Research article

Assessment of correlational selection on tolerance and resistance traits in a host plant–parasitic plant interaction

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Abstract. Resistance and tolerance are considered to be different plant strategies against disease. While resistance traits prevent hosts becoming parasitized or reduce the extent of parasitism, tolerance traits reduce the fitness-impact of parasitism on infected hosts. Theoretical considerations predict that in some circumstances mutual redundancy will give hosts with either high resistance or high tolerance a fitness advantage over hosts that exhibit both of these traits together. However, empirical evidence has provided mixed results. In this paper, I describe the pattern of phenotypic selection imposed by the holoparasitic mistletoe *Tristerix aphyllus* upon resistance (spine length) and tolerance (branching) traits in the cactus *Echinopsis chilensis*. Results indicate that branching was an efficient compensatory mechanism, reducing 75.5% of the fitness-impact attributable to parasitism. Even though both traits showed a negative correlation, as expected from the presence of allocation costs between strategies, no correlational selection coefficient was significant indicating that selection did not favor alternative combinations of traits. Consequently, I did not find evidence for selection promoting mutually exclusive defense strategies against the mistletoe, which suggests that tolerance and resistance traits may coexist stably in populations of *E. chilensis*.

Key words: host–parasite interaction, phenotypic selection, plant defense strategies

Introduction

Understanding the conditions under which hosts evolve defensive traits against natural enemies is one of the central questions in evolutionary ecology (see reviews in Karban and Baldwin, 1997; Strauss and Agrawal, 1999; Agrawal, 2000; Stowe *et al.*, 2000). Most host organisms can respond to enemy attack either through resistance and/or tolerance mechanisms. There is an important conceptual distinction between resistance and tolerance. While resistance refers to traits that prevent infection or limit its extent, tolerance refers to traits that do not necessarily reduce or eliminate infection, but instead reduce its fitness consequences (Burdon, 1987; Fineblum and Rausher, 1995; Roy and Kirchner, 2000). Unlike resistance, tolerance mechanisms often involve some degree of compensation capacity, such as the ability of plants to regrow and/or reproduce after damage (Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999). Although different lines of correlative and experimental evidence support an adaptive role for resistance traits (e.g., Rausher and Simms, 1989; Simms and

Rausher, 1989; Núñez-Farfán and Dirzo, 1994; Mauricio and Rausher, 1997; Mauricio et al., 1997; Shonle and Bergelson, 2000), much less is known about the maintenance and evolution of tolerance traits in natural plant populations. Understanding the set of conditions under which natural selection favors one or both strategies is currently an active line of research. Van der Meijden et al. (1988) first suggested that resistance and tolerance represent alternative rather than complementary plant strategies to cope with disease. Implicit in this argument is the presence of allocation costs measurable as a fitness reduction. While some studies on the evolution of plant defense suggest that negative genetic covariances between resistance and tolerance will select hosts with high resistance or high tolerance over hosts that exhibit both of these traits together (e.g., Fineblum and Rausher, 1995; Stowe, 1998), other studies have documented patterns of separate and joint selection on resistance and tolerance traits indicating complementary rather than alternative strategies (e.g., Mauricio et al., 1997; Agrawal et al., 1999; Tiffin and Rausher, 1999; Juenger and Bergelson, 2000).

Tolerance mechanisms against disease usually involve an alteration in the host phenotype. While this phenomenon has been extensively documented in the host–parasite literature (e.g., Lobue and Bell, 1993; Mouritsen and Jensen, 1994; Ballabeni, 1995; Vance, 1996; Ness and Foster, 1999), the extent to which host phenotype modification is adaptive remains controversial (e.g., Stamp, 1981; Poulin, 1994; Poulin and Thomas, 1999). From the host perspective, the phenotypic change may be adaptive only if the modification is accompanied by a reduction in fitness-impact from parasites, and parasitized hosts still contribute offspring to the next generation. Parasites are known to affect animal host fitness through changes in a wide range of phenotypic traits including physiological (e.g., Poulin and Thomas, 1999), behavioral (e.g., Moore, 1983; Gotelli and Moore, 1992; Hechtel et al., 1993; Yan et al., 1994), and morphological characters (e.g., Mouritsen and Jensen, 1994; Ballabeni, 1995; Vance, 1996). Situation in plants is less understood. For instance, the extent to which parasitism has a real fitness impact and evolutionary significance for plant host populations has been only recently begun to be assessed (e.g., Haukioja, 1991; Roy, 1993; Rosenthal and Kotanen, 1994; Tuomi et al., 1994; Marquis, 1996; Shykoff et al., 1997; Shykoff and Kaltz, 1998; Medel, 2000).

