



Leaf functional traits predict cloud forest tree seedling survival along an elevation gradient

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Received: 8 July 2019 / Accepted: 14 November 2019 / Published online: 11 December 2019
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Abstract

• **Key message** Cloud forest tree seedlings of higher leaf mass to area ratio and leaf dry matter content displayed higher survival along an elevation gradient in the forest understorey. Phenotypic plasticity in leaf functional traits was not related to seedling survival.

• **Context** Understanding the relationship between seedling survival and phenotypic plasticity of leaf functional traits is of great importance for predicting tree species responses to climate change.

• **Aims** We analysed whether phenotypic plasticity and mean values of leaf functional traits could serve as predictors of cloud forest tree seedling survival along an elevation gradient.

• **Methods** We measured survival, leaf mass area (LMA) and leaf dry matter content (LDMC) in planted tree seedlings of 13 shade-tolerant tropical cloud forest species in nine forest understorey sites along an elevation gradient in southern Mexico. Phenotypic plasticity in LMA and LDMC was calculated based on inter-individual phenotypic variation to different elevations.

• **Results** Intraspecific differences in LMA and LDMC occurred with elevation. Across the elevation range, seedlings with higher mean LMA and LDMC had higher survival. Plasticity in leaf traits was small and was not related to survival.

• **Conclusion** Our results support that mean LMA, and to a lesser extent mean LDMC, could be good predictors of cloud forest tree seedling survival along elevation gradients. The small leaf trait plasticity found does not affect the survival of seedlings in the forest understorey along the elevation gradient.

Keywords Climate change · Leaf dry matter content · Leaf mass area · Phenotypic plasticity · Regeneration strategy · Shade tolerance · Temperature

Handling Editor: Erwin Dreyer

Contribution of the co-authors TTA conceived and designed the experiment; MAGH conducted the fieldwork and performed statistical analyses; and TTA, MAGH and HP wrote the manuscript.

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1 Introduction

The ability of tree species to cope with rapid climate change is of major concern in terms of biodiversity loss. In response to climate change, individuals have the possibility to either tolerate or acclimate to the environmental variation via phenotypic plasticity (Gratani 2014; Liu et al. 2016). However, the relative importance of these two responses has rarely been addressed in tropical forests, particularly during the regeneration phase, even though this developmental stage is subject to the highest selective pressures (Reich et al. 2003). Plant functional traits and their plasticity can affect plant performance under varying climatic conditions, especially changes in temperature, potentially representing predictors of plant capacities to cope with new climatic scenarios (Soudzilovskaia et al. 2013; Gratani 2014).

In tropical forests, the majority of tree species are shade tolerant and adapted to long-term survival under shaded conditions (Denslow 1987; Uhl et al. 1988). Linked morphological

and physiological leaf traits can strongly contribute to plant carbon economy and performance of tree saplings in shaded conditions (Sterck et al. 2006). The shade-tolerance strategy involves maintenance of captured resources rather than high resource gain, so shade tolerance is associated with biomass and energy conservation traits (including extended leaf life span, higher leaf mass area, and lower photosynthetic capacities) that maximize survival under low light conditions, at the expense of low growth rates (Kitajima 1994; Wright et al. 2010; Reich et al. 2003; Dent and Burslem 2009). Species that regenerate in the shaded understory can reduce carbon drain by increasing their leaf survival rates and presenting low respiration rates, which allows the plant to maintain a positive carbon balance, enhancing plant survival (Reich et al. 2003; Poorter and Bongers 2006). Such long-lived leaves require additional mechanical and chemical protection against herbivory (Coley and Barone 1996) and physical hazards (Alvarez-Clare and Kitajima 2007), resulting in a high leaf mass area (LMA) and low photosynthetic capacity (Sterck et al. 2006).

This conservative strategy of resource use has been linked to reduced phenotypic plasticity (Sánchez-Gómez et al. 2008; Poorter et al. 2009; Gratani 2014; Liu et al. 2016; Valladares et al. 2016). In diverse ecological studies, such phenotypic plasticity has been broadly estimated as the magnitude of inter-individual phenotypic variation in response to varying environmental conditions (Valladares et al. 2006, 2014). The reasoning behind this is that both components of inter-individual variation in natural populations, genotypic and plastic response, may contribute to the capacity of a species to deal with environmental changes (Feeley et al. 2012). Phenotypic plasticity (adjustment) is considered potentially advantageous for plants, since it could increase the probability of persistence under climate change (Richter et al. 2012; Gratani 2014). However, high phenotypic plasticity may imply metabolic costs that compromise long-term survival under resource limiting conditions (Liu et al. 2016; Bongers et al. 2017) and may thus impede the survival of species with high phenotypic plasticity in understory environments (Valladares and Niinemets 2008). It remains an open question whether individuals of shade tolerant species can display high phenotypic plasticity (high inter-individual variation) to changes in temperature as a result of climate change, and whether this capacity would act to increase their probability of survival in the understory.

