

Vertical distribution of Hymenophyllaceae species among host tree microhabitats in a temperate rain forest in Southern Chile

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Abstract

Question: Are differences in microhabitat preferences of co-occurring epiphytic Hymenophyllaceae species (filmy ferns) correlated with differences in ecophysiological responses to light availability and humidity in the host tree?

Location: The Andean foothills in south-central Chile.

Methods: We evaluated the distribution pattern of nine filmy fern species in microhabitats that differ in light availability and humidity in four host tree species. A DCA was developed to assess Hymenophyllaceae species microhabitat preference in terms of canopy openness (CO) and relative humidity. We assessed whether differences in chlorophyll content, maximum photochemical efficiency (F_v/F_m), photosynthetic capacity (A_{max}), evapotranspiration (E) and instantaneous water use efficiency (WUE) are consistent with any pattern.

Results: CO and relative humidity differed significantly with height in the host trees. While CO increased with height in a host tree, relative humidity decreased. DCA analysis showed that filmy fern species distribution within and among trees was mainly explained by the relative humidity of the microhabitat. Chlorophyll content, chlorophyll a/b ratio, A_{max} and E differed significantly among filmy fern species. A_{max} and E were correlated with axis 1 scores from the DCA analysis.

Conclusions: The vertical distribution and abundance of filmy fern species in Chilean temperate rain forest seems to be closely related to the different microhabitats offered by host trees. This pattern may reflect interspecific differences in ecophysiological traits related both to light availability and humidity. Our results suggest that humidity is the main environmental factor driving functional responses and habitat preferences of these filmy fern species.

Keywords: Chilean temperate rain forest; Chlorophyll content; Chlorophyll fluorescence; Filmy ferns; Gas exchange; Microhabitat preference; Niche differentiation.

Nomenclature: Marticorena & Rodriguez (1995).

Introduction

The diversity and vertical distribution of epiphytes has received much attention in the last two decades (Gentry & Dodson 1987; Dickinson et al. 1993; Wolf 1994; Nieder et al. 1999; Zotz 2007), mainly in tropical forests, where vascular epiphytes represent 25% of total plant diversity (Hofstede et al. 2001; Nieder et al. 2001). Epiphyte diversity is usually related to variations in microclimatic and microenvironmental conditions in the host tree (Dickinson et al. 1993; Freiberg 1996; Werneck & Espirito-Santo 2002). Thus, differences in species composition and performance of epiphytes may, in part, be explained by their physiological requirements (Hietz-Seifert et al. 1996), leading to niche diversification within epiphyte communities (Ter Steege & Cornelissen 1989).

Among the epiphytes, the Hymenophyllaceae (filmy ferns) normally lack a cuticle (or have highly reduced cuticles), differentiated epidermis and stomata. This causes a close dependence between their occurrence and environmental humidity because they have no mechanism to prevent loss of water from their tissues (Krömer & Kessler 2006). However, aside from basic characterization of habitats where filmy ferns occur, there is scarce quantitative information on abundance, host tree preference, vertical distribution (Zotz & Buche 2000) and functional response to environmental heterogeneity of this fern group.

The host tree microenvironment presents a pattern of vertical change, where factors such as temperature, light availability and wind speed increase with host tree height; while moisture and nutrient availability simultaneously decrease with height (Johansson 1974; Meinzer & Goldstein 1996). Within host trees, this generates a variety of niches (Krömer et al. 2007) that are differentially occupied by epiphytes and lianas (Muñoz et al. 2003). Characterization of epiphytic communities in terms of

microhabitat and plant association on host trees in New Zealand temperate forests has shown that subtleties in microclimate, combined with environmental variables such as branch orientation and humus depth, lead to complex patterning of communities within the crown (Dickinson et al. 1993). In the temperate forests of South America, in spite of the high number of vascular epiphytes (Arroyo et al. 1995), there is still scant information on basic aspects of filmy fern ecology (Muñoz et al. 2003).