Parasitic plants constitute about 1% of flowering plants with approximately 3000 described species (Kuijt, 1969; Musselman and Press, 1995; Norton and Carpenter, 1998). About 20% of species are holoparasitic and, unlike hemiparasitic species, they lack chlorophyll and cannot fix atmospheric carbon dioxide. Because holoparasites lack leaves, or possess leaves reduced to small scales, they depend entirely on their hosts for water, inorganic nutrients, and carbon-containing compounds. This singularity makes them suitable organisms for studying the impact of parasitism on the plant host phenotype. In this

paper I present data on the adaptive value of defense mechanisms in *Echinopsis chilensis* (Cactaceae) against the holoparasitic mistletoe *Tristerix aphyllus* (Loranthaceae). I analyze the magnitude, sign, and form of the phenotypic selection coefficients on tolerance and resistance traits. More specifically, I address the following questions: (1) Does branching compensate for the fitness-impact of parasitism? Because the spines of *E. chilensis* have been previously documented to represent the first line of resistance against *T. aphyllus* (Medel, 2000), simultaneous consideration of the within-population variation of resistance (spines) and tolerance (branching) traits will allow to address comparative questions such as (2) Does parasitism select for independent and/or correlated tolerance and resistance traits?, and (3) Is there a trade-off in the selection surface upon tolerance and resistance in *E. chilensis* against the mistletoe?

Materials and methods

Natural history and study site

Tristerix aphyllus is a leafless holoparasitic mistletoe that parasitizes only species of the family Cactaceae in the arid and semiarid regions of Chile. The only vector species for the holoparasite is the Chilean mockingbird, *Mimus thenca* (Mimidae). Once defecated by the bird, the mucilaginous seed adheres to the surface of cactus, most of the time to taller columns (Martinez del Río et al., 1995). The seed elongates a reddish radicle which often contacts the cactus cuticle to form an haustorial disk from which the entrance to the internal tissues is effected (see morphological details in Mauseth et al., 1984, 1985). Once inside, the mistletoe develops vegetatively and adheres to the phloematic vessels of the cactus. The only portion that emerges from the cactus tissues is the red inflorescence, ~1 year after successful infection (Botto-Mahan et al., 2000). *Echinopsis* (*Trichocereus*) *chilensis* is a columnar cactus species endemic to the arid and semiarid regions of Chile. Individuals are tall (mean (m) $\pm$ SD, 2.10 $\pm$ 0.51, $n = 225$), and the growth pattern is basitonic with 1–5 columns arising directly from the ground. The fitness impact of *T. aphyllus* on *E. chilensis* ranges from a reduction in flower and fruit production to a complete suppression of reproduction (Silva and Martinez del Río, 1996; Medel, 2000).

This study was conducted during 1994–1995 at the Reserva Nacional Las Chinchillas (31°30′ S, 71°06′ W, IV Región, Chile), ~300 km north Santiago, and 60 km east from the Pacific coast. Climate of the 4229 ha topographically rugged area is of a semiarid Mediterranean type with long lasting droughts, and unusual years with high precipitation that seemingly concurs with El Niño Southern Oscillation (ENSO) events. The prevalence of parasitism is variable

across populations, ranging from 15.6–44.4% ($n = 10$ populations) (mean number of *E. chilensis* per site = 254.1, range: 225–282). Vegetation is thornscrub with *Bahia abrosioides*, *Fluorensia thurifera*, and *Porlieria chilensis* as the more common shrub species. Cactus species inhabit equatorial facing-slopes and consist on the columnar *E. chilensis* and *Eulychnia acida*, and the globular *Opuntia berteroniana* and *Eriosyce sandillon*.

