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Natural selection on ecophysiological traits of a fern species in a temperate rainforest

Alfredo Saldaña · Christopher H. Lusk · Wilfredo L. Gonzáles · Ernesto Gianoli

Abstract   Unlike other species of the genus *Blechnum*, the fern *Blechnum chilense* occurs in a wide range of habitats in Chilean temperate rainforest, from shaded forest understories to abandoned clearings and large gaps. We asked if contrasting light environments can exert differential selection on ecophysiological traits of *B. chilense*. We measured phenotypic selection on functional traits related to carbon gain: photosynthetic capacity (A_{max}), dark respiration rate (R_d), water use efficiency (WUE), leaf size and leaf thickness in populations growing in gaps and understorey environments. We assessed survival until reproductive stage and fecundity (sporangia production) as fitness components. In order to determine the potential evolutionary response of traits under selection, we estimated the genetic variation of these traits from clonally propagated individuals in common garden experiments. In gaps, survival of *B. chilense* was positively correlated with WUE and negatively correlated with leaf size. In contrast, survival in shaded understories was positively correlated with leaf size. We found positive directional fecundity selection on WUE in gaps population. In understories, ferns of lower R_d and greater leaf size showed greater fecundity. Thus, whereas control of water loss was optimized in gaps, light capture and net carbon balance were optimized in shaded understories. We found a significant genetic component of variation in WUE, R_d and leaf size. This study shows the potential for evolutionary responses to heterogeneous light environments in functional traits of *B. chilense*, a unique fern species able to occupy a broad successional niche in Chilean temperate rainforest.

A. Saldaña (✉) · E. Gianoli
Departamento de Botánica, Universidad de Concepción, Casilla 160-C, Concepción, Chile
e-mail: asaldana@udec.cl

C. H. Lusk
Deparment of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

W. L. Gonzáles
Departamento de Ciencias Biológicas y Fisiológicas, Facultad de Ciencias y Filosofía,
Universidad Peruana Cayetano Heredia, Lima 3, Peru

Introduction

Ferns (Pteridophyta) have been on earth for more than 300 million years and
comprise over 11,000 living species distributed worldwide and exhibiting remarkable
diversity in form and habit (Raven et al. 1999). Most pteridophytes live in moist and
shady environments (Page 2002; Aldasoro et al. 2004; Karst et al. 2005). Fern species
are dependent upon a moist environment for the growth of their nonvascular
gametophyte generation (Page 2002). Hydraulic characteristics of fern foliage
determine a poor control of water conduction and loss (Woodhouse and Nobel 1982;
Robinson 1994; Brodribb and Holbrook 2004). Despite these constraints some fern
species are able to establish in high-irradiance sites (Saldaña et al. 2005) and tolerate
soil water deficits (Page 2002), thus having a wide ecological breadth.

The maintenance of a positive carbon balance in a wide range of environments is
a key feature of plant species with ample ecological breadth (Chazdon 1992; Spencer
et al. 1994; Sultan et al. 1998). Leaf ecophysiological traits such as photosynthetic
capacity, dark respiration rate, instantaneous water use efficiency (WUE), leaf size
and leaf thickness have significant influence on net carbon gain, and hence on
components of plant fitness (Givnish 1988; Chazdon 1992; Reich et al. 1998; Lambers
et al. 1998; Ackerly et al. 2000; Wright et al. 2004). Several studies have reported the
adaptive value of leaf ecophysiological traits (Chapin et al. 1993; Dudley 1996;
Ackerly et al. 2000; Geber and Griffen 2003). In order to establish that a functional
trait is adaptive for a given environment, a significant influence on plant fitness for
that trait should be determined (Phillips and Arnold 1989; Dudley 1996; Ackerly
et al. 2000). Phenotypic selection analysis describes the relationship between traits
and fitness and can be used to test for adaptive hypotheses (Lande and Arnold 1983;
Endler 1986). If the traits under selection are also heritable, evolutionary change in
these traits could proceed in the population (Simms and Rausher 1992; Geber and
Griffen 2003). There is evidence of genetic variation and differential selection of
ecophysiological traits in contrasting environments in flowering plant species
(Dudley 1996; Ackerly et al. 2000; Arntz and Delph 2001; Ludwig et al. 2004).
However, there is paucity of research on the adaptive value and potential evolu-
tionary response of functional traits in populations of fern species.

