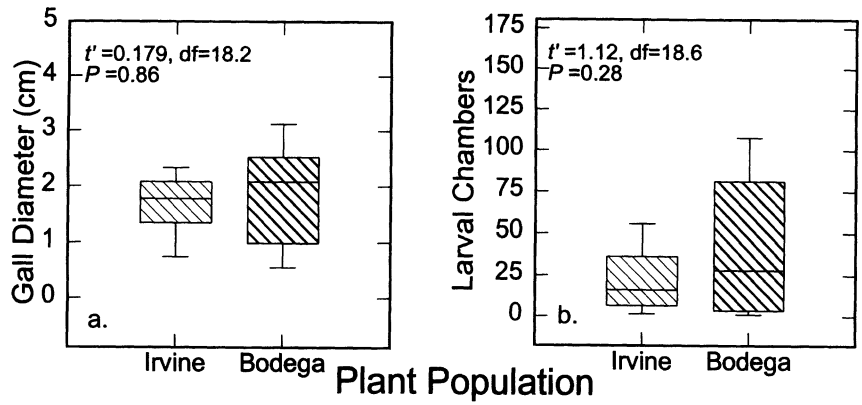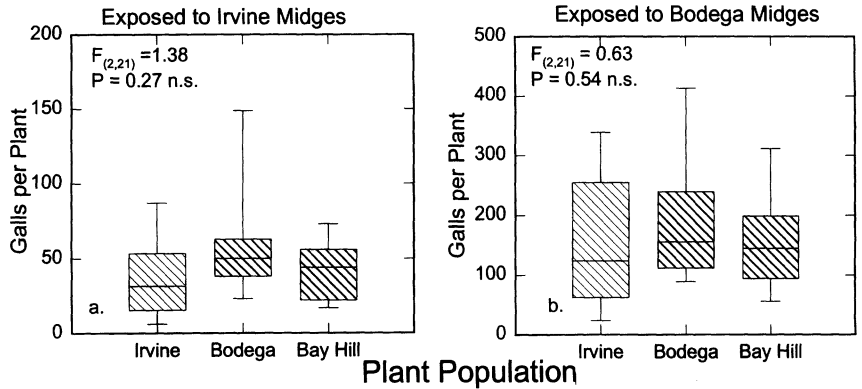
$t' = 0.179$, df=18.2
$P = 0.86$

$t' = 1.12$, df=18.6
$P = 0.28$

Fig. 2. Number of galls on greenhouse plants exposed to *R. californica* from Irvine and Bodega populations.

Exposed to Irvine Midges
$F_{(2,21)} = 1.38$
$P = 0.27$ n.s.

Exposed to Bodega Midges
$F_{(2,21)} = 0.63$
$P = 0.54$ n.s.

When allowed free access to plants in greenhouse rooms, Bodega and Irvine *R. californica* infested the two plant populations equally. In neither of the tandem experiments did the total number of galls per plant differ between plant populations (Fig. 2). As in other experiments, responses of plants from the BML and Bay Hill areas of the Bodega population were indistinguishable. Galling rates on the different plant populations by Bodega midges were indistinguishable even when calculated on the basis of galls per potential oviposition site (Fig. 3). Thus, neither *R. californica* population showed evidence of strong preferences for their native host population within the confines of the greenhouse.

Morphological comparisons and susceptibility in the field

Identical genotypic arrays of Bodega and Irvine plants were compared after growing for six months in contrasting environments (UCI and BML). All MANOVA main effects (plant population, garden location, and genotype within population) and their interactions, had significant effects on morphology (Table 1). However the individual plant characters had various responses to the treatments, as revealed by univariate ANOVA (Table 2). Among the three leaf characters (length,

width and number of teeth), only the first differed between the two populations, with Irvine leaves being the longer (Fig. 4a). However, genetic variation within populations was evident for all three. No leaf traits differed due to the direct effects of garden location, but length and width were significantly affected by the interaction of population origin with garden location.
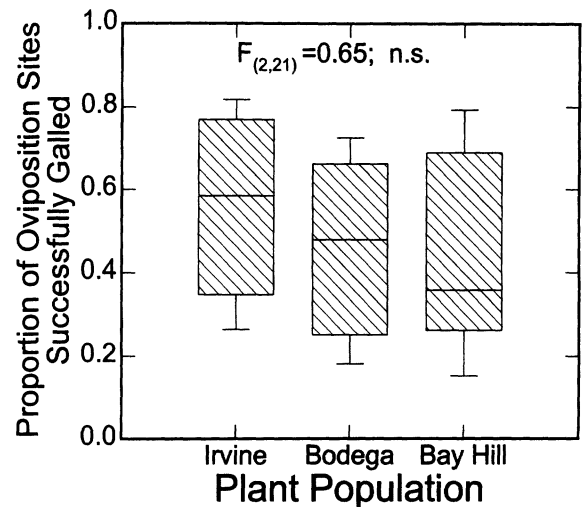
$F_{(2,21)} = 0.65$; n.s.