From an ecophysiological perspective, leaf chlorophyll (Chl) content and its variation within species along a light gradient can reflect the ecological performance of filmy fern species in different light environments. The amount of solar radiation absorbed by a leaf is largely a function of foliar concentration of photosynthetic pigments, and therefore low concentrations of chlorophylls can directly limit photosynthetic potential and hence primary production (Curran et al. 1990; Filella et al. 1995). The relative concentration of chlorophylls is known to change with light environment (e.g. sun leaves have a higher Chl *a/b* ratio; Larcher 1995; Lambers et al. 1998). In addition, chlorophyll fluorescence measurements have shown considerable potential for measuring changes in leaf photochemical efficiency (Demmig-Adams et al. 1995; Maxwell & Johnson 2000). Finally, maintenance of a positive carbon balance in a range of environments is a key feature of the ecological breadth of a plant species (Chazdon 1992; Spencer & Teeri 1994; Sultan et al. 1998). Leaf ecophysiological traits such as photosynthetic capacity (A_{max}), evapotranspiration (E) and instantaneous water use efficiency (WUE) have a significant influence on net carbon gain, and hence on species habitat preference (Chazdon 1992; Lambers et al. 1998; Ackerly et al. 2000).

In Chile, there are 23 species of filmy fern, being a major epiphytic component of Chilean temperate rain forests (Marticorena & Rodríguez 1995; Parra 2005). However, there is a lack of research on variations in ecophysiological traits in relation to light capture and photosynthetic performance, which potentially determine microhabitat preference of filmy fern species. This study addressed the distribution pattern of filmy fern species inside a temperate rain forest in southern Chile in relation to microhabitats that differ in light and humidity on the host tree trunk. Additionally, we assessed if the fern ecophysiological traits chlorophyll content, chlorophyll fluorescence and gas exchange are consistent with that pattern. We evaluated the hypothesis that differences in ecophysiological traits related to light availability and humidity in filmy

fern species explain their distribution and habitat preferences on the host trees.

Methods

Study site

This study was performed in a second-growth forest stand at Katalapi Park in Pichiquillaie, south-central Chile (41°31'S, 72°45'W), in the Andean foothills 9 km from the Seno de Reloncaví, and without a clear influence of prevailing winds (Luebert & Pliscoff 2006). Climate is characterized by short, relatively dry summers and long, wet and rainy winters (Luebert & Pliscoff 2006). Mean annual air temperature is 11°C; mean minimum monthly air temperature (5°C) occurs in August, and mean monthly maximum temperature (20°C) occurs in February. The climate at Pichiquillaie is considered temperate and strongly humid, with an oceanic tendency (Di Castri & Hajek 1976), although winter frosts do occur. Annual precipitation is around 2200 mm or more (Armesto et al. 1995). Even though the daily mean relative humidity is high throughout the year, there are periods of lower humidity (Reyes-Díaz et al. 2005). The second-growth rain forest at this altitude in the western foothills of the Andes is comprised exclusively of broadleaf evergreens (Saldaña & Lusk 2003; Luebert & Pliscoff 2006).

Species abundance and microenvironmental measurements

A total of 18 filmy fern species were found in the study area. Of these, we selected nine species (Table 1) that were commonly present on the four dominant host tree species: *Amomyrtus luma* (Mol.) Legr. et Kausel, *Laurelia philippiana* (Looser) Schodde, *Drimys winteri* J.R et G. Foster and *Rhaphythamnus*

Table 1. The most common filmy fern species in the study site. Abbreviated names are in capital letters.

Species	Abbreviated name
<i>Hymenophyllum caudiculatum</i> var. <i>productum</i>	HCAU
<i>Hymenophyllum cuneatum</i>	HCUN
<i>Hymenoglossum cruentum</i>	HCRU
<i>Hymenophyllum dentatum</i>	HDEN
<i>Hymenophyllum dicranotrichum</i>	HDIC
<i>Hymenophyllum krausseanum</i>	HKRA
<i>Hymenophyllum pectinatum</i>	HPEC
<i>Hymenophyllum tortuosum</i>	HTOR
<i>Serpyllopsis caespitosa</i>	SCAE

spinosus (A.L. Juss) Mold. We measured abundance of the nine filmy fern species, light availability [canopy openness (CO)] and humidity at three trunk heights (0–60 cm, 61–120 cm and 121–180 cm above ground level) on a total of 10 host tree individuals (from 25 to 30 cm d.b.h.) of each of the four tree species. Given that filmy fern species generally propagate vegetatively by rhizomes (Marticorena & Rodríguez 1995), we measured the abundance of each species by counting the number of fronds whose petioles were inside the quadrant, as a proxy for the number of individuals (*sensu* Zotz & Buche 2000), in six 25 cm × 25 cm plots at each of the abovementioned heights in the host trees. Frond sizes of filmy fern species range from 2.5 ± 0.1 cm (*S. caespitosa*) to 9.0 ± 0.2 cm (*Hymenoglossum cruentum*). CO measurements were made with a pair of LAI-2000 canopy analysers (Li-Cor, Lincoln, NE, USA). One instrument was used to take measurements at 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 CO over the quasi-hemispherical (148°) view field of the LAI-2000 sensors. Relative humidity was measured sequentially over 10 days (February 2007) with a thermo-hygrometer (Delmhorst HT-3000, NJ, USA) attached to each host tree trunk.