This study addressed natural selection on ecophysiological traits of the fern
species *Blechnum chilense* (Pteridophyta, Blechnaceae) in a temperate rainforest in
southern Chile. Unlike some of its congeners, *B. chilense* has considerable ecological
amplitude, growing in different successional positions ranging from shaded forest
understories to abandoned clearings and large gaps (Saldaña et al. 2005). Variation
in leaf functional traits appears to be an important mechanism of acclimation of *B.
chilense* to this wide range of light environments (Saldaña et al. 2005). We asked
whether selection on ecophysiological traits of *B. chilense* acts differentially in open
and shaded understorey environments. This was considered likely as the life cycle of
B. chilense is short relative to the lifespans of the tree species whose growth and
mortality control most of the variation in light environments associated with patch
dynamics. First, we measured phenotypic selection on several ecophysiological traits

of ferns growing in large gaps and forest understories. In this analysis two components of plant fitness—survival and reproductive output—were assessed. Second, we estimated the genetic variation in those ecophysiological traits by means of cloned ferns originating from gap and understorey individuals of *B. chilense*. We hypothesized that selection in the forest understorey should favour ecophysiological traits that optimize light capture while in gaps it should favour traits that reduce water loss.

Materials and methods

Study species and sites

Blechnum chilense (Kaulf.) Mett. is a fern species native to central and southern Chile (30°40′S–52°36′S). This species has an erect rhizome of 10–30 cm height, dimorphic leaves (vegetative and fertile fronds, 50–150 cm length), petiole of 1/4–1/3 of leaf length, and sori covered by continuous indusium (Marticorena and Rodríguez 1995). The pinnae of the fertile fronds are very fine, being markedly reduced in width. Sporangia are accordingly very small (ca. 90 μm length). Plants reach reproductive maturity around 10–12 months after the emergence of the sporophyte (Rodríguez 1973). *B. chilense* is able to spread by rhizomes sending up new crowns around the main plant (Rodríguez 1973). We studied *B. chilense* populations located in large gaps (>2.500 m^2) and shaded forest understories. In order to maximize the sample size and minimize the occurrence of particular ''site'' effects other than those related to the light environment, we pooled four gap populations (located less than 2 km apart) and three understorey populations (located less than 2 km apart). To avoid spurious relationships between fitness and ecophysiological traits in the analysis of the pooled data, we assessed whether there were significant differences in fitness and ecophysiological traits among the study sites within each environment. We did not find any significant effect of sites in plant fitness or leaf functional traits (data not shown). Consequently, we hereafter refer to one gap population and one understorey population, and analyses were performed accordingly. Gaps and understories differed greatly in light availability but not in average density of *B. chilense* (Saldaña et al. 2005). All sites lay in the old-growth temperate rainforest at Parque Nacional Puyehue (40°39′S, 72°11′W; 350–400 m a.s.l.), in the western foothills of the Andes in southern Chile. The climate is maritime temperate, with an average annual precipitation of 3,500 mm (Almeyda and Sáez 1958). The old-growth rainforest of the lower western slopes of the Andes is composed exclusively of broad-leaved evergreen species (Saldaña and Lusk 2003).

Field data

For the selection analysis, one hundred juvenile individuals of *B. chilense* were randomly marked in each of two populations located in contrasting light environments: large gaps (30.0–65.0% canopy openness) and shaded understorey (2.0–4.0% canopy openness). Ten metres was the minimal distance among marked individuals, to ensure the independence of samples. Two LAI-2000 plant canopy analysers (LI-COR, Lincoln, Nebraska, USA) were used to quantify the light environment of

each individual. One instrument was used to take measurements at 50 cm height above each sampling point, while the other, placed at the centre of a 2-ha clearing, was programmed to take readings at 30 s intervals. Integration of data from the two instruments enabled estimation of percentage diffuse non-intercepted irradiance at each sampling point within the forest, equivalent to percentage canopy openness over the quasi-hemispherical (148°) view field of the LAI-2000 sensors.

