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Costs *versus* risks: Architectural changes with changing light quantity and quality in saplings of temperate rainforest trees of different shade tolerance

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Abstract Light requirements and functional strategies of plants to cope with light heterogeneity in the field have a strong influence on community structure and dynamics. Shade intolerant plants often show a shade avoidance strategy involving a phytochrome-mediated stem elongation in response to changes in red : far red ratio, while shade-tolerant plants typically harvest light very efficiently. We measured plant size, stem diameter, internode and leaf lengths in randomly chosen saplings of 11 woody species differing in their shade tolerance in both a secondary forest and an old-growth temperate evergreen rainforest in southern Chile. We also recorded the irradiance spectrum and the diffuse and direct light availabilities at each sampling point. Significant differences were found for the mean light environment of the saplings of each species, which also differed in basal stem diameter, internode length and leaf length, but not in plant height. Both plant slenderness (plant height/stem diameter) and mean internode length increased with increasing light availability, but no relationship was found between any of these two traits and red : far red ratio. The change in plant slenderness with light availability was of lesser magnitude with increasing shade tolerance of the species, while internode change with light availability increased with increasing shade tolerance of the species. Shade tolerators afford higher costs (thicker stems and plants), which render more biomechanically robust plants, and respond more to the light environment in a trait strongly influencing light interception (internode length) than shade intolerant species. By contrast, less shade-tolerant plants afforded higher risks with a plastic response to escape from the understorey by making thinner plants that were biomechanically weaker and poorer light interceptors. Thus, species differing in their shade tolerances do differ in their plastic responses to light. Our results contribute to explain plant coexistence in heterogeneous light environments by improving our mechanistic understanding of species responses to light.

Key words: elongation, light capture, phenotypic plasticity, red : far red ratio, shade avoidance, shade tolerance, temperate rainforest, understorey.

INTRODUCTION

Plant survival in low light conditions heavily relies on maximization of light interception and utilization for carbon fixation coupled with a minimization of carbon loss by respiration (Valladares & Niinemets 2008). Shade-tolerant plants are also known for their capacity to persist for long periods of time in the understorey, coping with other factors in addition to limiting light such as herbivory and risk of mechanical damage (Kitajima 1994). While many studies have addressed leaf features conferring shade tolerance (e.g. Craine & Reich 2005; Lusk & Warton 2007), only a few have explored whole-plant features associated with survival in dim understorey light (Reich *et al.* 2003; Baltzer & Thomas 2007). This is remarkable because light interception is a whole crown property (Pearcy *et al.* 2005; Baltzer & Thomas 2007). Light interception by a plant is influenced by a number of traits such as leaf inclination angles, branching patterns and internode lengths, all affecting crown architecture and leaf display (Poorter & Werger 1999; Poorter *et al.* 2003; Valladares & Niinemets 2007). Understorey plants of

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contrasting growth form and shape are known to converge in their light interception efficiency (Valladares *et al.* 2002b), but they do segregate regarding their plastic phenotypic responses to available light (Valladares *et al.* 2000). Shade intolerant plants often exhibit the shade avoidance syndrome (Smith & Whitelam 1997) which involves high morphological and architectural plasticity in order to maximize elongation and apical dominance (Ballare 1999; Weinig 2000). In general, shade-tolerant plants are less plastic than shade intolerant plants (Valladares *et al.* 2002a; Portsmuth & Niinemets 2007), but this typically applies to leaf level traits, and even at the leaf scale, evidence for this is consistent only for certain physiological traits like photosynthetic capacity and stomatal conductance (Valladares & Niinemets 2008). We hypothesized that phenotypic variation of saplings along the light gradient in a forest understorey would reflect interspecific differences in shade tolerance. In particular, shade-tolerant plants are expected to cope with light shortage by affording the costs of producing robust individuals of a high light harvesting efficiency, a conservative strategy that should yield high fitness compared with a shade avoidance syndrome. In contrast, less shade-tolerant plants are expected to show phenotypic variation functional for shade avoidance, investing in vertical growth at the expense of poor light interception and carbon gain, thus risking their survival in the understorey if shading prevails.