Fig. 3. Proportion of nodes and axillary branches with galls along the mature branches of Bodega and Irvine plants. Plants were reared in the greenhouse and exposed to Bodega midges.

Table 1. Results of multivariate analysis of variance based on July 1994 morphological comparisons of Bodega and Irvine plants in reciprocal field plots at UCI and BML. Significance levels for Wilks' Lambda are presented.

Effect	λ	F-value	d.f.	P
Population origin	0.07	192.53	7,102	<0.0001
Garden location	0.21	56.16	7,102	<0.0001
Genotype(Population)	0.007	618.7	77,618.7	<0.0001
Location × Population	0.57	10.93	7,102	<0.0001
Location × Genotype(Pop.)	0.22	2.34	77,618.7	<0.0001

Table 2. Univariate analyses of variance on the effect of plant origin, location of planting, and genotype on seven morphological traits of *Baccharis pilularis*. Measures were taken in July 1994, approximately six months after establishment of field plots.

Source	d.f.	MS	Error	F values						
				Leaf length	Leaf width	Teeth per leaf	Plant height	2° Branch length	Nodes per 2° branch	Internode length
Population origin	1	M1	M3+M4−M5	5.50**	1.26	0.64	1.41	0.93	33.02**	4.75
Garden location	1	M2	M4	1.12	0.15	2.02	5.52	5.82	14.09	1.61
Genotype(Population)	11	M3	M5	31.08***	12.1**	4.85**	1.37	3.15*	2.43†	3.79*
Location × Population	1	M4	M5	14.13**	23.23***	0.04	16.82**	6.40*	0.69	5.24*
Loc × Geno.(Pop.)	11	M5	M6	0.60	0.87	1.68	2.70**	2.12*	1.88*	6.36***
Error	108	M6								

†$P < 0.10$; *$P<0.05$; **$P<0.01$; ***$P<0.001$.

Overall, leaves on Bodega plants were smaller in the alien UCI garden than their native BML garden, while Irvine plants were more constant between the two.

Among the stem characters (plant height, secondary branch length, nodes per branch and internode length), only number of nodes differed between populations (Fig. 5, Table 2). Within-population genetic variation was observed for branch length, internode length and node number, but not height (Table 2).

Populations differed in susceptibility to wind pruning, as was revealed by strong effects of the population × location interaction effect on plant height, branch length and internode length (Fig. 5). Irvine plants were twice as tall in their native UCI garden than when grown as aliens in the BML location. Bodega plants were also taller in the UCI garden than their native BML location, but only by one third. This suggests that the non-native Irvine plants were severely wind pruned on the BML coastal bluff. Bodega plants are genetically shorter, and so were less affected by wind. In the absence of strong and persistent winds at the UCI location, the genetically determined taller stature of the Irvine plants became apparent. Number of nodes per branch did not show a significant population × location interaction (Fig. 5c). All stem characters showed small but significant effects caused by the interaction between genotype within populations and garden location (Table 2).

The differential performance of Irvine and Bodega plants at BML was obvious when plant survivorship was compared after 16 months, in spring of 1995. Of 26 plants that died since planting at BML, 22 of them were the alien Irvine genotypes ($G_{adj} = 13.46$, d.f. = 1, $P < 0.001$). Thus, Bodega genotypes were better adapted to

the northern, coastal environment than Irvine types. At Irvine, survivorship of plants from both populations was high. Only two Irvine and three Bodega plants died. However, Irvine plants did grow larger than Bodega plants in the UCI environment, as measured by crown volume (Irvine, 0.411 ± 0.038 m³; Bodega, 0.285 ± 0.027 m³; $F_{(1,65)} = 7.89$; $P < 0.007$). While architectural differences among plant populations contributed to the disparity in plant sizes, general appearances suggested that Bodega plants were less vigorous at UCI than the Irvine plants.

Patterns of susceptibility to midge attack mirrored differences in stem characters. At BML plants from the two populations had similar attack rates but at UCI, Irvine plants had on average 4 times more galls than Bodega plants (Fig. 6, Table 3). This difference is greater than can be attributed to crown volume alone, especially when one considers that the less-preferred Bodega plants had more nodes, and thus more oviposition sites, per stem than the more-preferred Irvine plants (Fig. 5c).