Several ecophysiological traits were measured on vegetative leaves of each marked individual at the beginning of the study in March 2004. All tagged individuals were 7–9-month-old juvenile sporophytes, characterized by the presence of the first fern leaf (primofrond) and low number of fronds (Rodríguez 1973; Pérez-García et al. 1996). We carried out gas exchange measurements between 24 and 31 March 2004 using a CIRAS II portable infrared gas analyser and leaf chamber (PP Systems, Hitchin, England). Photosynthetic capacity (A_{max}) and stomatal conductance were measured at PAR 1,000 μmol m^{-2} s^{-1}, assumed to be a saturating level. Dark respiration rate (R_d) was measured at PAR 0 μmol m^{-2} s^{-1}. Cuvette temperatures were 18–20°C. Gas exchange was measured between 9:00 a.m. and 3:00 p.m. Instantaneous WUE was calculated as the ratio of photosynthetic capacity to stomatal conductance. Leaf size (area) was estimated by means of digital photography and later analysis with Sigma-Scan Pro5 software (SPSS Inc, Chicago, IL, USA). Leaf thickness was measured with a digital calliper (0.01 mm sensitivity; Mitutoyo, Kanagawa, Japan). Leaf size and thickness were measured on two fully expanded leaves per plant. The average of the two measurements was used as an individual value.

Survival of marked plants was recorded monthly for 13 months, between March 2004 and April 2005. Fecundity was measured in each surviving individual of *B. chilense* that presented fertile fronds 12 months after the ecophysiological traits measurements. Reproductive output was estimated from sporangia production. The number of sporangia per mm^3 was counted in one pinna using a stereomicroscope (Nikon, Fukuoka, Japan), then multiplied by total number of pinna of the frond and total number of fertile fronds, thus estimating reproductive output of individuals. A total of 23 understorey plants and 25 gap plants lost their number tags during the study and hence were omitted from the analyses.

Genetic variation

In order to estimate the genetic variation of fern ecophysiological traits, common garden experiments were established on May 2004 in both open and shaded environments. Three 25 m^2 plots were established in open environments (30.0–65.0% canopy openness) and three 25 m^2 plots in shaded understories (2.0–4.0% canopy openness). A pair of LAI-2000 canopy analysers was used to verify canopy openness at each plot.

Blechnum chilense can be propagated by rhizome separation (Rodríguez 1973; Saldaña et al. 2005). Fifteen juvenile mother plants were obtained in each light environment, and each plant was separated into three fragments. Thus, one clone from each of 15 genotypes was planted in each one of three 25 m^2 plots established in both light environments (one clone × three plot × 15 genotypes = 45 individuals per light environment). Seven months later (December 2004) measurements of A_{max}, R_d, WUE, leaf size and leaf thickness were carried out in each fern individual.

Data analysis

To characterize the study populations, we compared means of ecophysiological traits and fecundity with *t*-tests, and survival with a log-rank chi-square test. To test adaptive hypotheses, for each light environment we calculated selection gradients, which assessed the covariance between fitness (survival and sporangia production) and the standardized ecophysiological traits (Mean = 0; SD = 1). These metrics estimate selection on a trait in terms of the effect on relative fitness in units of phenotypic standard deviations of the trait, allowing comparisons among traits and fitness components (Kingsolver et al. 2001). Selection gradients estimate the selection acting directly upon the focal trait, independent of selection on correlated traits that have also been included in the analysis. Linear selection gradients (β) assess the magnitude of directional selection; nonlinear selection gradients (γ) assess the form (curvature) of the selection function (Lande and Arnold 1983).

Although we calculated both linear and quadratic coefficients of the regression to estimate directional and stabilizing/disruptive selection gradients, respectively, the latter were not regarded. This was done because significant quadratic terms in the analysis ($\gamma \neq 0$) were due to a change in the slope of the fitness function rather than to the occurrence of minimum/maximum fitness values (data not shown) and hence did not reflect true stabilizing/disruptive selection (Mitchell-Olds and Shaw 1987). Directional selection gradients were obtained from linear regression of relative sporangia production on each functional trait (GLM, Statistica 6.0, StatSoft Inc., Tulsa, OK, USA). We estimated selection gradients only for R_d, WUE, leaf size and leaf thickness to avoid spurious correlations caused by including traits that are mathematical functions of each other (Dudley 1996). Consequently, A_{max} was not included in this analysis because it is a mathematical function of WUE. Because the survival measure was dichotomous (alive or dead) and may violate parametric assumptions of normality, we used multivariate nonparametric logistic regressions (Janzen and Stern 1998) to evaluate if specific ecophysiological traits were related to survival in each light environment. Finally, we estimated coefficients of phenotypic correlations among traits obtained from Pearson correlation matrix to rule out collinearity among traits.