Changes in temperature might act as a selection pressure on plant functional traits (Bresson et al. 2011). Therefore, the analysis of the variation of plant functional traits in response to this environmental factor and the implications of this variation for the capacity of populations to respond to changing environmental conditions is of great importance (Körner 2007; Soudzilovskaia et al. 2013). Leaf mass area (LMA) and leaf dry mass content (LDMC) are two morphological traits at the core of the resource acquisition–conservation capacity trade-off, directly affecting the performance and

survival of individuals (Reich 2014). LMA correlates with stress tolerance, particularly during the seedling and sapling stages (Janse-Ten Klooster et al. 2007; Poorter 2009; Wright et al. 2010). In principle, high carbon investment on a per-leaf basis is associated with resistance to the freezing temperatures that can occur at higher elevations (Körner et al. 1989; Körner 2012; Read et al. 2014). LDMC is a trait associated with resistance to drought or physical damage (Markesteyn et al. 2011; Bongers et al. 2017); leaves with high LDMC tend to be relatively tough and are potentially more resistant to physical damage caused by wind and hail (Pérez-Harguindeguy et al. 2013). To date, very limited information is available regarding the relationship between plasticity or inter-individual variation in LMA and LDMC and the ecological performance of tree seedlings in response to temperatures in the field.

Due to the existence of a trade-off between tolerance to shade and tolerance to other environmental factors, shade tolerance may influence the response of plants to different drivers of global change, such as elevated temperatures (Valladares and Niinemets 2008). This could be because leaves with a higher capacity for light capture (low LMA) can incur increased respiration costs caused by high temperatures, which are more difficult to compensate with the low photosynthetic rates prevalent in the shade (Valladares et al. 2016). This scenario may favour conservative species capable of reducing carbon losses, rather than those species capable of plastically adjusting their morphology or physiology in response to temperature increases.

In this study, we performed an experimental evaluation of tree seedling performance and functional trait variation in shade tolerant cloud forest species along an elevation gradient in order to contribute to elucidation of the potential response of tropical tree species to the observed or predicted effects of climate change. The specific questions we addressed were as follows: (1) Do mean leaf functional traits affect species success (seedling survival) differentially under the scenarios of high to low temperature present along the elevation gradient? (2) How does temperature affect intraspecific variation in LMA and LDMC along an elevation gradient, and are there general patterns in the plastic response? (3) Does the plastic response enhance survival across the elevation gradient? Together, the answers to these questions allow us to discern whether the mean values of LMA and LDMC (attributes conferring resistance) or their phenotypic plasticity are more closely related with probability of survival among species along the temperature gradient expressed by the selected elevation range. Since leaf functional traits that confer greater tolerance could be associated with a higher chance of survival in the forest understory, we expected tree species with higher LMA and LDMC to present higher survival in this environment. We expected a decrease in LMA and LDMC within species, in response to higher temperatures at lower elevation. Since resource limitation or environmental stress can reduce the potential phenotypic plastic response of a given trait (van Kleunen and Fischer 2005; Valladares et al.

2007; Gratani 2014), and shade tolerant species tend to have a conservative leaf morphological pattern, low phenotypic plasticity can act to enhance performance in the shaded forest understorey. Thus, while higher mean LMA and LDMC could be associated with higher survival in the understorey, we expected no relationship between phenotypic plasticity in these leaf functional traits and tree seedling survival along the elevation gradient.

2 Methods

2.1 Species

Thirteen tropical montane cloud forest tree species were selected based on seed availability and shade tolerance (Table 1). All species are associated with late successional stages and have been reported as intermediate to shade tolerant (Ramírez-Marcial et al. 2012; Toledo-Aceves et al. 2017). Due to the scarcity of mature trees of most of the studied species, seeds of three to five individuals per species were collected from cloud forest fragments in the study region in 2014. Some of the studied species have been overharvested by local communities and their populations have disappeared locally in the study region (Paré and Gerez 2012; Ortiz-Colín et al. 2017). Immediately after collection, the seeds were cleaned and sown in seedbeds with forest soil in a common garden experiment. The resulting seedlings were transplanted into polythene bags (30 × 16 cm) with forest soil at approximately two months after germination. Plants were kept in a common rustic nursery (located at 2088 m a.s.l.) covered with 30% shade mesh and no chemicals were applied. Seedling age varied from 10 to 18 months at the time of transplantation, due to differences in phenology and germination rates among species.

2.2 Study sites

The experiment was conducted along an elevation gradient from 1250 to 2517 m a.s.l. in Veracruz, Mexico (Table 2). Along this gradient, the reported mean annual temperature ranges from 8 to 18 °C (Vidriales-Chan et al. 2012) and mean annual precipitation varies between 1800 and 2000 mm (Vidriales-Chan et al. 2012). Nine forest sites were selected based on shared attributes (forest fragment area > 1 ha, presence of forest cover for at least the last 40 years, absence of cattle grazing inside the forest, ≤ 40° slope). One 50 × 55 m plot was delimited in each forest for transplantation of the tree seedlings. Given that the central objective of the study was to evaluate the influence of temperature on seedling performance in the forest understorey, all of the plots were established under canopy cover. To assess forest structure, one 50 × 10 m transect was delimited along the middle of the plot and the diameter at breast height (DBH; at 1.3 m height) of all trees > 5 cm DBH

recorded. The forest characteristics for each plot are shown in Table 2, and a more detailed description of the forest sites is available elsewhere (García-Hernández et al. 2019). To record air temperature and air humidity, one sensor (iButton ThermoChron) was placed in the centre of each plot, recording these data at 10-min intervals from October 2015 to June 2017. The maximum and minimum temperatures recorded along the gradient are shown in Table 2. The soil characteristics are detailed in Table 6 in the Appendix. Due to the high spatial heterogeneity of soil nutrient contents and because strong tolerance to low soil nutrient availability is observed in cloud forest ecosystems (Bruijnzeel and Veneklaas 1998), the effects of soil nutrients on leaf traits were not analysed.