Discussion

We found that coyote brush populations from contrasting habitats are genetically differentiated. For some characteristics the degree of genetic differentiation expressed phenotypically depended on the developmental environment. Susceptibility to attack by the gall midge *R. californica* was one such environment-dependent difference; the Bodega and Irvine populations were equally susceptible in the BML location, but in the UCI garden, Bodega plants suffered less attack. Vulnerabil-

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Fig. 4. July 1994 comparison of selected leaf traits on Bodega and Irvine plants grown in reciprocal common gardens at Bodega Marine Lab and the U. C. Irvine Arboretum. Standard errors shown.
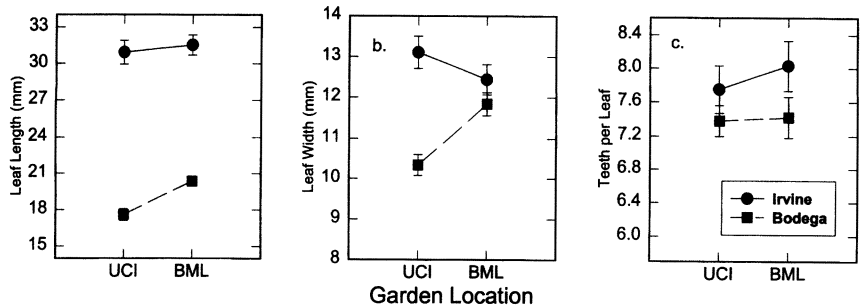
ity to attack was associated with plant height. In this final section we will discuss the nature of the environment-dependent expression of genetic differences, and how they relate to Price's Plant Vigor Hypothesis (Price 1991).

Plant differentiation

Previous greenhouse experiments had revealed population differentiation between plants from the Bodega and Irvine populations (Miller 1996). The garden experiment demonstrated that two differences, leaf length and nodes per branch, had genetic components that were consistent between the contrasting developmental environments at BML and UCI (population effect significant, Table 2). More often, population differences were seen only in the UCI environment. These interpretations must be viewed with caution. While each genotype was replicated several times in each garden, each population was represented by a small number of genotypes. This left limited degrees of freedom to test the population effect, and so small genetic differences that are stable across environments may have gone undetected. On the other hand, even with the limited number of genotypes, environment-dependent differences were seen in 5 of the 7 morphological traits examined.

The phenotypic convergence of Irvine and Bodega plants at the BML garden was apparently caused by
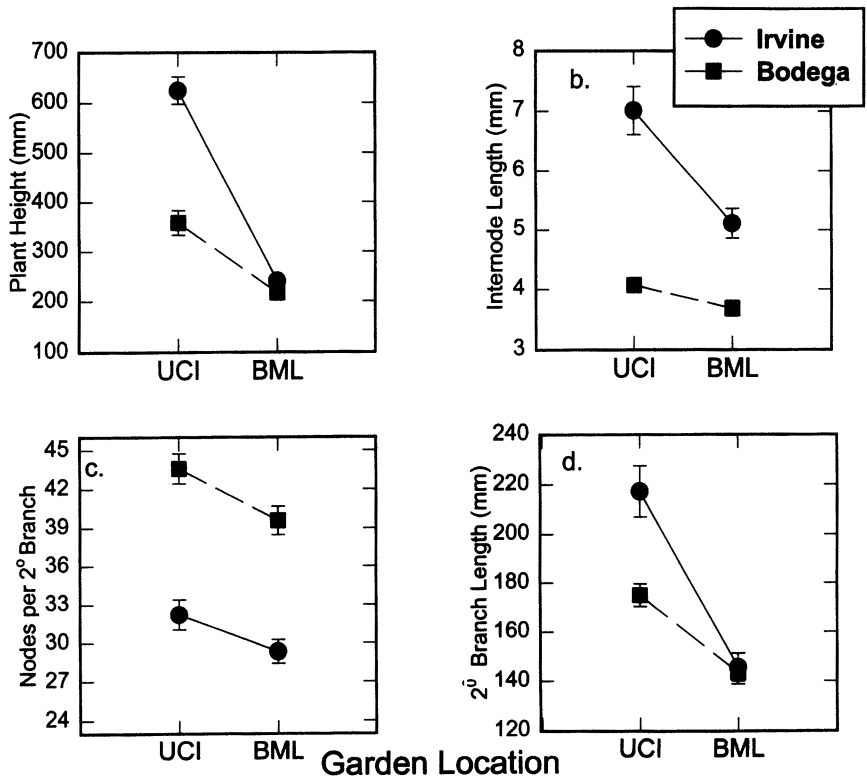

Fig. 5. July 1994 comparison of selected morphological traits on Bodega and Irvine plants grown in reciprocal common gardens at Bodega Marine Lab and the U. C. Irvine Arboretum. Standard errors shown.