There is discrepancy in the relative importance of the specific cue eliciting plastic responses to light (Dorn *et al.* 2000). One group of studies, primarily physiological, emphasizes the phytochrome-mediated responses elicited by changes in the red : far red ratio (R : FR) that is typically low in the dim understorey light (Smith 1995). Another group of studies, primarily ecological, focuses on the responses elicited by the actual intensity of the irradiance and not by its spectral characteristics (e.g. Sánchez-Gómez *et al.* 2006). Recent studies are showing more complex combinations of eliciting cues, so the shade avoidance syndrome might result not only from changes in the light but also in the chemical environment of the plant (Pierik *et al.* 2004; Mullen *et al.* 2006). It has been argued that the phytochrome-mediated responses allow the plant to anticipate competition providing an early neighbour detection (Ballare 1999). But it is the amount of light that eventually determines survival and performance of understorey plants (Dorn *et al.* 2000; Niinemets & Valladares 2006; Sánchez-Gómez *et al.* 2006). Consequently, we hypothesize that traits related with elongation, and thus with shade avoidance, would respond more to R : FR than to light quantity, while traits involved in light harvesting efficiency would respond more to light quantity than to R : FR. These patterns should be evident in the phenotypic variation of saplings along the light gradients occurring in forest understoreys where light is a key environmental factor driving plant individual performance and community dynamics.

We tested these two groups of hypotheses with a field study of saplings of 11 woody species differing in their shade tolerance in the understorey of the temperate evergreen rainforest in southern Chile. The ecology of these temperate hyper-humid forests is only beginning to be understood but they are ideal for the present study because many plant species coexist in these forests and light availability has been shown to play an important role in vegetation dynamics and niche differentiation (Lusk 1996; Saldaña & Lusk 2003; Lusk *et al.* 2008).

MATERIALS AND METHODS

Study site and sampling

The study took place in the lowland rainforest of Parque Nacional Puyehue (350–440 m a.s.l.; 40°39′S, 72°11′W), located in the western foothills of the Andean range in south-central Chile. Both old-growth and secondary rainforest stands at this altitude are composed exclusively of broad-leaved evergreen tree species (Saldaña & Lusk 2003; Lusk & Piper 2007). The climate is maritime temperate, with an average annual precipitation of around 3500 mm and 13.8°C and 5.4°C mean maximum and minimum temperature, respectively. The dominant canopy species in the mature lowland forest are *Laureliopsis philippiana* (Atherospermataceae), *Aextoxicon punctatum* (Aextoxicaceae), *Nothofagus dombeyi* (Fagaceae) and *Eucryphia cordifolia* (Cunoniaceae). Less abundant canopy trees are *Dasyphyllum diacanthoides* (Asteraceae), *Luma apiculata* (Myrtaceae) and *Weinmannia trichosperma* (Cunioniaceae). Advanced regeneration in the understorey is composed of these tree species in addition to *Amomyrtus luma* (Myrtaceae), *Azara serrata* (Flacourtiaceae), *Caldcluvia paniculata* (Cunionaceae), *Gevuina avellana* (Proteaceae), *Myrceugenia planipes* (Myrtaceae) and *Rhaphitamnus spinosus* (Verbenaceae) (Saldaña & Lusk 2003). Common woody species in treefall gaps are *Lu. apiculata*, *C. paniculata*, *Embothrium coccineum* (Proteaceae) and *Aristotelia chilensis* (Elaeocarpaceae) (Lusk 2002). In general, most of these tree species have intermediate light requirements (Kneeshaw *et al.* 2006).

Sampling was carried out across mature forest and secondary forest understoreys, which significantly differed in light availability and in the spectral features of the irradiance (Table 1). A minimum of five saplings of the 11 most common woody species were randomly chosen (Table 2).

We recorded for each plant the following morphological traits: sapling height (length of the main stem), basal stem diameter (using a digital calliper with a resolution of 0.01 mm), internode length (average of two consecutive internodes at the middle of the shoot) and the length of leaves associated with the measured internodes. We calculated a slenderness index for each sapling as the plant height : stem diameter ratio. Shade tolerance of each species was assigned from the values of the minimum light requirement given by Lusk *et al.* (2008).