2.3 Experimental design and functional trait measurements

In each of the nine plots, 30 seedlings per species were planted at random in a grid pattern, ~ 2.6 m apart, at the beginning of the rainy season (May–June 2015). The height of all individuals was measured after planting. To reduce non-woody competitors, a ~ 1-m radius around each seedling was weeded at the time of planting and again at 3 and 6 months after planting. Seedling survival was recorded for all of the plants after 2 years.

From each plot, 10 seedlings per species were selected at random and one new mature leaf (including the petiole), produced after transplanting and presenting no damage, was collected in order to determine LMA and LDMC, following the procedures described by Pérez-Harguindeguy et al. (2013) (processing details can be found in Table 9 in the Appendix). The following formulas were used to determine the functional traits: LMA = leaf dry mass / leaf area, and LDMC = leaf dry mass / leaf water saturated fresh mass (Pérez-Harguindeguy et al. 2013).

Seedling performance and leaf traits can be affected by light; in a previous analysis, canopy cover and temperature affected seedling survival and growth of the same ensemble of species along an elevation gradient (García-Hernández et al. 2019). Canopy cover was estimated one year after transplanting by taking hemispherical photographs above each of the 10 seedlings selected per species for leaf functional trait measurements in each plot (see details in García-Hernández et al. 2019).

2.4 Data analysis

To assess the relationship between mean species functional traits and seedling survival, we used a generalized linear model (GLM). LMA and LDMC were correlated ($R = 0.648$, $P < 0.001$). One GLM (quasibinomial family and logit link function) was fitted separately for each leaf functional trait. LMA and canopy cover were correlated ($R = -0.267$, $P = 0.003$),

LMA and temperature were correlated ($R = -0.197$, $P = 0.034$), and LMA and LDMC and initial height were correlated ($R = 0.437$, $P < 0.001$, $R = 0.329$, $P > 0.001$, respectively). Canopy cover and temperature were also correlated ($R = 0.487$, $P > 0.001$). To evaluate the relationship between LMA and LDMC, the Pearson correlation coefficient was used, while the Spearman correlation coefficient was calculated for the rest of the variables. In order to maximize the explanatory power of the model while maintaining its performance, only variables with low correlation (correlation coefficient $R < 0.5$) were maintained in the GLM, following Dormann et al. (2013). Mean values per site of canopy cover, temperature, and mean LMA or LDMC and seedling initial size (height) per species per site were included as covariates. To evaluate possible changes in the relationship between survival and leaf functional traits at the different elevations or dependent on canopy cover, the interactions leaf functional trait \times temperature and leaf functional trait \times canopy cover were also included. While temperature extremes could be expected to have a stronger effect on seedling functional traits and performance, given that mean temperature values were highly correlated to the minimum ($R = 0.953$, $P < 0.001$), and maximum ($R = 0.967$, $P < 0.0001$) temperature values recorded, we used the mean temperature values because these adequately represented the microclimate at each study site.

To determine the effect of the environmental variables (temperature, humidity and canopy cover) on intraspecific variation in leaf functional traits (LMA and LDMC) along the elevation gradient, a general linear model (LM) was fitted for each tree species separately. Mean temperature and air humidity per site and canopy cover above each seedling were included as covariates. Air humidity had no significant effect on the majority of the species and was therefore excluded from the models based on the Akaike Information Criterion (AIC). In all cases, the AIC was used for selection of the best model, i.e. that which presented the lowest AIC value (Crawley 2013). The Box–Cox transformation was used to increase homoscedasticity in the residuals where necessary.

To assess whether the plastic response of leaf traits to temperature is associated with seedling survival along the temperature gradient, we followed two procedures. First, for each functional trait, we tested a correlation between the slopes of plastic change in LMA (or LDMC) and the slopes of seedling survival in relation to temperature, where each data point represented one species. In this analysis, for example, a negative correlation would suggest that a plastic response would generally act to compromise survival while a positive association would suggest that a more plastic response would enhance survival among species. Secondly, we calculated the Relative Distance Plasticity Index (RDPI) proposed by Valladares et al. (2006), which quantifies phenotypic distances between individuals of a given species exposed to different environments (in our case, to different elevations). This index

was calculated for each leaf trait and for each species following Valladares et al. (2006) as follows:

$$\text{RDPI} = \sum(d_{ij \rightarrow i'j'} / \max\{x_{i'j'}, x_{ij}\}) / n$$

where RDPI is the result of the sum of the differences among trait values $d_{ij \rightarrow i'j'}$ for all pairs of individuals of a given species grown in different environments (i.e. elevations), divided by the maximum value of the trait (of the pair of individuals). The total number of distances is denoted by n (in our case, 3600 for each species). To assess the relationship between the species phenotypic plasticity of the functional traits based on the RDPI and seedling survival, a GLM was fitted (quasibinomial family and logit link function) using the RDPI for LMA or LDMC and overall survival per species along the gradient. All analyses were conducted with the program R, version 3.6.0 (R Core Team 2019).