In each light environment, the genetic variation of ecophysiological traits was separately estimated using ANOVA. Plot and Genotype were considered random factors. A significant effect of Genotype for a given trait would indicate that there is genetic variation for that trait. A potential limitation of this experiment is that the phenotype of ferns obtained from clonal propagation may include a carry-over effect from the maternal environment (Lynch and Walsh 1998).

Results

Field data

The five ecophysiological traits measured showed significant differences between *B. chilense* populations from gaps and forest understories (Table 1). Fern individuals at open sites showed thicker fronds and higher photosynthetic capacity (A_{max}) and dark respiration rate (R_d) than individuals at shaded sites. WUE was greater and leaves were smaller in gaps. Whereas average fecundity in the gap population was

Table 1 Mean values (± SE) of ecophysiological traits and survival of *Blechnum chilense* in each light environment

Trait	Gaps	Forest understorey
Photosynthetic capacity (μmol CO_2 m^2 s^{-1})	6.75 ± 0.33	3.18 ± 0.16
Dark respiration (μmol CO_2 m^2 s^{-1})	0.94 ± 0.04	0.34 ± 0.03
Water use efficiency (μmol CO_2/mol H_2O)	0.068 ± 0.003	0.043 ± 0.003
Leaf size (cm^2)	86.32 ± 6.33	157.09 ± 11.50
Leaf thickness (mm)	0.27 ± 0.01	0.14 ± 0.01
Survival	80%	83%

Gaps population: $N = 100$; Understorey population: $N = 100$. All ecophysiological traits showed significant differences between environments (*t*-test, $P < 0.01$)

Table 2 Phenotypic correlations between ecophysiological traits of *Blechnum chilense* in two light environments

	Photosynthetic rate	Dark respiration	Water use efficiency	Leaf area	Leaf thickness
Photosynthetic rate	–	0.41**	0.42***	0.18	0.33**
Dark respiration	–0.18	–	0.34**	0.15	0.33**
Water use efficiency	–0.01	–0.12	–	0.19	0.32*
Leaf area	0.61***	–0.03	0.11	–	0.39**
Leaf thickness	–0.06	0.36**	–0.11	0.13	–

The Pearson coefficients of correlation are shown for the forest understorey population (*below the diagonal*) and the gap population (*above the diagonal*)

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

significantly greater than in the understorey population (*t*-test, $F_{1,122} = 13.64$, $P < 0.001$), fern survival did not differ between these two environments ($\chi^2 = 0.244$, $P = 0.621$; Table 1). The phenotypic correlations among traits varied in each environment (Table 2). In gaps, leaf thickness was positively correlated with all ecophysiological traits. Leaf thickness was positively correlated with dark respiration in understorey plants (Table 2). WUE, dark respiration and photosynthetic rate were positively interrelated in gaps. At shaded sites, leaf size showed a positive correlation with photosynthetic rate and leaf thickness with dark respiration (Table 2).

The multivariate logistic approach showed that smaller leaf size and WUE increased fern survival in the gap population, and higher leaf size increased fern survival in understories (Table 3). Regarding fecundity selection gradients, positive and significant directional selection was detected only for WUE in gaps (Table 4; Fig. 1), while in the forest understorey population there was negative directional selection on R_d and positive directional selection on leaf size (Table 4; Fig. 2).

Common garden experiment

Significant differences in functional traits among genotypes (clones) were found in both environments (Table 5). No trait showed significant effects of plot (Table 5). At open sites, only WUE and leaf size exhibited genetic variation. At shaded sites

Table 3 Partial coefficients of multiple logistic regression of *Blechnum chilense* survival against ecophysiological traits in each light environment

Trait	Partial Coeff	
	Gaps	Forest understorey
Dark respiration	0.50	0.72
Water use efficiency	2.09**	2.02
Leaf size	–1.85**	4.55**
Leaf thickness	1.27	2.23

Gaps population: $N = 75$; Understorey population: $N = 77$. The overall model for each environment was significant (Gaps: $\chi^2 = 34.47$, $P < 0.001$; Understorey: $\chi^2 = 39.08$, $P < 0.001$)

** $P < 0.01$

Table 4 Linear standardized selection gradients of *Blechnum chilense* fecundity against ecophysiological traits in each light environment

Trait	β	
	Gaps	Forest understory
Dark respiration	0.05 ± 0.07	$–0.14 \pm 0.05$**
Water use efficiency	0.29 ± 0.06***	$–0.01 \pm 0.04$
Leaf size	$–0.09 \pm 0.07$	0.37 ± 0.04***
Leaf thickness	0.03 ± 0.05	$–0.01 \pm 0.04$

Gaps population: $N = 60$; Understorey population: $N = 64$. The overall model for each environment was significant (Gaps: $R^2 = 0.49$, $P < 0.001$; Understorey: $R^2 = 0.48$, $P < 0.001$)

** $P < 0.01$

*** $P < 0.001$

there was genetic variation in R_d, leaf size and leaf thickness (Table 5). There was genetic variation in each ecophysiological trait that was under directional selection in the same light environment (Table 4). Thus, we detected potential for evolutionary responses in these traits.