Physiological measurements

We measured chlorophyll content and fluorescence on five individuals of each filmy fern species present at each height in each host tree in the field. Chlorophyll content was measured on one completely expanded frond by means of five separate measurements using a hand-held chlorophyll meter (SPAD-502, Minolta Camera Co., Osaka, Japan). The SPAD-502 calculates an index in “SPAD units” based on transmittance of red and infrared light from two light-emitting diodes (650 and 940 nm). We used the arithmetic mean of these measurements for all subsequent analyses. This noninvasive optical method provides reliable estimates of relative leaf Chl (Richardson et al. 2002). To estimate total chlorophyll content and Chl *a/b* ratio we used standard extraction techniques and a spectrophotometer to measure Chl *a*, Chl *b* and total Chl content (Lichtenthaler & Wellburn 1983), and these values were compared with nominal Chl index values obtained with the hand-held Chl absorbance meter and

the reflectance index (SPAD units) was correlated with foliar Chl. The maximum photochemical efficiency (F_v/F_m) was estimated from fluorescence measurements made with a modulated fluorometer (type FMS 2, Hansatech Instruments, Norfolk, UK). Leaves of each species were dark-adapted for 30 min to obtain open reaction centres of photosystem II (PSII). In this paper, F_v/F_m (where variable fluorescence $F_v = F_m - F_o$) was used as an indicator of the potential quantum yield (photochemical efficiency) of PSII (Genty et al. 1989).

We carried out gas exchange measurements on ten individuals of each filmy fern species, using an LCi portable infrared gas analyser and leaf chamber (PP Systems, Hitchin, UK). A_{\max} and E were measured at $200 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR, assumed to be a saturating level for these fern species. Cuvette temperatures were 18–20°C. Gas exchange was measured between 09:00 and 15:00. WUE was calculated as the ratio of photosynthetic capacity to evapotranspiration.

Data analysis

The response variables light availability and relative humidity were analysed using a two-way ANOVA, with the explanatory variables tree host species and height on the trunk. Combined filmy fern density was analysed in a similar way. A DCA (Detrended Correspondance Analysis, MVSP) was used to assess filmy fern species ordination in terms of microhabitat characteristics. The eigenvalues obtained were correlated with the environmental parameters CO and relative humidity. A one-way ANOVA was used to test interspecific differences in chlorophyll content, chlorophyll *a/b* ratio, F_v/F_m , A_{\max} , E and WUE. Finally, we correlated the species scores from the DCA analysis (Axis 1; eigenvalue = 0.78) with the physiological traits measured for each filmy fern species in order to quantify the relationship between ecophysiological responses of the species and their distribution on host tree microhabitats. These statistical analyses were performed with JMP (SAS Institute, NC, USA).

Results

The four host tree species differed significantly in light availability with height on the trunk (Table 2). Relative humidity showed significant differences among tree host species and with height on the host tree (Table 2), with *D. winteri* and *R. spinosus* having the highest and lowest trunk humidity, respectively.

Whereas CO increased with height on the tree host, relative humidity decreased. CO ranged from 0.1% to 31.0% and relative humidity from 47% to 87%.

A total of 40 host trees were studied, on which we recorded nine species of filmy fern (Table 1), with *Hymenophyllum dicranotrichum* being the most abundant and *H. cruentum* the least abundant (Fig. 1a, b, c). Species abundance changed significantly with height on the tree trunk, and among tree host species (Table 3), with *D. winteri* being the host tree with the highest abundance of filmy fern species (Tukey test, $F = 2.375$, $P < 0.05$).

The ordination of filmy fern species showed that the two axes explained 90% of the variation in distribution of filmy ferns. The correlation of each axis eigenvalues with CO and relative humidity indicated that filmy fern species distribution was explained mainly by the relative humidity gradient (Axes 1 and 2) and secondarily by light availability (Axis 2) (Table 4). This ordination indirectly reflects the position of each filmy fern species on the host tree

trunk, given that, as mentioned above, the micro-environmental parameters changed with height in the host tree.

