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RESEARCH ARTICLE

Effects of light availability and growth rate on leaf lifespan of four temperate rainforest Proteaceae

Efectos de la luminosidad y de las tasas de crecimiento sobre longevidad foliar de cuatro Proteáceas del bosque templado lluvioso

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ABSTRACT

Although comparative studies have revealed much about the environmental correlates of leaf lifespan and its integration with other leaf traits, a comprehensive theory of leaf lifespan is still lacking. The influence of growth rate on self-shading may be a key proximate determinant of both inter- and intra-specific variation in leaf lifespans. If this were the case, we would expect leaf lifespans of fast-growing light-demanding species to respond more strongly to light environment than those of shade-tolerant species. We monitored growth and leaf survival of juvenile trees of four temperate rainforest Proteaceae in southern Chile, in order to explore the influences of light environment and self-shading on leaf lifespan. Leaf lifespans tended to decrease with increasing diffuse light availability, and slopes of these relationships were steeper in two light-demanding species (*Embothrium coccineum*, *Lomatia hirsuta*) than in two more shade-tolerant species (*Lomatia ferruginea*, *Gevuina avellana*). This pattern mirrored interspecific variation in relationships of height growth with light availability, height growth rates of the two light-demanding species responding more strongly to light availability than did growth of *L. ferruginea* and *G. avellana*. Path analysis suggested that light availability influenced leaf lifespans primarily through the influence of growth on self-shading: when rate of leaf production was held constant by multiple regression, light availability per se had no significant influence on leaf lifespans of any of the four species. However, 29 to 79 % of intraspecific variation in leaf lifespan remained unexplained by light environment and leaf production rate. If self-shading is fact the main proximate control on leaf lifespan, information on the elevational distribution of photosynthetic photon flux may enhance the explanatory power of studies of this nature.

Key words: height growth, LAI-2000, path analysis, self-shading, shade tolerance.

RESUMEN

Los estudios comparativos han documentado importantes correlaciones ambientales de la longevidad foliar, y también los vínculos con otros rasgos foliares. Sin embargo, una teoría comprensiva de la longevidad foliar aún no emerge de dichos estudios. El efecto de las tasas de crecimiento sobre el autosombramiento podría ser determinante en la variación tanto intra- como interespecífica en la longevidad foliar. De ser así, se esperaría que la longevidad foliar de las especies heliófitas, de crecimiento rápido, respondiera más marcadamente a la luminosidad que la de las especies tolerantes a la sombra, de crecimiento lento. Medimos crecimiento en altura, sobrevivencia foliar y producción de nuevas hojas, en árboles juveniles de cuatro Proteáceas Chilenas, con el objetivo de explorar los efectos de la luminosidad y del autosombramiento sobre la longevidad foliar. La longevidad foliar mostró una relación inversa con la disponibilidad de luz difusa, y la pendiente de esta relación fue más elevada en dos especies heliófitas (*Embothrium coccineum*, *Lomatia hirsuta*) que en dos especies más tolerantes a la sombra (*Lomatia ferruginea*, *Gevuina avellana*). Dicho patrón mostró cierta simetría con la variación interespecífica en el efecto de la luminosidad sobre el crecimiento en altura, ya que el crecimiento de las dos especies heliófitas respondió más notoriamente a la luminosidad que el crecimiento de *L. ferruginea* y *G. avellana*. Un análisis de vías sugirió que la luminosidad influyó en la longevidad foliar principalmente por el efecto del crecimiento sobre el autosombramiento: cuando la tasa de producción de nuevas hojas se mantuvo constante mediante la regresión múltiple, la luminosidad en sí no tuvo efecto significativo sobre la longevidad foliar de ninguna de las cuatro especies. Sin embargo, entre 29 y 79 % de la variación intraespecífica en la longevidad foliar no pudo explicarse por la luminosidad o la tasa de producción foliar. Si el autosombramiento efectivamente es el principal determinante inmediato de la longevidad foliar, datos sobre la distribución elevacional del flujo fotónico fotosintético podrían aumentar el poder explicativo de los estudios de esta índole.

Palabras clave: análisis de vías, autosombramiento, crecimiento en altura, LAI-2000, tolerancia a la sombra.

INTRODUCTION

Despite a vast amount of empirical work on leaf demography in recent decades (e.g., Reich et al. 1997, Reich et al. 2004, Wright et al. 2004), a comprehensive theory of leaf lifespan is still lacking. Some environmental correlates of leaf lifespan have been clearly established (e.g., Aerts 1995, Poorter & Bongers 2006), and interspecific work shows associations of leaf lifespan with other leaf traits such as photosynthetic capacity and leaf mass per area; these cross-species correlations are very strong in global datasets spanning more than two orders of magnitude in leaf lifespan (Wright et al. 2004). Yet these trait associations break down, and in some cases are even reversed, when intraspecific comparisons are made across a range of light environments (Lusk et al. 2008a).