3 Results

3.1 Seedling survival and leaf functional traits

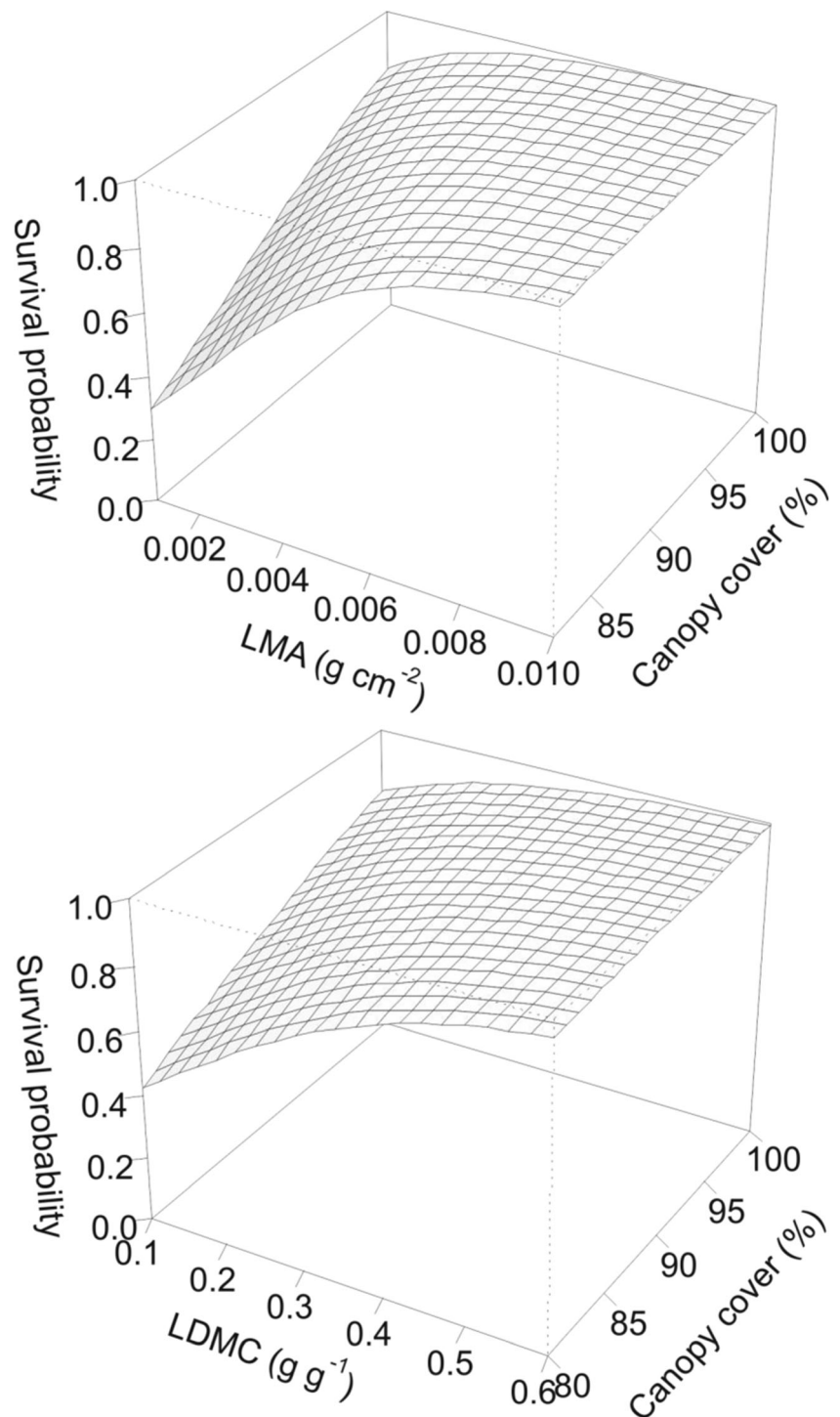
After 2 years, seedling survival ranged from 68% in *Meliosma alba* to 98% in *Quercus germana*. The ranking of species based on their survival at the sites with lowest temperature differed from the ranking based on survival in the sites with highest temperature (Table 7 in the Appendix). However, not all species that presented higher survival at the highest temperature presented the lowest survival at the lowest temperature. Most individuals were located under high levels of canopy cover (Fig. 3 in the Appendix).

The GLMs showed that mean functional traits had a highly significant effect on seedling survival among species; survival increased with LMA and LDMC (Table 3; Fig. 1). There was a canopy cover effect on seedling survival, which was additional to the contribution it had already made through its relationship with LMA; seedling survival increased with canopy cover. In the GLMs, 35.64% of deviance was explained by LMA and canopy cover, and 21.67% of deviance was explained by LDMC and canopy cover. Temperature and initial seedling size had no significant effect on survival (Table 8 in the Appendix). The interactions between leaf functional traits and temperature and canopy cover were also non-significant (full models can be found in Table 8 in the Appendix).