Discussion

The differences in trait expression between light environments (Table 1) are in accordance with the functional value ascribed to these traits (Geber and Dawson 1990; Sultan et al. 1998; Dudley 1996; Ackerly et al. 2000; Arntz and Delph 2001). For instance, whereas smaller and thicker leaves allow a reduction in transpiring leaf surface in exposed, dry environments, the opposite trend is beneficial in shade because light capture surface is maximized per unit of leaf mass (Givnish 1987). We found that different ecophysiological traits were selected in *B. chilense* populations growing in gaps and understories. This pattern may be related to the distinctive ecological breadth of this fern species. As predicted, selection favoured traits related to water economy in the gap population, while in the understorey population traits linked to light capture and net carbon balance were optimized (Fig. 1, 2; Tables 3, 4). Ecophysiological traits associated to carbon gain can be linked with plant survival

Fig. 1 The relationship between relative fecundity (*sporangia production*) and water use efficiency in gaps population. *X*-axis was standardized (Mean = 0, SD = 1)
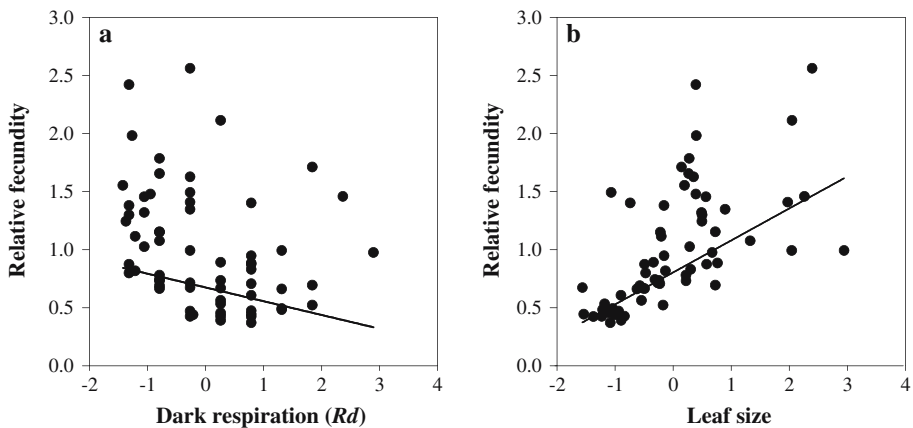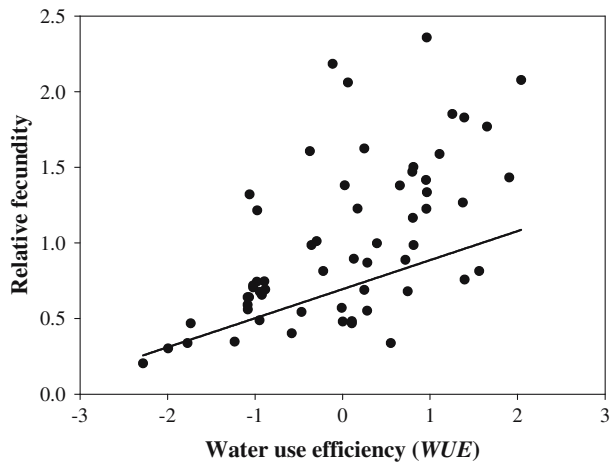
Fig. 2 The relationship between relative fecundity (*sporangia production*) and (**a**) dark respiration rate, and (**b**) leaf size in understorey population. Both leaf traits were standardized (Mean = 0, SD = 1)

through its influence on biomass allocation, morphological characteristics and defence against herbivores (Kitajima 1994).