BML Garden

Galls per Plant (y-axis: 0, 5, 10, 15, 20, 25, 30, 35)

$F_{(1,11)} = 0.12$
$P = 0.73$ n.s.

a.

Irvine   Bodega

UCI Garden

Galls per Plant (y-axis: 0, 5, 10, 15, 20, 25, 30)

$F_{(1,11)} = 39.2$
$P < 0.0001$
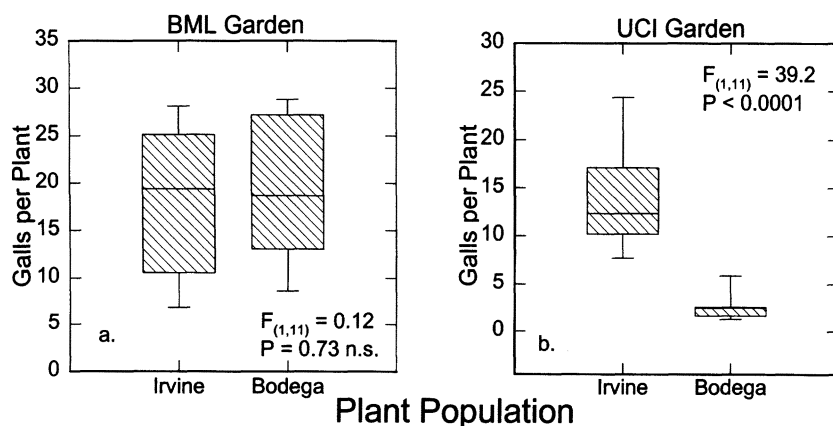
b.

Irvine   Bodega

Plant Population

Fig. 6. Number of galls on plants from the Irvine and Bodega populations grown in the two field plots, UCI and BML. Plants were exposed to the *R. californica* native to the plot location.

wind pruning. Irvine plants are much lankier than those from Bodega and breakage and tip dieback were frequently observed on Irvine plants at the windy BML garden. After six months, the branch length and total height of the Irvine plants was essentially the same as the Bodega plants at this location. Bodega plants were also shorter at the BML garden than at UCI.

It seems paradoxical that survivorship for the two populations differed most in the environment in which they were morphologically similar while their survivorship was the same in the environment in which they were morphologically different. This paradox is easily resolved. The shortened stature of Bodega plants at the BML location is apparently a developmental adaptation that reduced wind pruning. In contrast, a similar phenotype is caused in the Irvine populations at BML by non-adaptive vulnerability to wind. Wind pruning was probably one cause of high mortality of Irvine plants at BML, but differences in temperature, soil type and salinity, and additional osmotic stress from marine aerosols may have also contributed. In the more benign UCI location, the full genetic potential of the Irvine plants became apparent and they outgrew the Bodega plants; however, the benign conditions also allowed high survivorship for both populations. It appears that adaptation to the maritime environment has not come at the cost of survivorship in more inland habitats.

Susceptibility and reactivity to *R. californica*

How does the genetic differentiation of *B. pilularis* populations influence susceptibility and reactivity to the gall midge? Greenhouse experiments revealed no differences. In the no-choice experiment that used Bodega gall midges, Irvine and Bodega plants produced the same size of galls with the same mean number of larvae (Fig. 1). Although the number of eggs per oviposition site were not counted, our observations during and after oviposition gave no suggestion that one plant population receive more eggs than the other. One intriguing, but unexplained, observation is the higher variance in the number of larvae per gall on the Bodega plant population.

The free-choice experiments in the greenhouse and the reciprocal transplant experiments in the field show seemingly inconsistent differences in midge preference for the two plant populations. When plants were offered to the two midge populations in the neutral greenhouse setting there were no plant population differences in the total number of galls formed or in the number of galls per potential oviposition site. Likewise, at the BML garden there was no difference in infestation per plant. However, at the UCI garden Irvine plants had significantly more galls than those from the Bodega population.

We believe that the apparent inconsistency is a result of a midge preference for plants projecting above the surrounding canopy. The greenhouse used plants that were a few months post-germination, before population differences in stature were apparent. Thus there may not have been sufficient size contrast between the two plant populations in the greenhouse experiment for midges to discriminate between them. At the BML site, wind pruning prevented the Irvine plants from achieving their potential height, and so this cue was not

Table 3. One-way ANOVA contrasts of gall number among Irvine and Bodega plants when exposed to native insects at either the UCI or BML experimental gardens. Gall number was logarithmically transformed for analysis.

