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Ecophysiological responses to light availability in three *Blechnum* species (Pteridophyta, Blechnaceae) of different ecological breadth

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Abstract In Chilean evergreen temperate forest, fern species of the genus *Blechnum* occur in diverse microhabitats ranging from large gaps to heavily shaded understoreys. We hypothesised that differences in the ecological breadth of three co-occurring *Blechnum* species would be associated with differences in magnitude of ecophysiological responses to light availability. We quantified the field distribution of each species in relation to diffuse light availability (% canopy openness), and measured in situ variation in photosynthetic capacity (A), dark respiration (R_d) and specific leaf area (SLA) across the light gradient. The response of SLA of each species was also evaluated in a common garden in two light conditions (understorey and forest edge). The three *Blechnum* species differed significantly in the range of light environments occupied (breadth: *B. chilense* > *B. hastatum* > *B. mochaenum*). Despite significant interspecific differences in average A and R_d, the response of these traits to light availability did not differ among species. However, there was significant interspecific variation in both the mean value and the plasticity of SLA to light availability, the species with least ecological breadth (*B. mochaenum*) showing a flatter reaction norm (lower response) than its two congeners. This pattern was also found in the common garden experiment. The adjustment of leaf morphology (SLA) to light availability appears to be an important mechanism of acclimation in these *Blechnum* species. The narrow range of light environments occupied by *B. mochaenum* may be at least partly attributable to its inability to display phenotypic plasticity in SLA to changes in light availability.

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Introduction

The relationship between patterns of phenotypic responses to light availability and ecological breadth of plant species has been studied in several taxa, most of them angiosperms (Bazzaz and Carlson 1982; Walters and Field 1987; Chazdon 1992; Baskauf and Eichmeier 1994; Sultan et al. 1998; González and Gianoli 2004). Ecological breadth has been related either to the presence of different ecotypes in each habitat type (Walters and Field 1987; Baskauf and Eichmeier 1994) or to plasticity of individuals in morphological and physiological responses to environmental variation (Bazzaz and Carlson 1982; Sultan et al. 1998). Plant species limited to a restricted range of distribution are expected to exhibit narrow tolerance to environmental variation, and species of widespread distribution should be able to cope with greater environmental changes (Futuyma and Moreno 1988; van Tienderen 1997). Accordingly, there is evidence that species restricted to poor resource environments present regular but low levels in functional responses and ecologically wide species show an effective light use both in sun and shade (Chapin 1991; Sultan and Bazzaz 1993; Sultan et al. 1998). Most studies addressing the relationship between phenotypic plasticity and ecological breadth of plants have not included a field quantification of ecological breadth for each species, nor in situ ecophysiological measurements.

Plant species established across the whole light gradient should be able to produce leaves morphologically and physiologically suited to a wide range of light environments (Björkman 1981; Walters and Field 1987). The maintenance of a positive carbon balance in a wide range of environments is a key feature of species that successfully occupy diverse habitats (Chazdon 1992;

Spencer and Teeri 1994). Leaf traits relevant to net carbon gain, and hence to components of plant fitness, include photosynthetic rate (A), dark respiration (R_d) and specific leaf area (SLA) (Givnish 1988; Chazdon 1992; Reich et al. 1998). Given the influence of photosynthetic capacity on plant growth and reproduction, plasticity in this ecophysiological trait could be associated with variation in ecological breadth (Sultan et al. 1998). R_d has been associated with acclimation to light variation (Reich et al. 1998). Plants adapted to shade should present less carbon losses by respiration, and a decrease of R_d in low light could be expected in order to compensate the low assimilation rate (Givnish 1988; Ellsworth and Reich 1992). R_d increases with light availability (Bazzaz and Carlson 1982; Lusk and Reich 2000) because increased assimilation demands a greater amount of enzymes and metabolites with a higher maintenance cost (Reich et al. 1998). SLA shows a positive correlation with interspecific variation in relative growth rate (RGR) (Poorter and Remkes 1990; Lambers et al. 1998). Under low light conditions, plants produce thin leaves (with greater SLA), hence optimising the surface of light capture (Givnish 1988).

This study addressed patterns of ecophysiological responses to light in three sympatric fern species of the genus *Blechnum* (Pteridophyta, Blechnaceae) that differ in ecological breadth. In Chilean evergreen temperate forest, *Blechnum chilense* (Kaulf.) Mett covers the broadest environmental range, from shaded understoreys to full sun; *Blechnum hastatum* Kaulf. occurs from low light habitats to the forest edge; and *Blechnum mochaenum* Kunkel. is restricted to shady and moist sites. We evaluated the hypothesis that the magnitude of phenotypic plasticity to light availability in leaf ecophysiological traits of the three *Blechnum* species would reflect their ecological breadth. In order to test this hypothesis, we first estimated quantitatively the ecological breadth (Colwell and Futuyma 1971) of the fern species in the field light gradient, and we compared in situ the values of A, R_d and SLA under different light levels. Furthermore, we carried out common garden experiments in two light environments (understorey and forest edge) in order to confirm whether there are differential plasticity patterns among the three species.