3.2 Intraspecific variation in LMA and LDMC

The LMs showed that intraspecific variation in leaf functional traits was explained by temperature and canopy cover (Table 4). The LMA decreased with temperature in eight species, with only *Sideroxylon contrerasii* presenting the opposite pattern. This trait decreased with canopy cover in 11 of 13

Fig. 1 Effects of leaf traits and canopy cover on seedling survival in 13 cloud forest tree species in the forest understory. Mean LMA and probability of survival ($P < 0.001$) (top) and mean LDMC and the probability of survival ($P < 0.001$) (bottom)



species (Table 4). The LMA of *Ocotea disjuncta* and *Oreomunnea mexicana* was unaffected by any of the environmental variables evaluated (Table 4).

For most of the species, LDMC displayed slight variation and the response to temperature was inconsistent among the taxa. The LMs showed that only *M. alba* and *Ulmus mexicana* presented decreased LDMC at higher temperatures, while the opposite pattern was found in *O. mexicana* and *S. contrerasii*.

LDMC decreased with higher canopy cover in seven species (Table 5). In *Carpinus tropicalis*, *O. disjuncta* and *Prunus rhamnoides*, LDMC was unaffected by any of the environmental variables measured. The mean values of LMA and LDMC are found in Table 9 in the Appendix, and their variation within species dependent on temperature is found in Fig. 4 in the Appendix. The primary data is deposited in TRY Plant Trait Database (Toledo-Aceves and García-Hernández 2019).

3.3 Phenotypic plasticity of leaf functional traits and seedling survival

No significant correlations were found between the slope of the change in LMA or LDMC as a function of temperature and the slope of survival ($P = 0.234$ and $P = 0.267$, respectively; Fig. 5 in the Appendix). In terms of the phenotypic plasticity of the leaf functional traits analysed with the RDPI, there was low variation for LMA and LDMC (Fig. 2). The RDPI for LMA and LDMC did not show a significant relation with seedling survival (Table 3; Fig. 2).

4 Discussion

4.1 LMA and LDMC as predictors of tree seedling survival

LMA is a key trait involved in carbon, nutrient and water economics and is part of a whole set of interconnected traits that

together shape the performance of plants (Poorter 2009; Reich 2014). Our results suggest that mean species LMA could be a good predictor of cloud forest tree seedling survival probability in shade tolerant species in the understorey. While survival and LMA did not present high interspecific differences, a pattern of coordination emerged among the shade tolerant tree species studied; the species with higher LMA displayed the highest early survival, regardless of variation in temperature and canopy cover along the elevation gradient. The prominent role of mean species values of LMA in plant survival has also been suggested in previous studies (Kitajima 1994; Garnier et al. 2001; Poorter and Bongers 2006; Wright et al. 2010). High LMA leaves have lower return per mass investment per time (Westoby et al. 2013); this trait is associated with the “slow strategy” which is advantageous in low resource settings because resource conservation acts to enhance survival (Reich 2014). Despite the confounding factors, and since leaf traits were correlated with canopy cover and temperature (although the correlations were weak), our results support the hypothesis that, under low-resource conditions such as those found in the shaded forest understorey, conservative

Fig. 2 Relationship between (top) the Relative Distance Plasticity Index (RDPI) of LMA and tree seedling survival ($P = 0.927$) and (bottom) the RDPI of LDMC and tree seedling survival ($P = 0.112$)