Prolongation of leaf lifespan appears to be associated with both adaptation and acclimation to shade. Several studies have reported that leaves live longer on shaded plants than on conspecifics growing in well-lit environments (e.g., Lusk 2002, Reich et al. 2004, Vincent 2006). Studies in diverse evergreen forests have shown that inherently slow-growing shade-tolerant species retain their leaves longer than light-demanding associates (e.g., Reich et al. 1995, Lusk 2002, Poorter & Bongers 2006). However, this parallel in evolutionary and plastic responses of leaf lifespan to shade is associated with divergent trends in leaf mass per area: whereas shade-tolerant evergreens have larger mass per area (LMA) than their light-demanding associates, plastic responses to shade invariably involve a reduction in LMA (Lusk et al. 2008a). Despite their lower LMA, shade leaves tend to have a larger structural fraction than sun leaves, which may enable long lifespan by reducing their attractiveness to herbivores (Lusk et al. 2010).

What may bridge inter- and intraspecific patterns is the influence of self-shading on leaf lifespan (Ackerly & Bazzaz 1995). As leaves age their carbon balance deteriorates because of increased shading by newer leaves, as well as declining physiological capacity (Reich et al. 2009). Although "self-shading" is a convenient term, shading by growth of neighbouring plants may be an equally important influence on leaf lifespans (Vincent 2006). Plants might be expected to shed leaves when their net carbon gain declines to zero; although a modelling study by Reich et al. (2009) found that almost all leaves had positive daytime carbon balances at the age of their mean life-span, their calculations did not include night-time leaf respiration, or the costs of supplying leaves with water. Zero net carbon balance seems likely to be reached sooner in fast-growing plants than in slow-growing plants, partly because of more rapid self-shading in the former (Ackerly & Bazzaz 1995), and partly because of the linkage between plant growth rates and respiration rates, which determine the minimum light levels required for positive net carbon gain (Walters & Reich 2000, Lusk 2002). As slow metabolism and slow growth are characteristic of both adaptation and short-term responses to shade, such an impact of self-shading is likely relevant to both inter- and intra-specific variation in leaf lifespan.

If rates of self-shading are the proximate determinant of leaf lifespans, we would expect leaf lifespans of light-demanding species to respond more strongly to light environment than those of shade-tolerant species. Photosynthesis and growth of the former are usually highly responsive to light availability, whereas shade-tolerant taxa often show modest photosynthetic plasticity, and growth of their seedlings often saturates at moderate light intensities (e.g., Read 1985, Poorter 1999, Valladares et al. 2000, Lusk 2002). We addressed this question by measuring juvenile height growth, leaf production rates and leaf lifespans of four Chilean rainforest Proteaceae across a wide range of light environments. The four tree species differ widely in reported light requirements.

METHODS

Study site

The study was carried out at Parque Katalapi (latitude 41°31' S, longitude 72°45' W, elevation 60 masl) near Cordillera de Quillaipe in southern Chile. Mean annual precipitation is estimated at 2322 mm, with a marked summer minimum, and nearly all of this falls as rain. Mean annual air temperature is 11 °C. The coldest months are June to August, with mean daily minimum and maximum temperatures of about 2 and 10 °C, respectively. February is the warmest month, with mean daily minimum and maximum temperatures of 8 and 23 °C, respectively. The site is a 30 ha mosaic of old fields, remnants of the previous forest cover, and patches of young regenerating forest. Cattle have been excluded from the study area for 15 years. Common tree species on the site included *Nothofagus nitida*, *Laureliopsis philippiana, Luma apiculata, Amomyrtus luma, A. meli, Weinmannia trichosperma*, *Caldcluvia paniculata, Eucryphia cordifolia* and *Drimys winteri*, as well as the four Proteaceae that were the focus of this study.