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Table 1. Mean values (± SE) of light quantity and light quality of gaps, secondary forest and old-growth forest sites in a Chilean rainforest

	Gaps	Secondary forest	Old-growth forest
	($n = 5$)	($n = 14$)	($n = 16$)
Light quantity			
Indirect site factor	0.97 ± 0.01 a	0.20 ± 0.01 b	0.09 ± 0.01 c
Direct site factor	0.98 ± 0.01 a	0.15 ± 0.01 b	0.06 ± 0.01 c
Light quality			
Red : far red ratio	1.13 ± 0.13 a	0.47 ± 0.02 b	0.26 ± 0.03 c
Blue : red light ratio	5.84 ± 0.78 a	6.97 ± 0.50 b	10.17 ± 0.47 c
UV-A : red light ratio	0.50 ± 0.23 a	0.88 ± 0.15 b	1.92 ± 0.14 c
UV-B : red light ratio	0.05 ± 0.04 a	0.06 ± 0.02 b	0.21 ± 0.02 c

Values with different letters have significant differences among sites (one-way ANOVA, $P < 0.01$). n = sample size.

Table 2. Mean values (± SE) of indirect site factor (ISF), direct site factor (DSF), red : far red ratio (R : FR), plant height, basal stem diameter (Basal d.), internode and leaf length of saplings of 11 evergreen species in a Chilean rainforest

Species	n	ISF***	DSF***	R : FR*	Height (cm)	Basal d. (mm)***	Internode (cm)*	Leaf length (cm)***
Aristotelia chilensis (Ac)	6	0.20 ± 0.02	0.16 ± 0.02	0.47 ± 0.07	20.70 ± 6.79	1.88 ± 0.66	1.31 ± 0.51	5.32 ± 1.91
Amomyrtus luma (Al)	5	0.09 ± 0.02	0.06 ± 0.02	0.28 ± 0.08	25.80 ± 7.44	3.38 ± 0.73	1.68 ± 0.55	3.28 ± 2.09
Aextoxicon punctatum (Ap)	17	0.16 ± 0.01	0.12 ± 0.01	0.34 ± 0.04	23.50 ± 4.04	3.29 ± 0.39	1.82 ± 0.30	7.81 ± 1.14
Embothrium coccineum (Ec)	5	0.09 ± 0.03	0.06 ± 0.02	0.13 ± 0.10	45.90 ± 9.61	6.00 ± 0.94	1.25 ± 0.72	10.52 ± 2.71
Dasyphyllum diacanthoides (Dd)	7	0.09 ± 0.02	0.07 ± 0.01	0.24 ± 0.07	22.94 ± 6.29	3.11 ± 0.61	0.93 ± 0.47	3.03 ± 1.77
Gevuina avellana (Ga)	8	0.16 ± 0.02	0.12 ± 0.01	0.53 ± 0.06	42.81 ± 5.88	7.54 ± 0.58	3.46 ± 0.44	19.41 ± 1.66
Luma apiculata (La)	8	0.21 ± 0.02	0.15 ± 0.01	0.37 ± 0.06	17.55 ± 5.88	1.77 ± 0.58	1.46 ± 0.44	2.96 ± 1.66
Lomatia ferruginea (Lf)	5	0.20 ± 0.03	0.16 ± 0.01	0.35 ± 0.10	14.43 ± 9.61	3.47 ± 0.94	1.73 ± 0.72	7.73 ± 2.71
Rhaphithamnus spinosus (Rs)	5	0.18 ± 0.02	0.14 ± 0.02	0.49 ± 0.08	27.44 ± 7.44	3.66 ± 0.73	1.56 ± 0.55	2.25 ± 2.09
Laureliopsis philippiana (Lp)	9	0.14 ± 0.01	0.10 ± 0.01	0.26 ± 0.06	30.73 ± 5.55	4.36 ± 0.54	2.56 ± 0.41	8.47 ± 1.56
Myrceugenia planipes (Mp)	16	0.15 ± 0.01	0.11 ± 0.01	0.36 ± 0.04	26.55 ± 4.16	3.56 ± 0.41	2.12 ± 0.31	6.36 ± 1.17

Significant differences among species after one-way ANOVA: *$P < 0.05$, **$P < 0.01$; ***$P < 0.001$. n = sample size.