Materials and methods

Study site

This work was conducted in old-growth evergreen temperate forest at Parque Nacional Puyehue (40°39′S, 72°11′W; 350–400 m.a.s.l.) located in the western foothills of the Andes in south-central Chile. The climate is maritime temperate, with an average annual precipitation of 3,500 mm (Almeyda and Saez 1958). The old-growth rainforest of the lower western slopes of the Andes is composed exclusively of broad-leaved evergreen species such as *Laurelia philippiana* (Atherospermataceae), *Aextoxicon punctatum* (Aextoxicaceae), *Nothofagus dombeyi* (Fagaceae) and *Eucryphia cordifolia* (Cunoniaceae).

Breadth of light gradient use

Five transects were laid out across the forest, including gap and understorey environments. In each transect, 15 random sampling points were chosen, yielding a total of 75 points. Density of each fern species and the percentage of diffuse light (canopy openness) were determined in a 1-m^2 quadrant at each sampling point. A pair of LAI-2000 canopy analyzers (Li-Cor, Lincoln, Nebraska) was used to quantify light environments. 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. LAI-2000 measurements are a good surrogate of spatial variation in mean daily photosynthetic photon flux density within a stand (Machado and Reich 1999).

Ecological breadth in light gradient use of each species was determined quantitatively by means of the niche breadth index of Levins (Colwell and Futuyma 1971). Levins suggested a measure of uniformity in which notation for the niche breadth of the ith species is

$$B_i = -\Sigma_j p_{ij} \log p_{ij}$$

where $p_{ij} = N_{ij}/Y_i$ is the proportion of individuals of species i associated with resource state j; N_{ij} the number of individuals of species i found to be associated with resource state j, and Y_i the total number of individuals of species i (Colwell and Futuyma 1971). This index was estimated by measuring the uniformity of the distribution of each species among the resource states, using density estimates (n° individuals/m^2) taken from 1% to 80% canopy openness at 5% intervals. These intervals were considered to equate resource levels in the Levins' index. This index retrieves values between 0 and 1: values near to zero indicate a narrow distribution on the light availability gradient and values close to one indicate a broad distribution.

Ecophysiological traits

Area-based photosynthetic capacity (A), area-based dark respiration rate (R_d) and SLA were measured in situ in 15 individuals of each fern species, distributed across the light gradient. A and R_d measurements were made using a portable infrared gas analyser and leaf chamber (PP Systems, Hitchin, England). Photosynthetic capacity was measured at PAR 1,000 μmol m^{-2} s^{-1} (assumed to be a saturating level) and R_d was measured at PAR 0 $\mu mol\ m^{-2}\ s^{-1}$, both at 20°C. These measurements were carried out in mid-growing season (October) on two fully expanded leaves per plant. The average of these measurements was used as an individual plant value. Leaf area was measured using leaf area meter ADC AM100 (ADC BioScientific, Hoddesdon, Hertfordshire, England). Foliage samples were then dried at 70°C for 48 h and weighed. SLA was determined for each sample.

Common garden experiment

This experiment was carried out under two light conditions: forest understorey (0.1 –5% canopy openness) and forest edge (10–35% canopy openness), which span most of the range of light environments where the three fern species co-occur. Four 25-m^2 plots were established in each of the two light treatments. Plots of forest understorey were distributed within a mature forest stand (2 km^2) and forest edge plots were located around this stand. From 16 "mother" plants of each fern species, sampled in the same forest, two cloned individuals per plant were obtained from rhizome division and one clone replicate of each species was randomly assigned to each of the two light conditions ($n=16$ plants × 2 treatments × 3 species = 96). Four individuals of each species were randomly planted in each of the four plots assigned to light treatments. Thus, each of the eight 25-m^2 plots contained 12 plants, four of each *Blechnum* species. The cloning procedure allowed us to distribute the same genotypes in both forest understorey and forest edge environments, hence phenotypic plasticity could be adequately evaluated. However, it is important to keep in mind that the phenotype of ferns obtained from clonal propagation included maternal environmental effects. All plants were juveniles, characterised by the low number of pinna and thinness of the leaves, herbaceous petioles and rachis, and scales of smooth texture (R. Rodríguez, personal communication; Herbarium of Universidad de Concepción [CONC]). Plots were established in November 2003 (austral spring). Four months later, SLA was measured in new completely expanded leaves on each surviving plant. SLA was the only trait measured because in the first part of this study it was the only trait showing differential interspecific responses to light availability (see Results).