Study species

The four Proteaceae represent a wide range of reported light requirements. *Embothrium coccineum* and *Lomatia hirsuta* are frequent colonisers of disturbed habitats such as old fields and road cuttings. *E. coccineum* was described as "very intolerant" of shade by Donoso (1989). Its seedlings were found to have the highest understorey mortality rates of eight rainforest species studied by Lusk (2002), and Figueroa & Lusk (2001) reported that juveniles of *E. coccineum* were associated with brighter light environments than most other Chilean rainforest evergreens. Although *Lomatia hirsuta* was also rated as "very intolerant" by Donoso (1989), its presence in old-growth forests, especially those with an overstorey of deciduous *Nothofagus obliqua* (e.g., Veblen et al. 1979), suggests that it tolerates slightly more shade than *E. coccineum.* This is consistent with data in Figueroa & Lusk (2001), showing that *L. hirsuta* seedlings on Isla Grande de Chiloé occupied shadier microsites than those of *E. coccineum*. *Gevuina avellana* and *L. ferruginea* have been described as being of intermediate shade tolerance (Donoso 1989), although juveniles of the former can often be found growing in as little as 2 % light, in the shaded understories of old-growth stands (Lusk et al. 2008b). Nomenclature follows Marticorena & Quezada (1985)

Sampling methods

Sampling was carried out on a series of transects run across the park, including a wide range of light environments, including shaded understories and open pasture. At intervals randomly spaced between 20 and 30 m apart, the nearest juvenile (500-2200 mm tall) of each species was chosen for sampling. This system worked satisfactorily for three of the study species, but the fourth (*L. hirsuta*) was not common enough to be sampled in this manner. Accordingly, we selected all juvenile *L. hirsuta* within the requisite size range that could be located.

The height of the principal axis of each juvenile was measured to the apex, and all fully-expanded leaves on this axis were counted. 12 months later, each plant was revisited, its height remeasured, and survival of leaves recorded. Abscission scars were counted to determine mortality of new leaves initiated after the start of the study period; this was particularly important for *E. coccineum*, as most leaves of this species appeared to live < 1 yr. Leaf longevity (years) was estimated as:

$$\frac{n^i}{(n^i - n^f) + m^n}$$

where n^i = initial number of leaves, n^f = final number surviving from n^i, and m^n = mortality of new leaves initiated since the first census.

The light environment of each juvenile tree was quantified using a pair of LAI-2000 canopy analysers (Li-Cor, Lincoln, NE). One instrument was used to take measurements at each sampling point, while the other, placed in an open field, was programmed to take readings at 30-s intervals. Integration of data from the two instruments enabled estimation of percentage diffuse irradiance at each sampling point within the forest, equivalent to percentage of canopy openness over the quasi-hemispherical (148°) field of view perceived by the LAI-2000 sensors. Measurements were made on overcast days, using the full 148° field of view. Measurements with the LAI-2000 are a good surrogate of spatial variation in mean daily photosynthetic photon flux density within a stand (Machado & Reich 1999).

Statistical analysis

One of our interests was in the slope of relationships of leaf lifespan and growth with light availability. Major axis tests are appropriate when the primary interest is in slopes and intercepts of relationships, rather than their strength (Warton et al. 2006). We therefore used SMATR (Falster et al. 2006) to calculate the slope and intercept of the major axis of these relationships, instead of ordinary least squares regression. All variables were $\log_{10}$-transformed prior to analysis, in order to meet the assumption of additivity of effects.

As leaf lifespans are likely to be influenced by production of new leaves, rather than by height growth per se, we also examined relationships of new leaf production with light availability. This approach is supported by the findings of Ackerly & Bazzaz (1995), who showed that the light environments of individual leaves deteriorate steadily as they are progressively shaded by production of new leaves. As the relationship of leaf production rate with light availability appeared to differ in shape across species, we explored various least squares fits to determine which best described the relationship for each species. Finally, as light availability could potentially influence leaf lifespan through mechanisms other than self-shading, we used path analysis to explore dependence of leaf lifespan on both light availability and new leaf production. This was achieved by multiple regression of leaf lifespan on light availability and leaf production rate, and simple regression of leaf production rate on light availability (Quinn & Keough 2002).

RESULTS

Leaf lifespan

Mean leaf lifespans in high light (> 10 %) ranged from 0.7 yrs in *Embothrium coccineum* to 4.3 years in *Gevuina avellana* (Table 1). All three of the species present at microsites receiving < 10 % diffuse light had somewhat longer leaf lifespans there than in high light.

Overall, leaf lifespan showed a weak negative relationship with diffuse light availability (Fig. 1). Scaling exponents of this relationship differed significantly among species (P = 0.047), being steeper in light-demanding *Lomatia hirsuta* and *E. coccineum* than in the more tolerant *L. ferruginea* and *G. avellana*. However, this relationship was a long way from being statistically significant in *Gevuina avellana*, and significant at P < 0.05 only in *Embothrium coccineum*.

Growth

Height growth was positively correlated with diffuse light availability, although this relationship was only marginally significant in *L. ferruginea* (Fig. 2). Scaling exponents differed significantly among species (P = 0.003), and were steeper in light-demanding *Lomatia hirsuta* and *E. coccineum* than in the more tolerant *L. ferruginea* and *G. avellana*.