Results support earlier contentions that the control of water loss is critical for the establishment of plants in open habitats (Smith and Huston 1989). In this temperate rainforest seasonal drought may occur after forest clearing (Huber and López 1993), thus *B. chilense* individuals growing in gaps may be under some degree of drought stress. High WUE was found to be adaptive for the *B. chilense* gap population (Fig. 1; Tables 3, 4). This agrees with functional predictions that high WUE is more critical when water availability is likely to be a limiting factor (Ehleringer 1993; Dudley 1996). As we found for *B. chilense*, Dudley (1996) reported that leaf size and WUE of a succulent herb typical of sandy beaches were positively correlated in a dry environment. In this regard, a general mechanistic linkage has been proposed: small leaf size is associated with small boundary layer that reduces leaf temperature and

Table 5 Genetic analysis of ecophysiological traits of *B. chilense* in open sites and shaded forest understorey

Gaps	Ms genotype	Ms plot	Ms error
Photosynthetic capacity	6.89	4.45	10.95
Dark respiration	0.11	0.22	0.20
Water use efficiency	0.01***	<0.01	0.01
Leaf size	4743.25***	18.28	5.75
Leaf thickness	0.01	0.02	0.01
Understorey	Ms genotype	Ms plot	Ms error
Photosynthetic capacity	0.46	0.76	0.43
Dark respiration	0.15***	0.10	0.03
Water use efficiency	<0.01	<0.01	0.01
Leaf size	12395.74***	12.10	13.46
Leaf thickness	0.01***	<0.01	0.01

Plot and Genotype were random factors in the ANOVA

*** $P < 0.001$

hence transpirational water loss (Givnish 1987). Although leaf size was not correlated with fecundity in open sites (Table 4), survival in this population was highest for individuals with small leaves (Table 3). This supports earlier claims that, because plant fecundity and survivorship are not necessarily related, both fitness components should be measured in order to estimate the overall effects of natural selection (Primack and Kang 1989).

Results are consistent with the idea that natural selection in shaded environments favours plants expressing traits, which maximize net energy capture in low light (Givnish 1988). In the forest understorey, phenotypic selection favoured ferns with low R_d and larger fronds. A study of 38 woody perennial species by Falster and Westoby (2003) reported that leaf size was positively correlated with light interception efficiency. Our finding of strong positive directional selection on leaf size in the understorey points to optimization of light capture. Similarly, our finding of selection for low-respiration rates in the shade is consistent with across-species studies reporting low-metabolic rates in shade-adapted taxa (e.g. Grime 1965; Loach 1967; Lusk and Reich 2000; Lusk 2002).

Those ecophysiological traits that underwent significant selection showed genetic variation and hence potential for evolutionary response. Genetic variation in ecophysiological traits such as A_{max}, WUE and leaf size has been reported previously only for flowering plants (Geber and Dawson 1990). Patterns of phenotypic selection on and genetic variation in WUE, in the gap population, and R_d and leaf size, in the understorey population, suggest that evolution in these traits may account for the ample ecological breadth of *B. chilense*. However, projections of evolutionary responses in the wild based only in clone analysis must be interpreted with caution because of maternal effects and probable overestimation of genetic variation (Simms and Rausher 1992; Lynch and Walsh 1998).

Forest gap dynamics determine the occurrence of spatial and temporal environmental variability (Denslow 1987), and habitats in different stages of gap regeneration differ in light availability and moisture (Chiariello 1984; Walters and Field 1987). Phenotypic selection and evolutionary response in ecophysiological traits could be elicited under changing environments such as when gaps are created or closed. We suggest that *B. chilense* ability to occupy a broad different successional

niche in this temperate forest may have arisen from differential selection of eco-physiological traits in environments differing in light and water availability. This study found considerable agreement between natural selection in the field and predictions from functional analysis of ecophysiological traits. We have shown that selection on ecophysiological traits of *B. chilense* acts differentially in gaps and understories, favouring functional traits that reduce water loss, and optimize light capture and net carbon balance, respectively. Finally, the observed ecophysiological differences between plants in gaps and understories could be explained by both genetic differentiation and phenotypic plasticity, but the experimental approach carried out does not allow a distinction between these two possibilities. Without ruling out the capacity of *B. chilense* to show plastic responses to the light environment (see Saldaña et al. 2005), it seems more likely that the underlying phenomenon is genetic differentiation. This is suggested by the fact that *B. chilense* was able to show differentiation at the microhabitat scale, thus making probable the occurrence of differentiation between light environments with contrasting selective pressures.

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