Field procedure

Echinopsis chilensis is distributed in relatively discrete populations. To assure that subsequent analysis includes only reproductive individuals, I tagged every cactus exceeding 0.5 m height in a population located at Quebrada Torca in the reserve. A total of 225 individuals (125 parasitized and 100 not parasitized) were considered, and their number of branches, spine length, and height were recorded as phenotypic traits. I considered stems longer than 15 cm as a branching unit in every analysis. Mean spine length per individual was estimated from five spines on the top of columns. Each spine was measured with a caliper (precision 0.1 mm). Different lines of correlative and experimental evidence have previously demonstrated spine length represents the first line of defense of *E. chilensis* against *T. aphyllus*. Long spine-lengthed individuals are avoided as perching sites by birds responsible of parasite transmission, which results in a lower infection rate by *T. aphyllus* in comparison to short spined individuals (Medel, 2000). The height of cacti was measured from the ground level to the top of the tallest column. To compare the branching process in the presence and absence of *T. aphyllus*, I quantified the branching curves of 53 *E. chilensis* by using Cody's procedure (1984, 1986). This method consists on recording the number of branches intersected by an imaginary plane set up at increasing height intervals above ground, and then drawing an envelope of the size-specific branching curves. This approach to cactus branching design assumes each individual is a vertical system unit from which branching occurs. To prevent a potential covariance of the architectural phenotype with the height or age of the plant (see Coleman *et al.*, 1994), I selected individuals as similar as possible in height (CV: 11.4%).

The impact of parasite load on cactus fitness was assessed on 125 parasitized *E. chilensis*, that is, excluding the not parasitized subpopulation. Two components of parasite load were considered. First, I recorded the number of inflorescences of the mistletoe on the cactus surface. Because more than one genet of *T. aphyllus* may eventually emerge from about the same position on the cactus surface, making difficult to assure plant individuality, I considered discrete inflorescence aggregates as the reproductive unit of the mistletoe. This assumption is justified because *T. aphyllus* presents a well defined reproductive unit at least 1 year after experimental infection on previously not parasitized cacti (Botto-Mahan *et al.*,

2000). Second, I recorded the number of ripe fruits (crop size hereafter) of *T. aphyllus* on cacti every 20–25 days from May to December, a period that comprises the entire dispersal season of the mistletoe. To assess the functional relationship between cactus defense traits and cactus fitness, I considered fruit production as the first fitness component (w_1) of cacti. I counted the number of fruits produced by *E. chilensis* during three consecutive months that included the entire dispersal season of *E. chilensis* (November–January). A second fitness component (w_2) consisted on the mean number of seeds produced per fruit of cactus. I removed fruits from every reproductive individual (mean number of fruits removed = 3.43, range: 1–13) and dissected them in the laboratory for seed counting. A third product-estimate fitness component (w_3) was calculated from $w_1 w_2$. Because *E. chilensis* reproduces once a year, I measured fitness separately for, 1994–1995. The role of spine length to prevent parasitism and the infection rate suffered by cacti did not vary between years (Medel, 2000). Consequently, I used cumulative fitness data for the 2 years in subsequent analyses.

Statistical analyses

To quantify the compensatory capacity of branching in parasitized *E. chilensis* I constructed a path diagram of causal relationships and assessed the adequacy of the hypothesized model by structural equation modeling (SEM) using EQS (Bentler, 1995). The power of SEM analysis to test evolutionary and ecological hypothesis has been stressed by several authors (e.g., Crespi and Bookstein, 1989; Crespi, 1990; Mitchell, 1992). This modeling procedure is a form of path analysis that allows one to analyze more complex sets of causal relationships (see reviews in Dunn *et al.*, 1993; Byrne, 1994). Advantages of SEM analysis include: (i) the potential to test statistically the fit between the hypothesized causal model with the covariance structure of the observed data, and (ii) the feasibility to introduce factors representing theoretical constructs into the causal network, provided they summarize the mean, variance, and covariance between the observed variables. I estimated a factor reflecting parasite load from the linear combination of equations for, (i) inflorescence number and, (ii) parasitic crop size, measured as the maximal number of ripe fruits in a cactus. Similarly, a second latent variable reflecting total fitness was estimated from the linear equations for fitness components w_1 and w_2.