The fastest height growth was recorded in light-demanding *E. coccineum* and *L. hirsuta* (Table 1), some individuals of these species growing > 1 m in high light (Fig. 2).

Leaf production of all species responded positively to light availability (Fig. 3), although this relationship was only marginally significant (P = 0.08) for *L. hirsuta*. The shape of the relationship between rate of leaf production and light availability differed among the four species. Whereas an exponential fit best described the relationship for light-demanding *E. coccineum* and *L. hirsuta*, a power function gave the highest r^2 values for the more shade-tolerant *L. ferruginea* and *G. avellana* (Fig. 3).

Path analysis

Path analysis suggested that light availability influenced leaf lifespan of all four species primarily through the influence of new leaf production on self-shading (Fig. 4). This relationship was strongest in *E. coccineum*, with leaf production rate explaining nearly 70 % of the variance in leaf lifespan of this species, and weakest in *L. hirsuta*, which was found in only a limited range of light environments. The lack of statistical significance in the case of *G. avellana* at least partly reflects the small sample size of this species (n = 14). When leaf production rate was held constant by multiple regression, light environment per se was not found to significantly affect leaf lifespan of any of the four species.

The explanatory power of our model of variation in leaf lifespan differed widely between species. Whereas the combined effects of leaf production rate and light availability explained nearly 71 % of the variance in leaf lifespan of *E. coccineum*, this figure was only 21 % for *L. hirsuta* (Fig. 4).

DISCUSSION

As reported in many other studies, leaf lifespans were closely-related to reported species light requirements (Table 1). Foliage turnover rates during the year of observation indicated that relatively shade-tolerant

TABLE 1

Sample size, height, growth and mean leaf lifespan data of four Proteaceae on which measurements of height growth and leaf lifespan were made. Potential height data obtained from Muñoz (1980).

Tamaño muestral, altura, crecimiento y longevidad foliar media de árboles juveniles de cuatro Proteáceas. Los datos sobre altura potencial fueron obtenidos de Muñoz (1980).

Species	Potential height (m)	Sample size	Mean initial height (mm)	90th percentile of height growth (mm)	Mean leaf lifespan (yr) Low light (< 10 %)	High light (> 10 %)
Embothrium coccineum	10	21	1354	1075	0.9	0.7
Gevuina avellana	18	15	1149	713	5.4	4.3
Lomatia ferruginea	10	17	1318	420	3.4	2.4
Lomatia hirsuta	15	16	1593	973	-	2.3

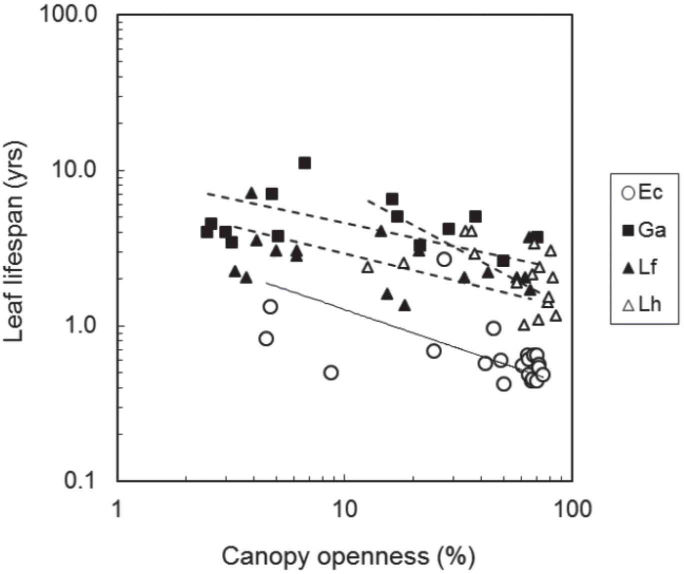

Fig. 1: Relationships of leaf lifespan of four Proteaceae with light availability. Lines show major axis of relationships: ***Embothrium coccineum*** (Ec) $y = 4.01x^{-0.498}$, $r^2 = 0.201$; ***Gevuina avellana*** (Ga) $y = 9.43x^{-0.310}$, $r^2 = 0.043$; ***Lomatia ferruginea*** (Lf) $y = 6.68x^{-0.360}$, $r^2 = 0.143$; ***Lomatia hirsuta*** (Lh) $y = 46.32x^{-0.784}$, $r^2 = 0.173$. Solid lines show significant relationships at $P < 0.05$, dashed lines show non-significant relationships.