Dependent variable	Sums of squares		F	P
	Among populations (d.f. = 1)	Error (d.f. = 11)		
No. of galls on plants in Bodega	0.006	0.574	0.12	0.73
No. of galls on plants in Irvine	1.8	0.51	39.2	<0.0001

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available to midges. Thus it is possible that the UCI garden was the only environment in which the genetic differences in height had the opportunity to result in differences in infestation. In several other systems it has been noted that gallmakers preferentially oviposit on long shoots or tall plants (Craig et al. 1986, Walton et al. 1990, Price and Ohgushi 1995, Abrahamson and Weis 1997).

The data give no indication that the midges exercise a preference between the plant populations after the midge lands on the plant. When confined, the Bodega midges readily oviposited on either plant. The free-choice experiment did not reveal a post-landing preference, but we must warn that a weak preference could have been hidden by the high infestation levels achieved in that experiment. If midges relax their preferences as favored sites are usurped by earlier ovipositions, those preferences can go undetected at high infestation levels, just as it would not be possible to detect moviegoers' preferences for seats in the center of the theatre if the show is sold out. The percentage of potential gall sites occupied in the greenhouse (over 40% on average, Fig. 5) was many times higher than is normally observed in the field, where parasitoids, predators and environmental factors keep *R. californica* at low densities (Ehler et al. 1984, McFayden 1985, Briggs 1993), and so mothers may have been forced to accept less desirable sites.

Population differentiation and the plant vigor hypothesis

Price (1991) has proposed that herbivorous insects, particularly specialized species like gallmakers, will preferentially infest vigorous plants because these often supply superior or more concentrated resources. As a consequence, herbivore carrying capacity may be set by the availability of *vigorous* plants and plant parts rather than plant biomass generally. A number of studies have lent support to the Plant Vigor Hypothesis (Price 1991, Price et al. 1995a, Preszler and Price 1995, Vieira et al. 1996, Woods et al. 1996). However, a variety of selective factors will act on plant vigor, such as plant-plant competition and abiotic conditions. This means that vigor-mediated susceptibility to attack can evolve in response to these other selective agents as a genetically correlated character.

In the Introduction we raised the possibility that when plant genotypes disperse into new regions, alien environmental stresses could lower vigor, which in turn could lower herbivore attack rates. Our experimental results do not support this hypothesis. At the BML garden, the maladapted Irvine genotypes did not suffer any less attack than the locally adapted Bodega genotypes. It is true that at the UCI garden the alien Bodega genotypes were less infested than the more vigorous, and locally adapted, Irvine genotypes. However, the

low vigor of Bodega plants was not induced by the stress of the alien UCI environment. In fact Bodega plants in the alien environment grew more vigorously than in their native region. It is quite possible that the lower susceptibility of Bodega plants could be frequency-dependent at a very local scale; Bodega plants might have been attacked at high rates by Irvine midges if none of the taller Irvine plants were available. Midge preferences for the Irvine plants might only be expressed when plants are presented in a mixture, where the size contrast is evident.

Some implications for understanding plant-herbivore evolution

In the decades since publication of seminal papers by Fraenkel (1959), Ehrlich and Raven (1964), Feeny (1976), Rhoades and Cates (1976), and more recently by Coley et al. (1985), the study of plant-herbivore interactions has been dominated by the notion that susceptibility to attack is determined mainly by plant traits that function solely or at least predominantly as defenses. Plant secondary chemicals have of course received the most attention in this regard, and convincing examples of a selective advantage to chemical defense have been described (e.g., Berenbaum et al. 1986, Mauricio and Rausher 1997). However, selection is opportunistic, and there is no logical reason to preclude the possibility that traits serving other important functions can be modified to enhance their defensive aspects (Craig et al. 1988, Berenbaum 1995). Taking the argument a step further, multi-functional traits that affect susceptibility may evolve primarily through selection on their non-defensive functions. Jermy (1976, 1993) has made similar arguments, but they are flawed by the incorrect assertion that insects act as selection agents only if they limit plant population recruitment. Our study shows that *Baccharis* susceptibility to *Rhopolomyia* attack is mediated in part by a fundamentally and non-defensive plant character, i.e., stature. This may seem a trivial result, but we would argue that nature could be full of instances in which seemingly "trivial" relationships have a large effect on variation and abundance of herbivorous insects. Concentrating only on traits with explicit defensive function could lead to a distorted picture of the role of plant evolution on the ecology of insect herbivores.

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