I estimated the linear and nonlinear selection coefficients for resistance and tolerance traits by following the standard procedure for phenotypic selection analysis (Lande and Arnold, 1983). Absolute individual fitnesses were relativized by dividing them by the population mean absolute fitness. Traits were log-transformed and standardized to have zero mean and unit variance before analyses. I assessed the form of the fitness surface by using the univariate version of the cross-validation cubic spline suggested by Schluter (1988).

Results

Relationship between parasitism and cactus phenotype

Comparison of the branching curves between parasitized and not parasitized individuals revealed that status of parasitism and height of measurement were important factors in accounting for the total variation in the number of intersected branches of *E. chilensis* (Two-way ANOVA, F_{status}: 120.09, $p < 0.001$; F_{height}: 94.57, $p < 0.001$; $F_{status \times height}$: 10.74, $p < 0.001$; df = 1,19; Fig. 1). Most significant effects between parasitized and not parasitized cacti occurred in the range 1.0–2.2 m (Tukey's difference method) and the greatest impact of *T. aphyllus* on the branching pattern occurred at 1 m height, where parasitized cacti showed 3.6 more branches on the average than not parasitized individuals (Fig. 1).

To evaluate whether parasitism influences the stem shedding process, I tagged columns from 171 parasitized and 85 not parasitized cacti and assessed them for stem shedding after 14 months. Seventy three stems out 171 parasitized cacti, and two stems out 85 not parasitized cacti were shed (42.7 and 2.3%, respectively) (Yates corrected χ^2 (1) = 42.67, $p < 0.001$), indicating that parasitism by *T. aphyllus* is an important factor affecting stem shedding in *E. chilensis*. However, this does not imply *T. aphyllus* is the only causal factor for stem shedding in the study site. Other factors such as fungus attack and wind exposure may also contribute to explain stem shedding in this species.
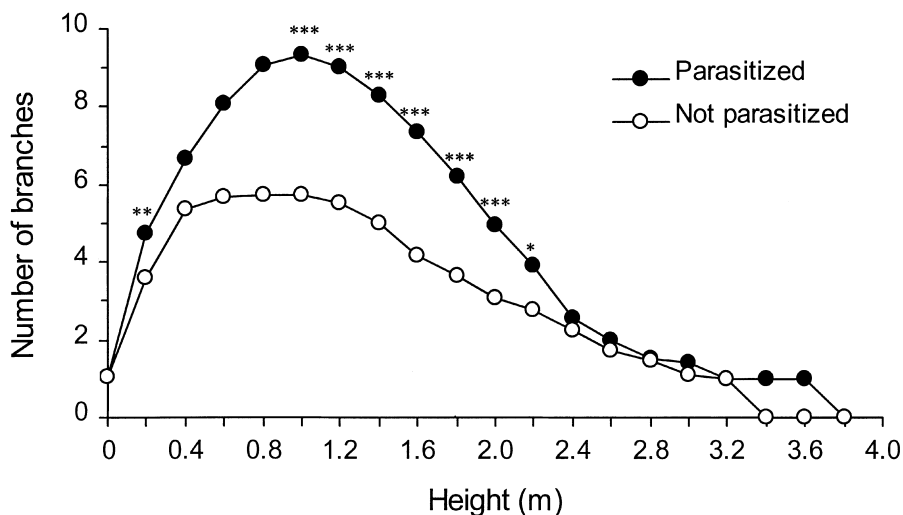

Figure 1. Branching curves of 28 parasitized and 25 not parasitized *E. chilensis* by using Cody's procedure (1984, 1986). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Results from SEM analysis revealed a negative path coefficient between parasite load and host fitness (−0.384). The parasite load factor, however, showed a positive and significant effect on the branching of cacti (0.61), which in turn had a significant effect on the host fitness factor (0.48) (Fig. 2). Applying the chain rule for sequential path coefficients, the indirect effect of parasite load on host fitness can be calculated from the product $0.61 \times 0.48 = 0.290$. Because the net impact of parasite load on the cactus fitness results from summing the direct and indirect effects, it follows that $(−0.384) + (0.290) = −0.094$, value that represents a 75.5% reduction in the fitness-impact relative to the direct effect. The hypothesized model showed a good fit with the covariance structure of data (Bentler-Bonner normed fit index = 0.983), which indicates that the hypothesized causal network was statistically supported.