Relaciones de longevidad foliar de cuatro Proteáceas con la disponibilidad lumínica. Las líneas muestran eje principal de las relaciones: ***Embothrium coccineum*** (Ec) $y = 4.01x^{-0.498}$, $r^2 = 0.201$; ***Gevuina avellana*** (Ga) $y = 9.43x^{-0.310}$, $r^2 = 0.043$; ***Lomatia ferruginea*** (Lf) $y = 6.68x^{-0.360}$, $r^2 = 0.143$; ***Lomatia hirsuta*** (Lh) $y = 46.32x^{-0.784}$, $r^2 = 0.173$. Las líneas continuas muestran las relaciones significativas ($P < 0.05$) y las discontinuas muestran relaciones no significativas.

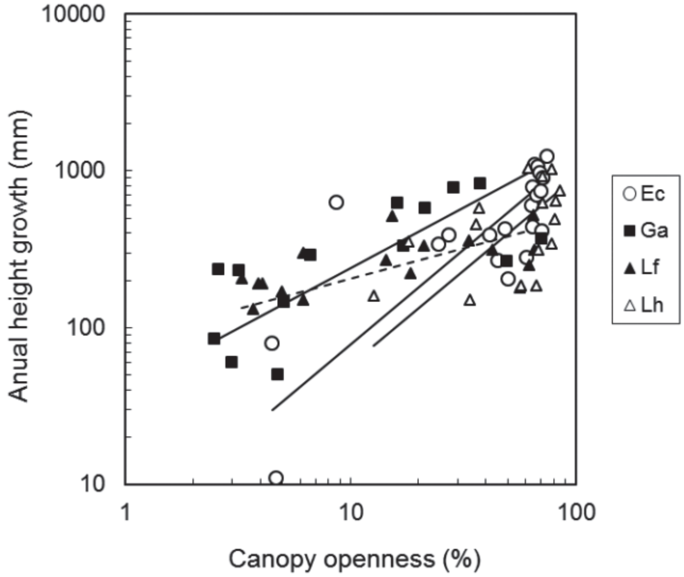

Fig. 2: Relationships of height growth of four Proteaceae with light availability, over a 12-month period. Lines show major axis of relationships: ***Embothrium coccineum*** $y = 4.86x^{1.205}$, $r^2 = 0.578$; ***Gevuina avellana*** $y = 41.15x^{0.768}$, $r^2 = 0.5$; ***Lomatia ferruginea*** $y = 84.35x^{0.386}$, $r^2 = 0.223$; ***Lomatia hirsuta*** $y = 3.57x^{1.205}$, $r^2 = 0.248$. Solid lines show significant relationships at $P < 0.05$, dashed lines show non-significant relationships.

Relaciones de longevidad foliar de cuatro Proteáceas con la disponibilidad lumínica. Las lineas muestran eje principal de las relaciones: *Embothrium coccineum* $y = 4.86x^{1.205}$, $r^2 = 0.578$; *Gevuina avellana* $y = 41.15x^{0.768}$, $r^2 = 0.5$; *Lomatia ferruginea* $y = 84.35x^{0.386}$, $r^2 = 0.223$; *Lomatia hirsuta* $y = 3.57x^{1.205}$, $r^2 = 0.248$. Las líneas continuas muestran las relaciones significativas ($P < 0.05$) y las discontinuas muestran relaciones no significativas.

Gevuina avellana typically retained its leaves for four to six years on average, whereas most individuals of the most light-demanding species (*Embothrium coccineum*) underwent a complete change of foliage during the 12 months (Fig. 1). In both tropical and temperate rainforests, strongly light-demanding trees and shrubs often have leaf lifespans of < 1 year, whereas the most shade-tolerant taxa often hold their leaves for > 4 years (Coley 1988, Lusk 2002, Poorter & Bongers 2006).

As predicted, responsiveness of leaf lifespan to light environment appeared to be related to species shade tolerance and growth rate. Leaf lifespan of light-demanding *E. coccineum* and *Lomatia hirsuta* scaled more steeply with light availability than that of relatively shade-tolerant *G. avellana* and *L. ferruginea* (Figs. 1 and 2). Similarly, a comparative study of the tropical rainforest genus *Piper* found that light availability was strongly negative correlated with leaf lifespan of two light-demanding species, whereas weaker relationships prevailed among more shade-tolerant species (Williams et al. 1989). On the other hand, Lusk (2002) reported rather "individualistic" species responses of foliage turnover to light availability in a temperate rainforest, without finding any clear relationship with shade tolerance. Reich et al. (2004) reported that prolongation of leaf lifespans in low light was a generalized phenomenon in an Amazonian rainforest, without documenting any relationship with species' light requirements.