Determination of light quantity and quality

Light availability over each sapling was quantified by hemispherical photography. Comparisons of methods revealed a good accuracy of hemispherical photography for the description of understorey light availability (Bellow & Nair 2003). The photographs were taken using a horizontally levelled digital camera (CoolPix 995, Nikon, Tokyo, Japan), mounted on a tripod and aimed at the zenith, using a fish-eye lens of 180° field of view (FCE8, Nikon). Photographs were analysed for canopy openness using Hemiview canopy analysis software version 2.1 (1999, Delta-T Devices Ltd, UK). This software is based on the program CANOPY (Rich 1990). Photographs were taken under homogenous sky conditions to minimize variations due to exposure and contrast. The direct site factor (DSF) and the indirect site factor were computed by Hemiview accounting for the geographic features of the site. These factors are estimates of the fraction of direct, and diffuse or indirect radiation, respectively, expected to reach the spot where the photograph was taken (Anderson 1966). The hemispheric distribution of irradiance used for calculations of diffuse radiation was standard overcast sky conditions. A total of 160 sky sectors were considered resulting from 8 azimuth × 20 zenith divisions.

Spectral composition above each sapling of each forest stand was measured using a portable spectroradiometer (SPEC PAR-NIR, Apogee Inc., Logan, UT, USA), equipped with the cosine corrected sensor with 180° field of view. Spectroradiometer SPEC PAR-NIR has a detection range of 190–2200 nm, with a wavelength accuracy of 0.5 nm. Two days representative of clear-sky conditions (18–19 December 2007) were selected for light-quality measures. We measured light quality at solar midday (12.00–15.00 hours), taking four spectra above each plant at each light environment. The average of these measurements was used as an individual plant value. At the same time we took three spectra in the centre of five large gaps (>2000 m^2), as a control of the full sunlight spectral composition. The sequential order of sampling in the field was randomized. Ratio of red to far-red light (R : FR) was estimated by dividing the total irradiance of red light (R: 660 ± 6 nm wavelength) by the total irradiance of far-red light (FR: 730 ± 6 nm wavelength). Additionally, we calculated the blue light (450 ± 6 nm) to red light ratio, UV-A (300 ± 15 nm) to red light ratio and UV-B (330 ± 15 nm) to red light ratio.

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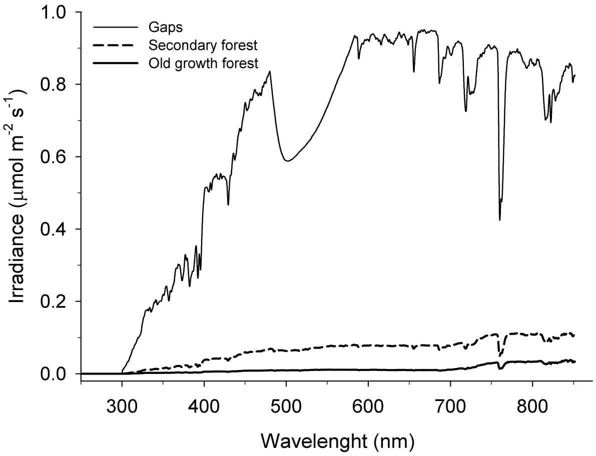

Fig. 1. Irradiance spectra characteristic of gaps and of the understorey of secondary and old-growth forest patches. We included the average spectra of five large gaps (>2000 m^2), as a reference for full sunlight spectral composition.

Data analysis

A one-way ANOVA was used to test for differences in light quantity and quality between forest stands (old-growth forest, secondary forest and gaps). Species characteristics (light environment and morphological traits) were also compared by a one-way ANOVA. Correlation analyses (Pearson product-moment coefficients) were used to test for the relationship between morphological traits of saplings (slenderness, internode : leaf length ratio and internode length) and light environment conditions (DSF and R : FR). In order to maximize the sample size and depict the general response patterns of plant traits to light quantity and quality, we pooled data from both old-growth and secondary forest stands for correlation analyses.