The evaluation of ecophysiological traits showed that chlorophyll content, chlorophyll *a/b* ratio, A_{max} and E differed significantly among filmy fern species (Figs. 2a, b, 3a, b), whereas photosynthetic efficiency (F_v/F_m) and WUE did not show significant interspecific differences (Figs. 2c, 3c). Among species, the Axis 1 scores from the DCA analysis – which are closely correlated with relative humidity in host trees – were positively correlated with evapotranspiration and negatively correlated with photosynthetic capacity (Table 5). Thus species with higher evapotranspiration are associated with more humid microhabitats and species with lower evapotranspiration are associated with less humid microhabitats.

Discussion

Our results agree with others that filmy fern distribution is strongly linked to the availability of water (Dickinson et al. 1993; Freiberg 1996;

Table 2. Two-way ANOVA of canopy openness and relative humidity on the host tree species *Amomyrtus luma*, *Laureliopsis philippiana*, *Drimys winteri* and *Rhaphythamnus spinosus* at three heights on the tree trunk (60, 120, 180 cm).

Source	df	SS	MS	F	P
Canopy openness (%)					
Tree species	3	0.007	0.002	2.38	0.0930
Height	2	0.049	0.024	17.3	<0.0001
T×H	6	0.058	0.001	10.4	<0.0001
Residual	108	0.066	<0.001		
Relative humidity (%)					
Tree species	3	2137	712.33	29.93	<0.0001
Height	2	3742	1871	52.42	<0.0001
T×H	6	272.6	45.43	1.909	0.0873
Residual	108	2727	25.26		

Table 3. Two-way ANOVA of density (individuals cm⁻²) of filmy fern species growing on the host tree species *Amomyrtus luma*, *Laureliopsis philippiana*, *Drimys winteri* and *Rhaphythamnus spinosus* at three heights on the tree trunk (0–60 cm, 61–120 cm, 121–180 cm).

Source	df	SS	MS	F	P
Tree species	3	0.059	0.019	5.079	0.003
Height	2	0.023	0.011	3.017	0.050
T×H	6	0.044	0.007	1.891	0.093
Residual	108	0.204	0.002		

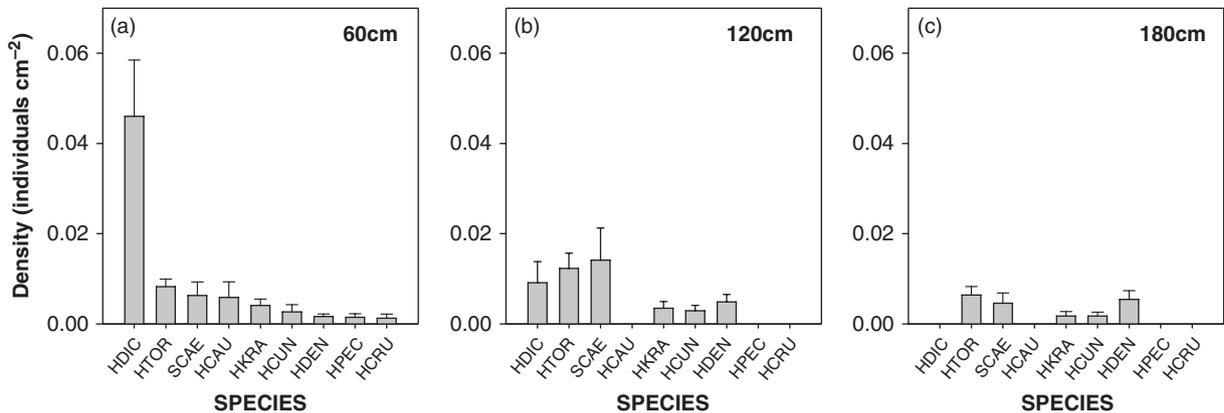


Fig. 1. Average density (\pm SD) of filmy fern species at three tree host trunk heights in a Chilean temperate rain forest. Codes represent abbreviated names of fern species (see Table 1).

Andrade & Nobel 1997; Muñoz et al. 2003; Roberts et al. 2005). However, more detailed ordination would require measurement of other factors, such as nutritional quality of the bark substrate of the host tree (Nadkarni 1984). The hygrophilous condition of this fern group is mainly thought to be due to its lack of stomata and single cell layer in the leaves, which restricts them to humid and shady places because they cannot control water loss (Dubuisson et al. 2003). However, several filmy fern species display different degrees of drought tolerance (Proctor 2003), which might allow certain species to inhabit higher layers of the canopy (Zotz & Buche 2000). In New Zealand, Dickinson et al. (1993) found that *Hymenophyllum* and *Trichomanes* species were found on middle to outer branches of host trees, indicating that filmy ferns are not necessarily confined to shady habitats. Our results show that only five out of the nine filmy fern species persist in upper parts of host tree trunks (Fig. 1c).