Path analysis supported the postulated role of self-shading as an important proximate control on leaf lifespan (Ackerly & Bazzaz 1995). Light availability per se had only a very weak negative influence on leaf lifespans of all species when leaf production rate was held constant (Fig. 4), suggesting that mechanisms other than self-shading played little part in the observed correlations of leaf lifespan with light availability (Figs. 1 and 4). The relatively high leaf mortality rates of open-grown individuals of all species therefore likely reflect rapid

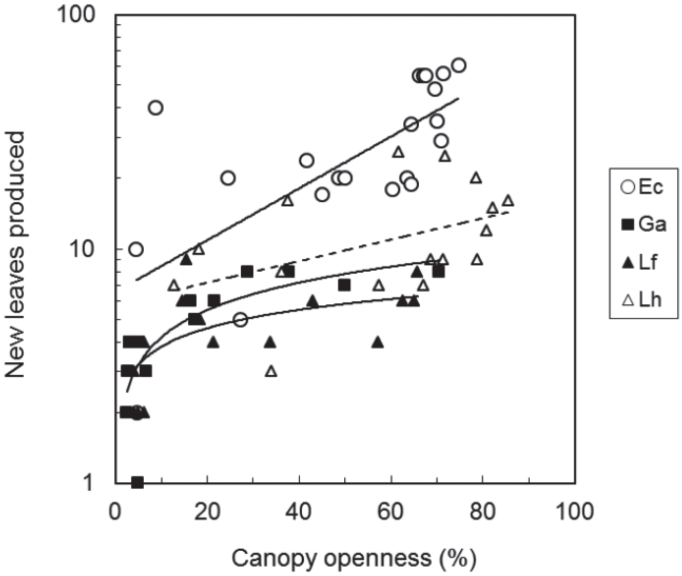

Fig. 3: Influence of light availability on production of new leaves of four Proteaceae, over a 12- month period. Fitted lines/curves show best fits for each species. Best fits were achieved with a power function for *Embothrium coccineum* (r^2 = 0.489) and *Lomatia hirsuta* (r^2 = 0.200), and with an exponential function for *Gevuina avellana* (r^2 = 0.582) and *L. ferruginea* (r^2 = 0.423). Solid lines and curves show significant fits at $P < 0.05$; dashed lines show non-significant relationships.

Influencia de la disponibilidad lumínica sobre la tasa de producción foliar de cuatro Proteáceas, mostrando el mejor ajuste para cada especie. Los mejores ajustes se lograron con funciones de potencia para *Embothrium coccineum* (r^2 = 0.489) y *Lomatia hirsuta* (r^2 = 0.200), y con funciones exponenciales para *Gevuina avellana* (r^2 = 0.582) y *L. ferruginea* (r^2 = 0.423). Las líneas y curvas continuas muestran las relaciones significativas ($P < 0.05$), y las discontinuas muestran relaciones no significativas.

declines in light interception and carbon gain of individual leaves as they age, because of shading by vigorous new growth (Ackerly & Bazzaz 1995). In contrast, light environments of leaves would be expected to change more gradually in slow-growing plants with low leaf production rates. The evidence for control of leaf lifespan by self-shading was strongest in *E. coccineum*, the fastest-growing and most light-demanding of the four species, and weakest in *L. hirsuta*. This latter result probably reflects the restricted range of light environments in which we were able to find juvenile trees of *L. hirsuta*.

The elevational distribution of canopy openness was not examined in this study, but may account for some of the unexplained variation in leaf lifespans. Depending on species, between 29 and 79 % of the variance in leaf lifespan could not be explained by global diffuse light availability or leaf production rate (Fig. 4). Leaves growing on the main stem of a plant receiving most of its light from high elevational angles (e.g., growing directly beneath an opening in an otherwise intact canopy) will undergo a rapid decline in light availability (e.g., Ackerly & Bazzaz 1995). However, such declines are likely to be more gradual in plants receiving abundant side-light (e.g., growing on forest margins), despite the potential for rapid growth in such environments. This hypothesis is consistent with experimental manipulations of seedling light environments in a glasshouse experiment (Ackerly & Bazzaz 1995): leaf lifespans of tropical pioneer seedlings were increased when self-shading was attenuated by using reflective material to increase light availability to old leaves. Similarly, Hikosaka et al. (1994) found that training *Ipomoea* vines to grow