Data analysis

An ANCOVA was applied (Species as main effect and Light as covariate) in order to test interspecific differences in A, R_d and SLA across the light gradient in the field. For the common garden experiments, a two-way ANOVA was used (main factors: Species and Light treatment) to test the hypothesis that the three fern species differed in phenotypic plasticity of SLA to light. In this analysis, a significant Species×Light interaction would indicate that species respond differently to light availability. If Species×Light interaction was significant, differences in SLA plasticity between species were evaluated by comparing the slopes of reaction norms (Gianoli 2001). The reaction norm is defined as the repertoire of phenotypic states for a given trait along an environmental gradient (Schlichting and Pigliucci 1998), and is represented by the regression line of the plot of trait expression against environment. Paired tests of parallelism (González and Gianoli 2004) were used to determine which pairs of species differed in plasticity of SLA. All analyses were done with the statistical software JMP (SAS Institute).

Results

Breadth of light gradient use

The three *Blechnum* species coexisted in between 2.5% and 40% canopy openness (Fig. 1). *B. mochaenum* ($n=368$ individuals) was the most abundant species at low light availability and *B. chilense* and *B. hastatum* occurred continuously across the entire light gradient ($n=93$ individuals and $n=126$ individuals, respectively). Accordingly, Levins index (B_a) indicated that *B. chilense* has the greatest ecological breadth ($B_a=0.4$) followed by *B. hastatum* ($B_a=0.2$). *B. mochaenum* showed the most restricted niche breadth ($B_a=0.05$).

Ecophysiological traits

Whereas the mean value (elevation of reaction norms) of A, R_d and SLA of the *Blechnum* species was different, plasticity (slope of reaction norms) of gas exchange traits to light availability did not differ among species (Table 1). In any given light environment, A was greater on average in *B. chilense* and *B. hastatum* than in *B. mochaenum* (Fig. 2a). Photosynthetic and dark respiration rates increased and SLA decreased with light availability in all three species (Fig. 2a–c). ANCOVA showed differences in slope among species only for SLA, albeit such differences were marginally significant (Table 1). Thus, although all three species displayed thicker leaves in high light, this decrease in SLA was less marked in *B. mochaenum* than in the other two species (Fig. 2c).

Common garden experiments

The common garden experiment confirmed that plasticity of SLA differed among fern species (Table 2). This variable changed significantly with light treatments, and the statistical interaction between the effects of species and light indicated that the three fern species differed

Fig. 1 Average density (± SD) of *Blechnum* fern species across the light gradient. B_a corresponds to niche breadth index of Levins (Colwell and Futuyma 1971)

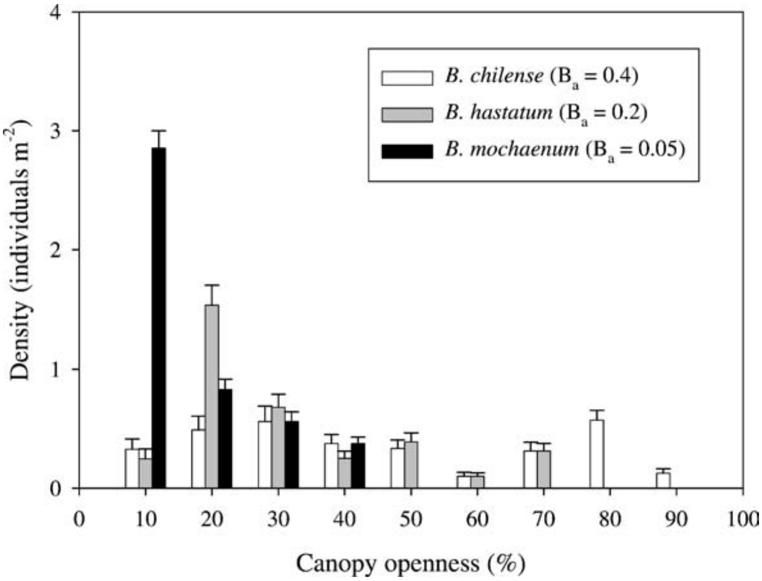


Table 1 ANCOVA of photosynthetic capacity (A, μmol m^{-2} s^{-1}), dark respiration rate (R_d, μmol m^{-2} s^{-1}) and specific leaf area (SLA, cm^2 g^{-1}) of *Blechnum chilense*, *B. hastatum* and *B. mochaenum* growing across a light gradient

	df	SS	*F*	*P*
A				
Species	2	0.15	7.21	0.003
Light	1	0.28	26.67	0.000
Species × Light	2	0.01	0.52	0.599
R_d				
Species	2	0.92	5.58	0.009
Light	1	1.50	18.12	0.000
Species × Light	2	0.08	0.49	0.618
SLA				
Species	2	0.35	41.01	0.000
Light	1	0.28	65.07	0.000
Species × Light	2	0.03	2.99	0.067

Main factor: Species; covariate: Light

significantly in their SLA response to light (Table 2).