In order to estimate the phenotypic change of saplings with light quantity and quality, we calculated the slope of the regression between morphological traits and light conditions across the forest (light availability DSF and R : FR) for each species. These species and trait specific slopes were correlated with the minimum light requirement of the species obtained from Lusk *et al.* (2008). MRL is the 10th percentile of the distribution of each species in relation to light availability (% canopy openness), which is an approximation of the lowest light levels tolerated by each species (Lusk *et al.* 2008).

RESULTS

Gaps had not only more light but also a different light quality than that of the two forest understoreys studied (Fig. 1, Table 1). Significant differences were also found for the light environment of the understorey of the two forests. The understorey of the secondary forest had more direct and diffuse light and a higher R : FR than that of the old-growth forest while the reverse was true for blue to red and UV to red light ratios (Table 1, Fig. 2). However, even though mean R : FR was higher in the secondary forest understorey, R : FR was scattered over a wide range of values in both forest types, with values as high as 0.45 in the darkest understorey and as low as 0.09 in the brightest one, with a remarkable overlap in sampling points from the two forests for the 0.1–0.4 range (Fig. 2). Sampling plants over the two types of forest allowed us to have saplings of each species growing over a wide range of light environments differing either in light quantity, light quality or both.

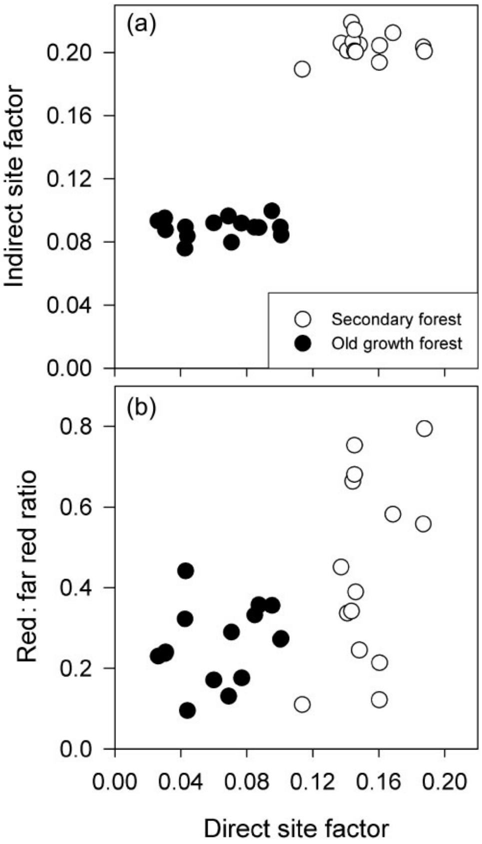

Fig. 2. Diffuse irradiance (indirect site factor) (a) and red : far red ratio (b) *versus* direct irradiance (direct site factor) in the secondary (open symbols) and old-growth (closed symbols) forest plots where the saplings were found.

Significant differences were found for the mean light environment of the saplings of the different species, which also differed in basal stem diameter, internode length and leaf length (Table 3). Differences in plant height among species were not significant (Table 3). Both plant slenderness (plant height/ stem diameter) and mean internode length increased with increasing light availability when all individuals from the species studied were plot together (Fig. 3). These two variables exhibited high variability for a

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Table 3. Range of light environments (direct site factor and red : far red ratio) where saplings of the 11 evergreen species where sampled in a Chilean rainforest

	Direct site factor range		Red : far red ratio range	
Species	Lower value	Upper value	Lower value	Upper value
Aristotelia chilensis (Ac)	0.14	0.19	0.12	0.79
Amomyrtus luma (Al)	0.03	0.10	0.23	0.36
Aextoxicon punctatum (Ap)	0.04	0.19	0.12	0.66
Embothrium coccineum (Ec)	0.03	0.10	0.13	0.36
Dasyphyllum diacanthoides (Dd)	0.04	0.08	0.10	0.18
Gevuina avellana (Ga)	0.04	0.19	0.17	0.79
Luma apiculata (La)	0.14	0.19	0.12	0.68
Lomatia ferruginea (Lf)	0.14	0.17	0.12	0.58
Rhaphithamnus spinosus (Rs)	0.04	0.16	0.10	0.75
Laureliopsis philippiana (Lp)	0.03	0.19	0.12	0.68
Myrceugenia planipes (Mp)	0.04	0.19	0.32	0.66