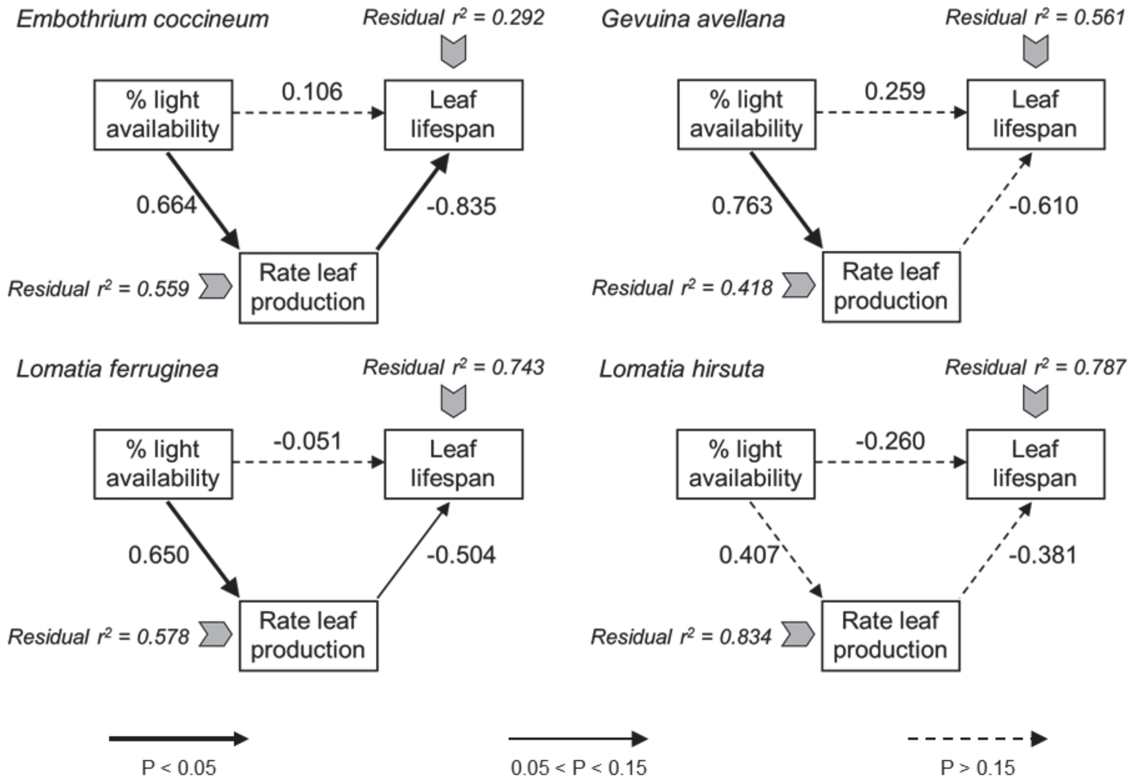

Fig. 4: Path diagrams showing dependence of leaf lifespans of four Proteaceae on light availability and growth. Values above black arrows show coefficients of determination. Residuals show proportion of variance not explained by the model.

Diagramas de vía mostrando la dependencia de la longevidad foliar de cuatro Proteáceas sobre la disponibilidad lumínica y el crecimiento. Las cifras sobre las flechas negras muestran los coeficientes de determinación. Los residuales indican la proporción de la varianza no explicada por el modelo.

horizontally led to prolongation of leaf lifespan, presumably as a result of reduced self-shading. Although canopy structure was quite variable at our study site, we did not obtain information on the elevational distribution of photosynthetic photon flux. This hypothesis could readily be tested in the field by using hemispherical photos to provide detailed information on the elevational and azimuthal distribution of light (Rich 1990).

In conclusion, two lines of evidence presented here support the postulated role of self-shading as a major proximate determinant of leaf lifespan. Firstly, the negative relationship of leaf lifespan with light availability was steepest in light-demanding species (Fig. 1), whose growth rates responded mostly dramatically to variation in light availability (Fig. 2). Second, when leaf production rate was held constant by multiple regression, light availability per se had little effect on leaf lifespan of any species (Fig. 4). Nevertheless, factors that remained unquantified in this study, such as the elevational distribution of canopy openness, must be invoked to explain 29 to 79 % of the intraspecific variance in leaf lifespan of the four Proteaceae that we studied. More sophisticated quantification of plant light environments could help address some of this unexplained variation.

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LITERATURE CITED

ACKERLY DD & FA BAZZAZ (1995) Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. Oecologia 101: 289-298.

AERTS R (1995) The advantages of being evergreen. Trends in Ecology & Evolution 10: 402-407.

COLEY PD (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia 74: 531-536.

DONOSO C (1989) Antecedentes básicos para la silvicultura del tipo forestal siempreverde. Bosque 10: 37-53.