Correlation and selection coefficients for tolerance and resistance

Mutually exclusive defense strategies have been suggested to evolve from simple trade-offs in allocation rules in limited resource environments (Van der Meijden *et al.*, 1988). I assessed for a potential allocation trade-off between
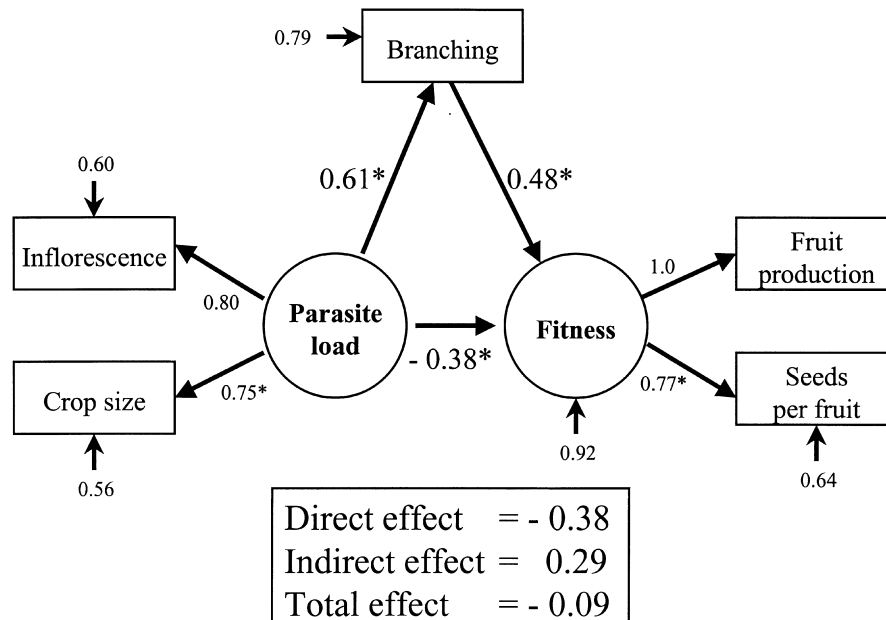

Figure 2. Path diagram of causal relationships among factors parasite load (inflorescence and crop size), total host fitness (fruit production and seeds per fruit), and branching. The indirect effect of parasite load on host fitness was calculated from the product of sequential path coefficients. *$p < 0.05$.

resistance and tolerance by comparing the magnitude of traits in parasitized and not parasitized population fractions. While the parasitized subpopulation had more branching than not parasitized individuals (Fig. 3a, mean ± SE, parasitized: 7.82 ± 0.45, not parasitized: 5.35 ± 0.10, $F(1.216) = 20.04$, $p < 0.001$), parasitized individuals had shorter spines than not parasitized cacti (Fig. 3b, mean (cm) ± SE, parasitized: 10.53 ± 0.21, not parasitized: 11.76 ± 0.20, $F(1.216) = 17.97$, $p < 0.001$). These results did not differ when cactus height was included as covariate (branching: $F(1.215) = 11.42$, $p < 0.001$; spine length: $F(1.215) = 12.73$, $p < 0.001$).