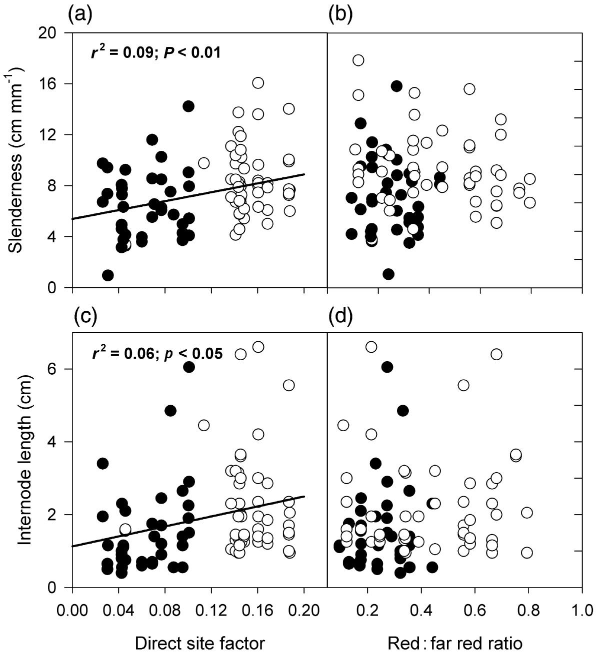

Fig. 3. Slenderness (a and b) and internode length (c and d) of the saplings of the 11 species studied *versus* direct site factor and red : far red ratio in the secondary (open symbols) and old-growth (closed symbols) forest plots where the saplings were found.

given light quantity level (r^2 was below 0.1 in the two regressions) due, at least in part, to the different crown architectures of the different species considered. A similarly positive trend was found for most species when regressions were calculated for each species independently (see Appendix S1–S4). No relationship was found between any of these two traits and R : FR (Fig. 3).

Change of plant slenderness with light availability, estimated from the slope of slenderness *versus* the DSF, increased with increasing light requirements of the species (i.e. with decreasing shade tolerance; Fig. 4). By contrast, change of internode length with light availability, estimated in an analogous way, decreased with increasing light requirements of the species. A similar pattern was found for change of slenderness with R : FR, that is, greater differences along the light gradient with increasing light requirements of the species, although with greater scatter than that observed for variation with DSF (r^2 of 0.24 *vs.* 0.48, respectively; Fig. 5). No relationship was found between changes in internode length with R : FR and light requirements of the species (Fig. 5).

DISCUSSION

Our study revealed that the phenotypic variation of saplings along the light gradient in a forest understorey was influenced by interspecific differences in shade tolerance. We expected that shade-tolerant plants cope with light shortage by affording the resource costs of producing robust individuals of a high light harvesting efficiency, which should pay off in the long run. Less shade-tolerant plants were expected to show phenotypic variation related to escape from the shade, investing in vertical growth at the expense of poor light interception and carbon gain, which compromises survival in the understorey if shading prevails. In our study, plants from shade-tolerant species increased their robustness (decreased slenderness) in deep shade. This pattern is somewhat coincident with the reported variation of leaf area on a mass basis (SLA, Specific Leaf Area), where thicker leaves are found in

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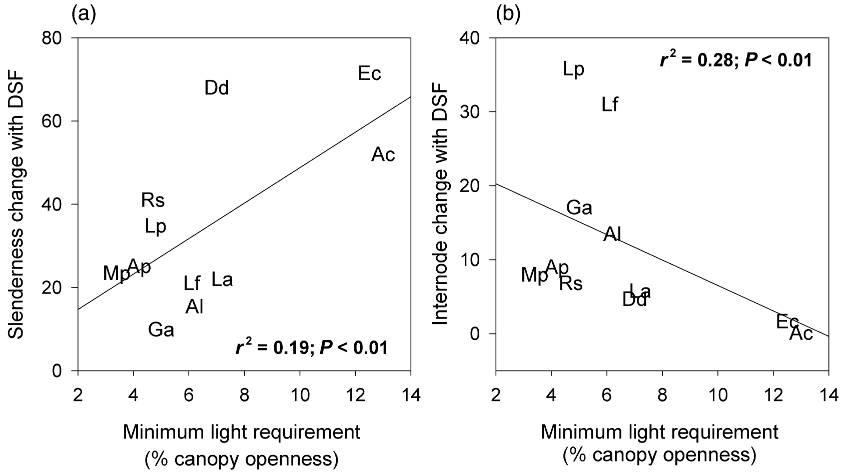