FALSTER DS, DI WARTON & IJ WRIGHT (2006) SMATR: Standardised major axis tests and routines. Version 2.0.

FIGUEROA JA & CH LUSK (2001) Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rain forest. New Phytologist 152: 483-489.

HIKOSAKA K, I TERASHIMA & S KATOH (1994) Effects of leaf age, nitrogen nutrition and photon flux density on the distribution of nitrogen among leaves of a vine (*Ipomoea tricolor* Cav.) grown horizontally to avoid mutual shading of leaves. Oecologia 97: 451-457.

LUSK CH (2002) Leaf area accumulation helps juvenile evergreen trees tolerate shade in a temperate rainforest. Oecologia 132: 188-196.

LUSK CH, Y ONODA, R KOOYMAN & A GUTIÉRREZ-GIRÓN (2010) Reconciling species-level versus plastic responses of evergreen leaf structure to light gradients: Shade leaves punch above their weight. New Phytologist 186: 429-438.

LUSK CH, PB REICH, RA MONTGOMERY, DA ACKERLY & J CAVENDER-BARES (2008a) Why are evergreen leaves so contrary about shade? Trends in Ecology & Evolution 23: 299-303.

LUSK CH, DS FALSTER, CK JARA-VERGARA, M JIMENEZ-CASTILLO & A SALDANA (2008b) Ontogenetic variation in light requirements of juvenile rainforest evergreens Functional Ecology 22: 454-459.

MACHADO JL & PB REICH (1999) Evaluation of several measures of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest understory. Canadian Journal of Forest Research 29: 1438-1444.

MARTICORENA C & M QUEZADA (1985) Catálogo de la flora vascular de Chile. Gayana Botanica 42: 1-155.

MUÑOZ M (1980) Flora del Parque Nacional Puyehue. Editorial Universitaria, Santiago.

POORTER L (1999) Growth responses of 15 rain forest tree species to a light gradient: The relative importance of morphological and physiological traits. Functional Ecology 13: 396-410.

POORTER L & F BONGERS (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology 87: 1733-1743.

QUINN GP & MJ KEOUGH (2002) Experimental designs and data analysis for biologists. Cambridge University Press, Cambridge.

READ J (1985) Photosynthetic and growth responses to different light regimes of the major canopy species of Tasmanian cool temperate rainforest. Australian Journal of Ecology 10: 327-334.

REICH PB, DS ELLSWORTH & C UHL (1995) Leaf carbon and nutrient assimilation and conservation in species of differing successional status in an oligotrophic Amazonian forest. Functional Ecology 9: 65-76.

REICH PB, MB WALTERS & DS ELLSWORTH (1997) From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences USA: 13730-13734.

REICH PB, C UHL, MB WALTERS, L PRUGH & DS ELLSWORTH (2004) Leaf demography and phenology in Amazonian rain forest: A census of 40000 leaves of 23 tree species. Ecological Monographs 74: 3-23.

REICH PB, DS FALSTER, DS ELLSWORTH, IJ WRIGHT, M WESTOBY, J OLEKSYN & TD LEE (2009) Controls on declining carbon balance with leaf age among 10 woody species in Australian woodland: Do leaves have zero daily net carbon balances when they die? New Phytologist 183: 153-166.

RICH PM (1990) Characterizing plant canopies with hemispherical photographs. Remote Sensing Reviews 51: 13-29.

VALLADARES F, SJ WRIGHT, E LASSO, K KITAJIMA & RW PEARCY (2000) Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81: 1925-1936.

VEBLEN TT, DH ASHTON & FM SCHLEGEL (1979) Tree regeneration strategies in a lowland *Nothofagus*-dominated forest in south-central Chile. Journal of Biogeography 6: 329-340.

VINCENT G (2006) Leaf life span plasticity in tropical seedlings grown under contrasting light regimes. Annals of Botany 97: 245-255.

WALTERS MB & PB REICH (2000) Trade-offs in low-light CO_2 exchange: A component of variation in shade tolerance among cold temperate tree seedlings. Functional Ecology 14: 155-165.

WARTON DI, IJ WRIGHT, DS FALSTER & M WESTOBY (2006) Bivariate line-fitting methods for allometry. Biological Reviews 81: 259-291.

WILLIAMS K, CB FIELD & HA MOONEY (1989) Relationships among leaf construction cost, leaf longevity, and light environments in rain-forest plants of the genus *Piper*. The American Naturalist 133: 199-211.

WRIGHT IJ, PB REICH, M WESTOBY, DD ACKERLY, Z BARUCH et al. (2004) The worldwide leaf economics spectrum. Nature 428: 821-827.

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