The significance of linear gradients of selection (β) for branching was contingent on the population subset that was analyzed. While positive significant gradients for an increasing branching were prevalent in the parasitized subpopulation, no significant negative directional selection coefficient for this trait was detected in the not parasitized subpopulation. Pooling subpopulations, significant directional selection for increasing branching was detected only in the fruit production fitness component (Table 1). Regarding spine length, β coefficients were generally low in magnitude (range: 0.043–0.154) and
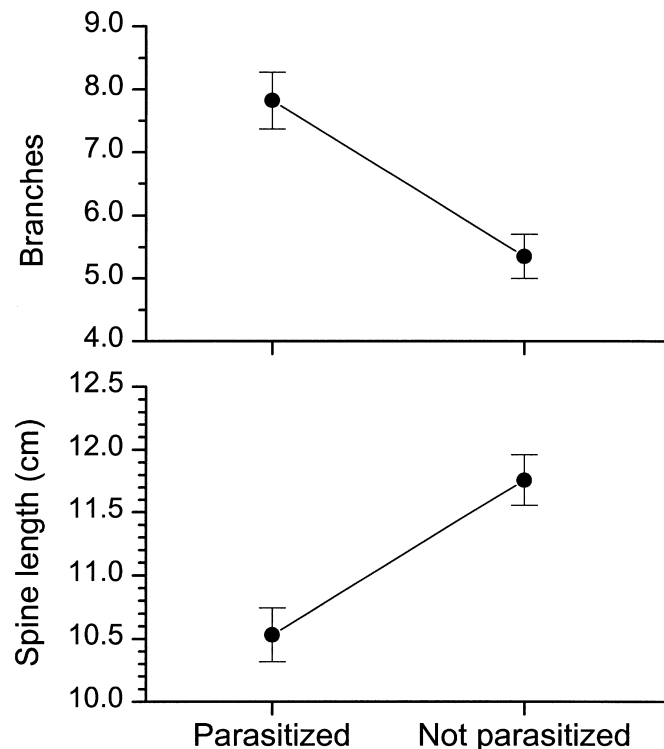

Figure 3. Mean branching (a) and spine length (b) values in the parasitized and not parasitized subpopulations of *E. chilensis*. Bars indicate ±1 SE.

nonsignificant, indicating absence of directional selection in every dataset that was analyzed.

Most nonlinear γ_{ii} parameter estimation showed convergence in the range of 10–20 iterations. Quadratic coefficients for branching were positive and significant in the parasitized subset and in the pooled population, indicating a disruptive-like form of selection upon this character (Table 1, Fig. 4). Nonlinear selection on spine length followed a different pattern. Positive and significant γ coefficients were detected in the not parasitized subpopulation, indicating a disruptive-like form of selection upon spine length. Finally, correlational γ_{ij} selection coefficients for branching and spine length were nonsignificant, indicating absence of joint selection for tolerance and resistance traits in *E. chilensis* (Table 1).

Discussion

Many studies have documented increased tolerance via the release of apical dominance and subsequent release of lateral dormant buds after experimental or natural damage (e.g., Paige and Whitham, 1987; Bergelson and Crawley, 1992). Tuomi *et al.* (1994) demonstrated that compensatory capacity is highest when dormant buds are most easily activated after apical damage. Most columnar cacti have strong apical dominance, and substantial branching occurs when apical dominance from the tip of columns is released (Gibson and Nobel, 1986). In this paper, I have presented evidence that branching compensates 75.5% of the overall fitness-impact of *T. aphyllus* on *E. chilensis*. Like most tolerance mechanisms in plants, this compensatory capacity may result from improved photosynthetic capacity. Because cactus morphology and stem height affect substantially the photosynthetically active radiation (PAR) interception (Nobel, 1980, 1981), it is possible that an increasing branching conveys an increasing surface area for PAR interception.

Theory predicts that if resistance and tolerance both have costs, their mutual redundancy will give hosts with either high resistance or high tolerance a fitness advantage over hosts that exhibit both of these traits together (van der Meijden *et al.*, 1988). In spite of, empirical evidence on the pattern of selection on resistance and tolerance has provided mixed results. For example, while Mauricio *et al.* (1997) failed to detect a joint pattern of selection promoting mutually exclusive evolutionary strategies in *Arabidopsis thaliana*, Tiffin and Rausher (1999) documented significant correlational selection gradients for *Ipomoea purpurea*. In this paper, the pattern of selection acting on branching was independent of spine length, indicating that selection did not favor combinations of traits. There are several potential reasons for the lack of correlational selection. First, it is possible that total lifetime fitness rather than

Table 1. Linear (β) and nonlinear (γ) gradients of selection for branching (B) and spine length (S) on parasitized, not parasitized and pooled data. Correlational selection coefficients are depicted for $B \times S$. w_1 is fruit production, w_2 is seed number per fruit, and $w_1 w_2$ is a product-estimate fitness component indicating total seed ouput