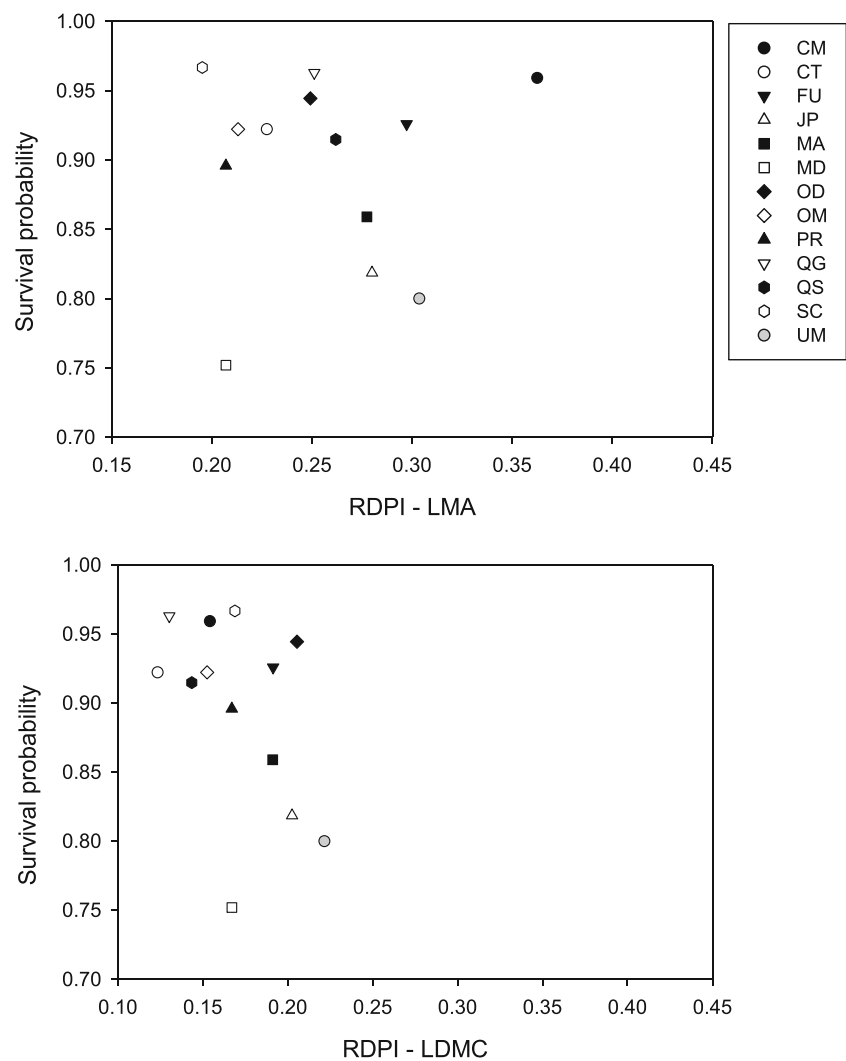


Table 1 Tropical montane cloud forest tree species studied. I = intermediate, S = shade tolerant. (^aRamírez-Marcial et al., 2012; ^bGolicher et al., 2008; ^cMuñiz-Castro et al., 2015; ^dMuñiz-Castro, 2008). ¹González-Espinosa et al. (2011), ²Furlow (1987), ³Vázquez-García et al. (2013)

Acronym	Species	Family	Shade tolerance	Elevation range (m a.s.l.)
CM	<i>Clethra macrophylla</i> M. Martens & Galeotti	Clethraceae	I ¹	750–1500 ¹
CT	<i>Carpinus tropicalis</i> (J. D. Smith) Lundell subsp. <i>tropicalis</i>	Betulaceae	S ^b	1200–2500 ²
FU	<i>Fraxinus uhdei</i> (Wenz.) Lingelsh.	Oleaceae	I ^b	1300–2240 ¹
JP	<i>Juglans pyriformis</i> Liebm.	Juglandaceae	S ^a	1200–1400 ¹
MV	<i>Magnolia vovidesii</i> A. Vázquez, Domínguez-Yescas & L. Carvajal.	Magnoliaceae	I ^a	600–1700 ³
MA	<i>Meliosma alba</i> (Schltdl.) Walp.	Sabiaceae	I ^a	700–1900 ¹
OD	<i>Ocotea disjuncta</i> Lorea-Hern.	Lauraceae	S ^a	1700–2500 ¹
OM	<i>Oreomunnea mexicana</i> J.F. Leroy	Juglandaceae	S ^a	1100–2000 ¹
PR	<i>Prunus rhamnoides</i> Koehne	Rosaceae	S ^a	1500–2400 ¹
QG	<i>Quercus germana</i> Schltdl. & Cham.	Fagaceae	S ^c	800–1800 ¹
QS	<i>Quercus sartorii</i> Liebm.	Fagaceae	I ^d	1300–2000 ¹
SC	<i>Sideroxylon contrerasii</i> (Lundell) T.D.Penn.	Sapotaceae	S ^a	800–1800 ¹
UM	<i>Ulmus mexicana</i> (Liebm.) Planch.	Ulmaceae	I ^b	150–2150 ¹

resource use seedling traits can be associated with higher survival (Kitajima 1994; Poorter and Bongers 2006; Wright et al. 2010; Reich 2014). It is important to highlight that this relationship was maintained despite the environmental heterogeneity along the gradient, e.g. variation in temperature, canopy cover and soil condition, as well as herbivory and pathogens, that can have significant effects on carbon economy, suggesting that the predictive value of mean functional traits analysed does not change along the elevation range studied.

Our results also show that, compared to LMA, the mean LDMC of species under the forest canopy is a weaker predictor of tree seedling survival among cloud forest tree species. LDMC is a trait associated with resistance to drought which might have a positive effect on tolerance to freezing in leaves (Medeiros and Pockman 2011); thus, increased resistance to freezing could facilitate the establishment of seedlings at higher elevations (Medeiros et al. 2012). However, we did not find support for such effect, despite recording temperatures below 0 at the highest elevations.

4.2 Effects of temperature on intraspecific variation in leaf functional traits

An increase in LMA caused by low temperatures has been reported in tropical trees (Bresson et al. 2011; Read et al. 2014). This allows the individuals to avoid or reduce leaf damage (Poorter et al. 2009; van de Weg et al. 2009). At low temperatures, greater leaf density and thickness lead to higher LMA, and higher leaf thickness can reduce the incidence and severity of freezing (Poorter et al. 2009). As expected, we found a consistent pattern in most species, with increasing LMA at lower temperatures. Our finding of such a relationship within multiple species, along with the previous reports from interspecific analysis (Wright et al. 2005; Poorter et al. 2009; Read et al. 2014), suggests that freezing protection associated with high LMA values may operate at both intra- and inter-specific levels, and that environmental filtering along elevational gradients can favour a convergence of traits, such as increased LMA (Read et al. 2014; Long et al. 2015).