Fig. 4. Mean change in slenderness and internode length with increasing direct irradiance (direct site factor (DSF)) (a and b, respectively) *versus* mean light requirement of each of the 11 woody species studied. See Table 2 for abbreviations of the species.

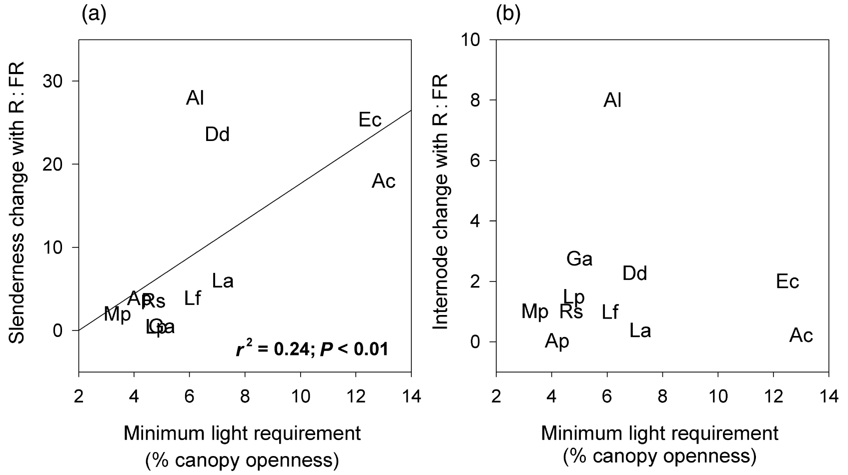

Fig. 5. Mean change in slenderness and internode length with increasing red : far red ratio (R : FR) (a and b, respectively) *versus* mean light requirement of each of the 11 woody species studied. See Table 2 for abbreviations of the species.

shade-tolerant species (Lusk & Warton 2007), which is often interpreted in terms of decreasing the risk of premature tissue losses via reduced palatability and fragility of leaves (Kitajima 1994; Lusk 2002). This costly strategy should only pay-off if leaf longevity extends over several years; otherwise the extensive mass and energy investment in aerial plant biomass would be maladaptive. Likewise, the observed robustness of saplings in the shade should be associated with enhanced, long-term survival in the understorey for this strategy to be adaptive.

Plants exposed to reductions in R : FR typically follow the shade avoidance syndrome and elongate their stems and increase their internode lengths to actively compete for light with neighbours (Smith 2000). But different responses, such as those reported here for shade tolerators, have been described in previous studies, particularly when competition for light is not symmetrical, that is, when it is established between plants of different sizes like trees and understory plants. For instance, Reinhart *et al.* (2006) found a reduction in internode length in *Acer platanoides* seedlings in response to a reduced R : FR, which was interpreted as a strategy to 'sit and wait' rather than compete for light with canopy trees (Reinhart 2010). Responses to shade seems to involve a coordinated response to low light intensity and to changes in both blue light and R : FR (Lin 2000; Valladares & Niinemets 2008), which leads,

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at least in certain plant species, to extend survival in the understory and to increase chances to take advantage of eventual canopy openings.

Interestingly, patterns of phenotypic change arose when light quantity was considered in the analysis, while no relationship was found between plant slenderness and light quality. Shade tolerance was more related to changes in these architectural traits with light quantity than with light quality (R : FR). We hypothesized that traits related with elongation, and thus with shade avoidance, would respond more to R : FR than to light quantity, while traits involved in light harvesting efficiency would respond more to light quantity than to R : FR. Both plant slenderness (plant height/stem diameter) and mean internode length increased with increasing light availability when all individuals from the 11 species studied were plotted together, but no relationship was found between any of these two traits and R : FR. The change in plant slenderness with light availability was of lesser magnitude with increasing shade tolerance of the species, while internode change with light availability increased with increasing shade tolerance of the species.