Fitness component	Character	Parasitized		Not parasitized		Pooled	
		β	γ	β	γ	β	γ
w_1	Branching (B)	$0.301 \pm 0.095^*$	$1.232 \pm 0.526^{**}$	0.131 ± 0.123	0.445 ± 0.724	$0.157 \pm 0.077^{**}$	$0.841 \pm 0.323^{***}$
	Spine length (S)	0.113 ± 0.092	2.129 ± 3.439	-0.116 ± 0.103	$6.684 \pm 2.766^{**}$	0.051 ± 0.071	2.193 ± 1.883
	$B \times S$		0.790 ± 1.071		0.070 ± 1.077		0.570 ± 0.663
w_2	Branching (B)	$0.265 \pm 0.096^*$	$1.561 \pm 0.575^*$	-0.061 ± 0.124	0.253 ± 0.827	0.022 ± 0.078	$1.032 \pm 0.366^*$
	Spine length (S)	0.043 ± 0.093	0.350 ± 3.754	-0.080 ± 0.104	$6.863 \pm 3.161^{**}$	0.048 ± 0.071	2.199 ± 2.131
	$B \times S$		1.273 ± 1.169		0.028 ± 1.231		0.490 ± 0.750
$w_1 w_2$	Branching (B)	$0.261 \pm 0.097^*$	1.627 ± 1.003	0.033 ± 0.124	0.159 ± 0.759	0.022 ± 0.077	$1.052 \pm 0.550^{\dagger}$
	Spine length (S)	0.047 ± 0.094	0.705 ± 6.555	-0.154 ± 0.103	$10.039 \pm 4.420^{**}$	0.048 ± 0.071	1.583 ± 3.206
	$B \times S$		0.993 ± 2.041		0.581 ± 1.397		0.392 ± 1.128

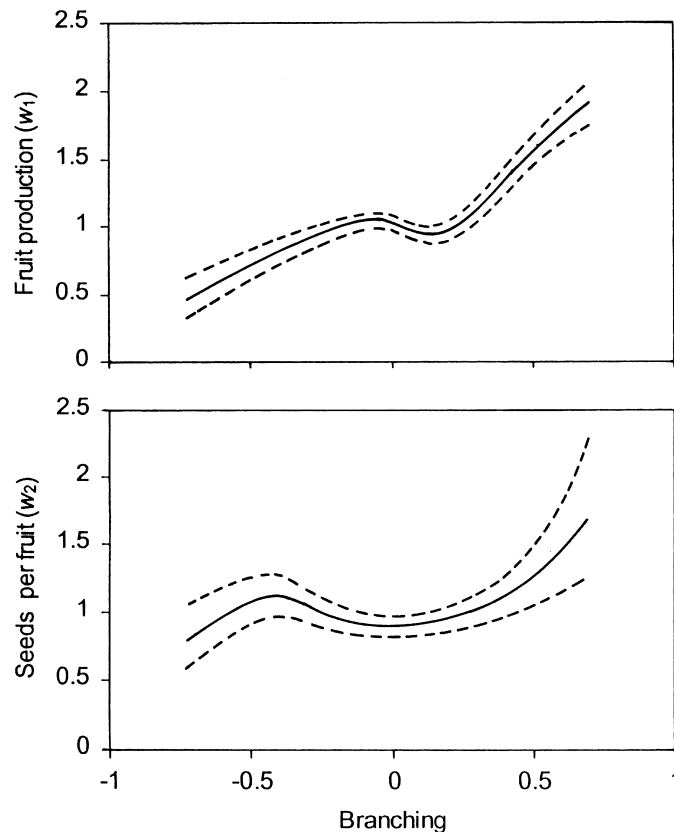$^* p < 0.01$; $^{**} p < 0.05$; $^{***} p < 0.001$; $^{\dagger} p = 0.057$.