We found that the overall abundance of filmy ferns was greater on the lower part of tree host trunks and that the number of filmy fern species decreased from nine at 60 cm trunk height to five at 180 cm (Fig. 1a, b, c). *H. cruentum*, *H. caudiculatum*

var. *productum* and *H. pectinatum* disappeared completely above a height of 120 cm on host trees, reflecting their adaptation to low light habitats. However, the ordination results suggest that this group of filmy ferns seems to be more limited by humidity than by light availability within this shady habitat (Table 4). Our findings that the host tree *D. winteri*, which had a significantly higher humidity on its trunk, also had a higher average abundance of filmy ferns (Table 3) highlights the humidity-dependence of this group. While filmy fern species restricted to the lower part of the trunk, where humidity is usually high, can decrease leaf-to-air vapor pressure deficit, thus promoting higher gas exchange (Martin & Siedow 1981; Callaway et al. 2002; Zotz 2007), filmy fern species that persist in upper parts of the host tree trunk (e.g. *H. dentatum* and *H. tortuosum*) had lower evapotranspiration and hence lower water loss. However, even though A_{\max} was higher in filmy fern species that persist in exposed microhabitats (Fig. 3a), interspecific differences in E did not induce significant interspecific differences in WUE (Fig. 3b, c). Despite this, it has been reported that some filmy fern species can tolerate drought stress and desiccation and can recover from desiccation at very low water potentials (Alpert 2000). Mechanisms such as recovery of water content, quantum efficiency (Fv/Fm), photosynthetic pigment and chloroplast ultrastructure, as well as prevention of damage to the plasma membrane have been related to the above desiccation tolerance (Sherwin & Farrant 1996).

There was a clear relationship between the distribution of filmy fern species among host tree microhabitats and ecophysiological measurements of both evapotranspiration and photosynthetic

Table 4. Correlation between component ordination values and environmental parameters, canopy openness (%) and relative humidity (%). Axis 1: eigenvalue = 0.78; Axis 2: eigenvalue = 0.12.

	Axis 1	Axis 2
Canopy openness	ns	$R^2: -0.56; F_{(1-54)}: 70.26; P: <0.0001$
Relative humidity	$R^2: 0.88; F_{(1-54)}: 415.47; P: <0.0001$	$R^2: 0.75; F_{(1-54)}: 164.34; P: <0.0001$

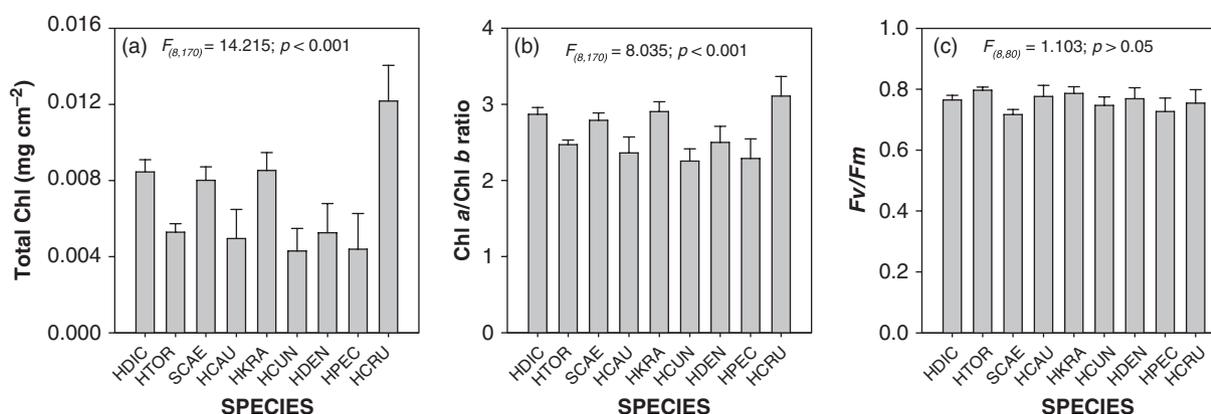


Fig. 2. Average chlorophyll content (\pm SD) (a), chlorophyll a/b ratio (\pm SD) (b) and photochemical efficiency (Fv/Fm) (\pm SD) (c) of nine filmy fern species from a Chilean temperate rain forest. Codes represent abbreviated names of fern species (see Table 1). Values of F and P were taken from one-way ANOVA tests.