The reduction in internodes lengths of plants experiencing deep shade is a case of counter-gradient variation (Conover & Schultz 1995) because typical intraspecific plastic responses to shade (elongated internodes) oppose interspecific patterns of phenotypic variation with increasing shade found here (shortened internodes). This can be interpreted considering that elongation in small saplings growing under the deep shade of a tall canopy is a futile and even risky resource investment (Valladares & Niinemets 2008). On the contrary, stem elongation in the secondary forest may be a rewarding strategy if it leads to overtopping competing plants (see also discussion in Henry and Aarssen 2001). Alternatively, the pattern of shortened internodes might be related allometrically with the reduced slenderness syndrome formerly described. The same explanation of a counter-gradient variation could apply to the positive slenderness-light trend observed across species. However, the same trends are found when data are explored within species (see Appendix S1–S4), suggesting that this might not be the case in our study system. However, further studies controlling phenotypic expression of individual genotypes are required to discard this explanation more conclusively.

Only light quantity showed a significant association with this pattern of phenotypic variation, suggesting that despite the considerable evidence accumulated on the role of phytochrome-mediated signalling on plant responses to shade, light quality could play a subordinate role with regards to light quantity. An earlier study with tropical vine juveniles showed that for two out of three species the reduction in light quantity (photosynthetic photon flux density) elicited greater responses in plant slenderness and internodes elongation than the reduction in light quality (R : FR) (Lee 1988).

Although the 11 woody species considered in this study significantly differed regarding their shade tolerance, the sampled individuals (saplings < 50 cm height) might not represent the shade tolerance of adult trees because this feature is known to change during the ontogeny (Kneeshaw *et al.* 2006; Valladares & Niinemets 2008). Lusk *et al.* (2004) suggested that differences in shade tolerance among evergreens co-occurring in temperate rainforests of southern Chile become increasingly important with increasing plant size and/or age. Interestingly, the effect of size on the light requirements of these plants seems to be related to the successional status of these temperate rainforest species. Species regarded as shade tolerant like *M. planipes*, *A. punctatum* and *L. philippiana*, had low light requirements that did not significantly change across height classes (Donoso 1989; Lusk 2002, 2004). By contrast, light requirement of the most shade intolerant species increased at increasing ontogenetic stages. Thus, care must be taken when extrapolating shade tolerance and functional features of saplings growing under low, understorey light to older plants and adult individuals even of the same species. Another word of caution is needed regarding the estimated phenotypic variance in response to the light environment; we argue that the variance estimated here is meaningful on an ecological basis (i.e. representative according to the co-occurring populations of each species) but this variance might not have captured well the real phenotypic variance of the species, particularly of those having low numbers of individuals in the forest understoreys studied.

In conclusion, our study suggests that shade tolerators afford higher resource costs (thicker stems and plants), which render more biomechanically robust plants, and respond more to the light environment in traits strongly influencing light interception (internode length in the present study) than shade intolerant species. By contrast, less shade-tolerant plants afforded higher risks in their plastic response to escape from the understorey by making thinner plants that are biomechanically weaker and poorer light interceptors. Species differing in their shade tolerances differed in their plastic responses to light, more clearly to light intensity than to light quality. Differences in plasticity arose not from overall or mean plasticity but from plasticity for specific traits with contrasting functional meanings. Our results thus contribute to explaining plant coexistence in heterogeneous light environments by improving our mechanistic understanding of species responses to light. While some species minimize risks and afford costs, others follow the opposite

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strategy, and both can render successful. The impact in fitness of following one or another is eventually determined by both the spatial and the temporal grain of environmental heterogeneity, which is highly variable depending not only on the type of ecosystem but also on the structure and dynamics of each particular forest patch. This locally idiosyncratic nature of the light environment further promotes coexistence at higher scales.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Slenderness *versus* direct site factor for each of the 11 species studied.

Appendix S2. Internode length *versus* direct site factor for each of the 11 species studied.

Appendix S3. Slenderness *versus* red : far red ratio for each of the 11 species studied.

Appendix S4. Internode length *versus* red : far red ratio for each of the 11 species studied.

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