Table 2 Two-way ANOVA of SLA of *Blechnum chilense*, *B. hastatum* and *B. mochaenum* growing in two light levels (understorey: 0.1–5% canopy openness; forest edge: 10–35% canopy openness) in a common garden experiment

Source	df	SS	*F*	*P*
Species	2	0.40	42.62	0.000
Light	1	0.25	53.94	0.000
Species × Light	2	0.06	6.80	0.002

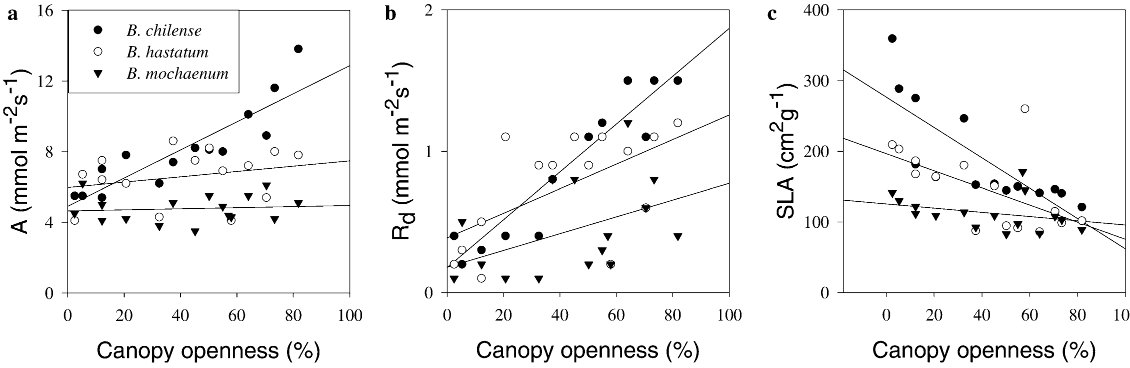
Main factors: Species and Light

B. chilense and *B. hastatum* showed plasticity in SLA, while SLA of *B. mochaenum* did not vary significantly with light availability, showing a flat reaction norm (Fig. 3). Parallelism tests showed that *B. mochaenum* differed from the other two species in terms of plasticity in SLA (Fig. 3). These results are almost identical to those of the in situ measurements.

Discussion

Blechnum fern species that coexist in the Chilean evergreen temperate forest differed in ecological breadth in

Fig. 2 Variation in photosynthetic rate *A* (**a**), dark respiration rate R_d (**b**), and specific leaf area *SLA* (**c**), in *B. chilense* (*squares*, *solid lines*), *B. hastatum* (*circles*, *dashed lines*) and *B. mochaenum* (*triangles*, *short-dashed lines*) across a light gradient in an evergreen temperate forest



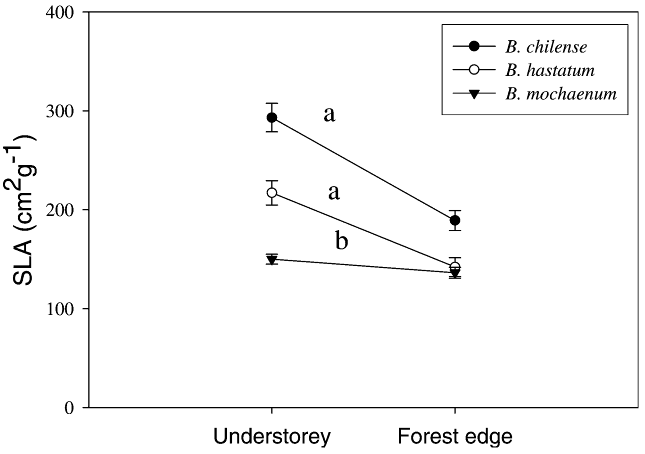


Fig. 3 Reaction norms of specific leaf area (*SLA*) to light (understorey: 0.1–5% canopy openness; forest edge: 10–35% canopy openness) in *B. chilense*, *B. hastatum* and *B. mochaenum* in a common garden. Mean ± SE are shown. *Lines with different letters* have significantly different slopes after a test of parallelism