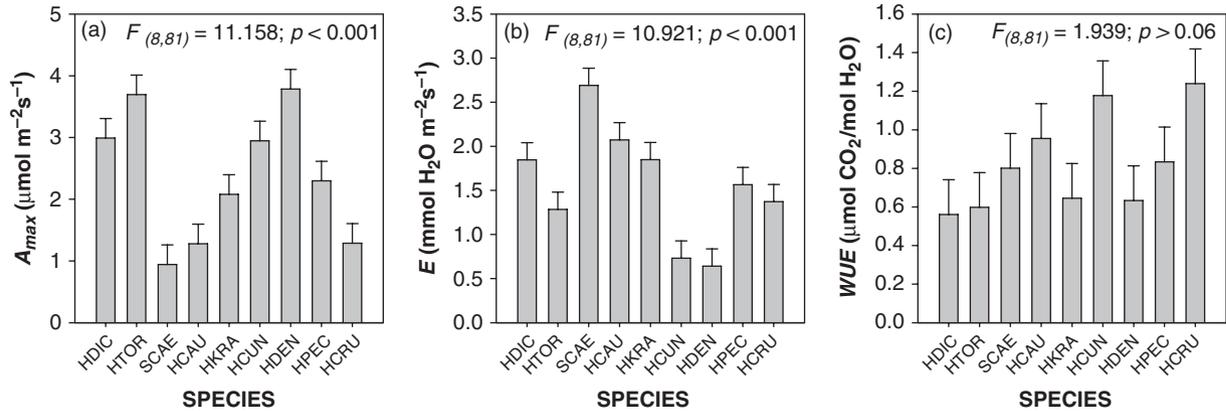


Fig. 3. Average photosynthetic capacity (A_{\max}) (a), evapotranspiration (E) (b) and water use efficiency (WUE) (c) of nine filmy fern species from a Chilean temperate rain forest. Codes represent abbreviated names of fern species (see Table 1). Values of F and P were taken from one-way ANOVA tests.

Table 5. Correlation analysis between species scores from the DCA (Axis 1) and physiological traits measured on each filmy fern species: average chlorophyll content, chlorophyll a/b ratio, photochemical efficiency (Fv/Fm), photosynthetic capacity (A_{\max}), evapotranspiration (E) and water use efficiency (WUE). R^2 : Pearson correlation coefficient.

	R^2	$F_{(1,7)}$	P
Total Chl (mg cm ²)	0.13	1.075	0.334
Chl a/b ratio	0.17	1.446	0.268
Fv/Fm	-0.08	0.355	0.570
A_{\max} ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	-0.56	9.028	0.019
E ($\text{mmol} \cdot \text{H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	0.83	35.438	<0.001
WUE ($\mu\text{mol CO}_2/\text{mol H}_2\text{O}$)	-0.12	0.111	0.748

capacity (Table 5). The effects of light availability on filmy fern performance are difficult to separate from those related to the humidity gradient, since adaptations to low light are a trade-off linked to high humidity (Andrade et al. 2004). Thus, tolerance of shade and susceptibility to photodamage might also influence distribution patterns (Andrade & Nobel 1997; Hietz & Briones 2001; Zotz & Hietz 2001). Our results show that filmy fern species present in the study area live in environments where light intensity does not exceed 30% CO and where relative humidity is high. Even though the species considered here had similar photosynthetic performance, species that disappear above a height of 60 cm on host trees had higher evapotranspiration and hence were more susceptible to desiccation, and also had lower photosynthetic capacity (Table 5).

The vertical distribution and abundance of filmy fern species in Chilean temperate rain forests seems to be closely related to the different microhabitats offered by host trees. Both light availability

and humidity change with host tree species and height on the tree trunk. Interspecific differences in ecophysiological traits related to light availability and humidity can explain distribution of the filmy fern species. Our results suggest that humidity is the main environmental factor driving functional responses and habitat preferences of this fern group, even in places where humidity is relatively high throughout the year. Further research on the ecological distribution of filmy fern species should also include nutrient availability on tree trunks and interspecific competition for resources offered by the host tree.

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