Table 2 Characteristics (mean \pm 1 SE) of forest sites along an elevation gradient in Veracruz, Mexico. Mean temp. = mean temperature, Min. temp. = minimum temperature, Max. temp. = maximum temperature

Plot	Elevation (m a.s.l.)	Basal area (m ² ha ⁻¹)	Mean canopy cover (%)	Mean temp. (°C)	Min. temp. (°C)	Max. temp. (°C)	Relative humidity (%)
1	1250	17.40	94.73 \pm 0.23	17.79 \pm 0.06	7.0	33.6	87.70 \pm 0.44
2	1526	31.60	94.70 \pm 0.30	16.79 \pm 0.06	2.5	31.6	89.97 \pm 0.41
3	1573	7.70	86.72 \pm 0.45	17.24 \pm 0.05	4.0	33.0	85.02 \pm 0.53
4	1680	45.20	94.65 \pm 0.21	15.67 \pm 0.05	2.5	31.5	91.28 \pm 0.39
5	1853	14.80	95.40 \pm 0.23	15.15 \pm 0.06	5.6	27.5	88.88 \pm 0.69
6	1995	16.50	94.97 \pm 0.25	14.38 \pm 0.05	2.0	31.5	85.18 \pm 0.54
7	2290	15.20	91.50 \pm 0.73	12.86 \pm 0.05	- 1.5	28.5	86.72 \pm 0.72
8	2498	16.00	82.75 \pm 0.86	11.31 \pm 0.06	- 1.0	28.5	89.12 \pm 0.45
9	2517	43.60	91.84 \pm 0.60	10.78 \pm 0.05	- 1.0	27.5	90.31 \pm 0.43

Table 3 Parameters of the generalized linear models to evaluate the effects of the mean values of the functional traits LMA and LDMC and of their plasticity on the survival of 13 species of cloud forest tree seedlings along an elevational gradient in Veracruz, Mexico. RDPI = Relative Distance Plasticity Index, B = coefficient \pm SE, P = probability of type I error

	B	P
Mean functional traits		
Intercept	-12.081 ± 2.198	< 0.001
LMA	549.424 ± 84.980	< 0.001
Canopy cover	0.130 ± 0.023	< 0.001
Intercept	-7.758 ± 2.198	< 0.001
LDMC	6.491 ± 1.453	< 0.001
Canopy cover	0.085 ± 0.023	< 0.001
Plasticity of functional traits		
Intercept	1.814 ± 0.992	0.095
RDPI-LMA	2.040 ± 5.924	0.737
Intercept	3.035 ± 0.987	0.011
RDPI-LDMC	-8.184 ± 8.799	0.372

In response to higher canopy cover, individuals displayed decreased LMA in most of the studied species. This was a widely described pattern; under low light conditions light interception is augmented by increasing the area per unit of leaf biomass (Gratani et al. 2006; Poorter 2009). This sensitivity is interesting since canopy cover was very high in all of the sites (mean canopy cover 83–95%), but most of the species were still responsive to variation within this narrow light range. Compared to temperature, this factor explained more variation in the LMA within species (Table 10 in the Appendix).

The variation of LDMC within species presented a similar trend to LMA in response to light, but the response was weaker, with a significant reduction at higher canopy cover in seven of the 13 studied species. In laminar leaves, LDMC is related to

LMA and leaf thickness, and a decrease in leaf thickness in more shaded microsites has been described previously (Lambers et al. 2008). In our study, variation in LDMC within species was relatively low, and little of this variation could be attributed to temperature. Furthermore, we found idiosyncratic responses; *M. alba* and *U. mexicana* presented a reduction in LDMC with increasing temperature at lower elevation, while *O. mexicana* and *S. contrerasii* presented the opposite pattern. To our knowledge, there are few studies assessing the effects of elevation on LDMC and, as with our findings, they do not offer conclusive patterns (Hernández-Calderón et al. 2014; Chai et al. 2015).

As previously described, LDMC is a trait associated with resistance to drought (Kursar et al. 2009). In our study, high levels of air humidity were consistently recorded (> 80%) and these results suggest that the seedlings were unlikely to have experienced hydric stress in the understorey of the forest sites. However, given the lack of soil humidity data for the entire study period, it is not possible to conclude with certainty that this was the case. Nevertheless, the low values of estimated phenotypic plasticity for LDMC found in this study coincide with previous assessments for woody Mediterranean species (Bongers et al. 2017).