Figure 4. Cubic spline estimates ($\lambda = 10$) for branching in the pooled population. Confidence intervals were estimated from 5000 bootstrap replications (see Schluter, 1988).

partial fitness measurements account better for the within-generation selective impact of parasitism on long-lived hosts. The impact of parasite-mediated selection seems to be contingent on the abiotic scenario experienced by cacti in the study site (Medel, 2000). For instance, the fraction of the total variance in cactus fitness that was accounted for by *T. aphyllus* during 1994–1995 was relatively small, ranging from 8.4–15.5%, depending on the fitness component that was considered (Medel, 2000). If long-lived hosts can adjust their reproductive effort according to environmental conditions, annual estimates of correlational selection may capture a small segment of the real within-population selection regime. Estimates of phenotypic selection on periods longer than the 2 years covered in this study are necessary to assess this possibility. Second, selection on plant defense traits is usually assessed in relation to female fitness components, assuming that pollen characters are not affected by allocation costs. However, recent work suggests that costs of tolerance may be

better expressed on male rather than on female fitness components (Agrawal *et al.*, 1999). Because direction, shape and magnitude of phenotypic selection usually differ between sex functions in plants (e.g., Campbell *et al.*, 1991; Conner *et al.*, 1996; Maad, 2000), estimates of selection coefficients for resistance and tolerance that are based only upon female fitness components may obscure the real pattern of selection on defense strategies. Third, the idea that resistance and tolerance constitute alternative evolutionary strategies lies on the critical assumption that allocation costs between traits exist. However, if costs of both resistance and tolerance are lacking, then the selection pattern on either defense component need not be constrained by the other. Even though genetic correlations were not measured in this study, absence of genetic correlation between resistance and tolerance traits has been observed in other plant systems, suggesting that the maintenance of defense traits may result as by-product from other unrelated selective regimes with no obvious cost for plant fitness (e.g., Simms and Triplett, 1994; Mauricio *et al.*, 1997; Tiffin and Rausher, 1999, but see Fineblum and Rausher, 1995; Stowe, 1998).

The observed pattern of selection was more complex than expected on the basis of a trade-off between traits. Phenotypic selection on branching was of a disruptive-like form, suggesting that absence and total tolerance may be favored over intermediate levels. Interestingly, other studies assessing the pattern of selection on resistance and tolerance have also unexpectedly detected disruptive selection for tolerance traits (Mauricio *et al.*, 1997; Tiffin and Rausher, 1999). There are at least two potential reasons for this pattern. First, it is possible that branching due to parasitism correlates with branching attributable to other environmental stressful conditions. For example, selection may indirectly increase branching under water and nutrient limitation (Maschinski and Whitham, 1989; Juenger and Bergelson, 1997), and in situations of high competition and shading from neighboring plant species (Bergelson and Crawley, 1992; Paige, 1992). For instance, the branching pattern of columnar cacti depends, among other things, from the surrounding habitat and growth habit of the coexisting cactus species (Cody, 1984, 1986). If this last situation applies to *E. chilensis*, then the fitness advantage of extreme phenotypes may be better explained by the immediate influence of neighboring plants rather than from adaptedness to parasite-mediated selection. Rausher (1992) raised the interesting possibility that environmental factors unrelated to selection may influence both phenotype and fitness occasioning a biased estimate of phenotypic selection gradients. According to this author, in the absence of information about potential environmental-induced correlations, conclusions from studies of phenotypic selection should be interpreted as preliminar to experimental studies. Clearly more work is necessary to examine this possibility in long lived cacti. Second, recent models predict that the evolutionary trajectories of resistance and tolerance are contingent to the prevalence of parasitism within populations (Roy and Kirchner, 2000). When a host

population receives low parasitism, that is, expresses high resistance, parasites may select for increased resistance rather than increased tolerance. On the contrary, when a host population shows high parasite prevalence, that is, expresses low resistance, parasites may select for increased tolerance rather than increased resistance. Current levels of resistance and tolerance may arise from a mixture of propagules coming from populations that differ in their levels of parasitism. Because the incidence of parasitism is variable across populations at the Reserve (see Natural history and study site section), it is possible that new populations of *E. chilensis*, by chance, are founded by propagules coming either from low parasitized populations and highly parasitized populations, thus evolving toward absence and complete tolerance. Recent geographic mosaic theory of coevolution emphasizes that variable gene flow among populations may lead to differences in the way populations respond to the same selective agent across sites (see Thompson, 1994, 1999; Lively, 1999). If sufficient gene flow exists across populations, the level of tolerance and resistance expressed in one environment may be constrained by levels expressed in other environment, obscuring any local correlational selection toward alternative defense strategies. Additional work is needed to understand the importance of geographical scale processes on the local evolutionary dynamics of host defensive traits.

Acknowledgements

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