relation to light availability. Their ecophysiological responses to light variation are consistent with interspecific differences in the ability to occupy different light environments. Light is the most important resource limiting plant survival and growth in the understorey of humid forests (Pacala et al. 1994; Finzi and Canham 2000; Saldaña and Lusk 2003). Therefore, the ability of ferns to capture and use this resource may determine to a large extent their ecological breadth in this forest ecosystem. The amplitude in light gradient use of these ferns species is: *B. chilense* > *B. hastatum* > *B. mochaenum*. *B. chilense* occurs in large gaps, forest edges, and shaded understoreys, and could be considered a generalist fern species in terms of ecological breadth for light availability. *B. hastatum* is mainly present at forest margins but also occurs at shaded sites. *B. mochaenum* is restricted to shaded sites in the forest understorey, hence can be considered a specialist fern species in terms of light environment.

All three *Blechnum* species displayed similar increases in photosynthetic capacity with greater available light. However, in any given light environment, *A* was greater on average in *B. chilense* and *B. hastatum* than in *B. mochaenum*. The latter species behaves photosynthetically like a typical "shade" plant (sensu Björkman 1981), with low rates of photosynthesis and dark respiration. The relatively low plasticity of *B. mochaenum* to higher light levels may therefore limit its distribution to shaded sites by means of several mechanisms. Low *A* determines low growth rates, with the result that *B. mochaenum* is outcompeted by faster-growing species in high light (Lambers and Poorter 1992). Alternatively, low photosynthetic capacity could render *B. mochaenum* susceptible to photoinhibition in high light (Long et al. 1994). As seen for *A*, there was no evidence of differential plasticity in R_d, with all species showing a similar increase in R_d with light availability. In any given light environment, R_d was higher on average in *B. chilense* and *B. hastatum* than in *B. mochaenum*. A decrease in respiration rate has been associated with plant acclimation to low light (Reich et al. 1998), which implies lower metabolic costs when carbon gains are low (Lusk and Reich 2000).

The interspecific differences in plasticity of SLA could be related to the more restricted ecological breadth of *B. mochaenum* with respect to the other two species. The more plastic SLA responses of *B. chilense* and *B. hastatum* may allow them to occupy a wider range of light environments by adjusting their surface of light capture. A change in SLA alters the amount of light that can be intercepted, and this is one of the most important acclimation mechanisms in maximizing carbon gain in response to light availability variation (Evans and Poorter 2001). Likewise, it has been shown that leaf area/mass ratio (SLA, or its reciprocal: LMA) has a regulatory role on photosynthetic capacity (Peterson et al. 1999), which stresses the importance of SLA variation during light acclimation. The common garden experiment confirmed that the species with the narrowest ecological breadth (*B. mochaenum*) showed the least phenotypic plasticity of SLA in response to light environment. Without this experimental approach, it could not be ruled out that the apparent in situ patterns of plasticity were actually a consequence of differentiated ecotypes along the light gradient. This apparent lack of morphological plasticity in response to prolonged exposure to high light may partly explain why *B. mochaenum*, a shade tolerant species (Rodríguez and Baeza 1991), does not occur on open sites. Whereas, some studies show that shade tolerant species are less plastic in SLA than pioneer species (Walters and Reich 1999; Lusk and Del Pozo 2002), others (Kitajima 1994; Montgomery 2004) did not find a clear-cut relationship between the degree of shade tolerance and SLA plasticity. This apparent conflict of evidences might be explained by the fact that some experiments did not control for the ontogenetic stage of plants, because SLA decreases with plant age (Lusk 2004). Our experiments were ontogenetically controlled because fern age and size varied little among species and light treatments.

To our knowledge, this is the first study addressing the relationship between phenotypic plasticity in ecophysiological traits and differences in ecological breadth in Pteridophyta. Adjustment of leaf morphology (SLA variation) appears to be an important mechanism of acclimation to light availability in *Blechnum* species in this temperate forest. SLA did not show significant phenotypic plasticity in *B. mochaenum* and this might partly explain the narrow ecological breadth of this species. Further research on the ecophysiological basis of fern ecological breadth should also include traits related to plant water economy. Thus, it is known that stomatal closure in ferns is slower than in angiosperms (Woodhouse and Nobel 1982), limiting the effectiveness of stomatal responses to local environmental variation (Robinson 1994). Therefore, the fact that some fern species, like

B. mochaenum, are restricted to moist and shaded habitats could be also related to their poor water loss control by transpiration (Robinson 1994).

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