4.3 Tree seedling survival is not predicted by leaf traits plasticity

One of the most interesting results of this study is that, while mean values of LMA and LDMC increased with decreasing temperature and canopy cover, within species, the phenotypic plasticity of LMA and LDMC did not show a relationship with the probability of survival among species along the elevation gradient. Our study provides support for the hypothesis that shade tolerant species that display high tolerance to stress show low phenotypic plasticity in shaded environments (Valladares

Table 4 Parameters of the general linear models for evaluating the effects of mean temperature and canopy cover on the leaf mass area (LMA) of seedlings of 13 cloud forest tree species along an elevation gradient in Veracruz, Mexico ($N = 90$ per species). B = coefficient \pm SE; P

Species	Intercept		Temperature		Canopy cover		R^2
	B	P	B	P	B	P	
<i>Carpinus tropicalis</i>	0.623 ± 0.017	< 0.001	$-0.002 \pm 5.1e-4$	< 0.001	$-0.001 \pm 1.8e-4$	< 0.001	0.385
<i>Clethra macrophylla</i>	0.744 ± 0.026	< 0.001	$-0.003 \pm 9.5e-4$	0.002	$-0.002 \pm 2.8e-4$	< 0.001	0.439
<i>Fraxinus uhdei</i>	0.732 ± 0.022	< 0.001	$-0.003 \pm 6.4e-4$	< 0.001	$-0.002 \pm 2.4e-4$	< 0.001	0.579
<i>Juglans pyriformis</i>	0.640 ± 0.022	< 0.001			$-0.002 \pm 2.5e-4$	< 0.001	0.323
<i>Magnolia vovidesii</i>	0.645 ± 0.017	< 0.001	$-0.002 \pm 4.1e-4$	< 0.001	$-0.001 \pm 1.8e-4$	< 0.001	0.485
<i>Meliosma alba</i>	0.652 ± 0.017	< 0.001	$-0.003 \pm 5.1e-4$	< 0.001	$-0.001 \pm 1.8e-4$	< 0.001	0.579
<i>Prunus rhamnoides</i>	0.608 ± 0.033	< 0.001			$-0.001 \pm 3.5e-4$	0.013	0.079
<i>Quercus germana</i>	0.663 ± 0.023	< 0.001	$-0.002 \pm 6.9e-4$	0.021	$-0.001 \pm 2.5e-4$	< 0.001	0.245
<i>Quercus sartorii</i>	0.658 ± 0.020	< 0.001	$-0.002 \pm 7.1e-4$	0.006	$-0.001 \pm 2.2e-4$	< 0.001	0.309
<i>Sideroxylon contrerasii</i>	0.545 ± 0.024	< 0.001	$0.002 \pm 6.1e-4$	0.003	$-0.001 \pm 2.5e-4$	0.046	0.124
<i>Ulmus mexicana</i>	0.664 ± 0.040	< 0.001	$-0.003 \pm 4.4e-4$	0.021	$-0.001 \pm 4.4e-4$	0.008	0.165

= probability of type I error; R^2 adjusted for the model. In *Ocotea disjuncta* and *Oreomunnea mexicana*, no significant effects of the environmental variables were identified

Table 5 Parameters of the general linear models for evaluating the effects of mean temperature and canopy cover on the leaf dry mass content (LDMC) of seedlings of 13 cloud forest tree species along an elevational gradient in Veracruz, Mexico ($N = 90$ per species). $B =$

coefficient \pm SE; $P =$ probability of type I error; R^2 adjusted for the model ($N = 10$). In *Carpinus tropicalis*, *Ocotea disjuncta* and *Prunus rhamnoides*, no significant effects of the environmental variables were recorded.

Species	Intercept		Temperature		Canopy cover		R^2
	B	P	B	P	B	P	
<i>Clethra macrophylla</i>	0.455 \pm 0.043	< 0.001			- 0.002 \pm 4.7e-4	< 0.001	0.188
<i>Fraxinus uhdei</i>	0.518 \pm 0.066	< 0.001			- 0.003 \pm 7.1e-4	< 0.001	0.174
<i>Juglans pyriformis</i>	0.550 \pm 0.054	< 0.001			- 0.003 \pm 5.9e-4	< 0.001	0.270
<i>Magnolia vovidesii</i>	0.228 \pm 0.019	< 0.001			- 0.003 \pm 0.001	0.032	0.051
<i>Meliosma alba</i>	0.551 \pm 0.042	< 0.001	- 0.006 \pm 1.3e-4	< 0.001	- 0.003 \pm 4.6e-4	< 0.001	0.479
<i>Oreomunnea mexicana</i>	0.223 \pm 0.035	< 0.001	0.009 \pm 0.002	< 0.001			0.153
<i>Quercus germana</i>	0.633 \pm 0.078	< 0.001			- 0.002 \pm 8.4e-1	0.007	0.081
<i>Quercus sartorii</i>	0.628 \pm 0.072	< 0.001			- 0.002 \pm 7.8e-4	0.003	0.097
<i>Sideroxylon contrerasii</i>	0.080 \pm 0.020	< 0.001	0.014 \pm 0.001	< 0.001			0.558
<i>Ulmus mexicana</i>	0.435 \pm 0.054	< 0.001	- 0.008 \pm 0.004	0.044			0.046

and Niinemets 2008). In support of our findings, in a meta-analysis, Liu et al. (2016) found that greater plasticity of LMA of species in response to shading was not associated with plant performance. Phenotypic plasticity is, in principle, an important mechanism to cope with rapid climate change; however, our results suggest that it may not be the case for shade tolerant species that exhibit a conservative strategy for resource use and a low capacity for plastic response in their leaf structural traits. For this type of species, survival under temperatures outside their optimal range seems to be more related to the capacity of seedlings to tolerate, rather than to plastically adjust to, increases or decreases in temperature. However, phenotypic plasticity can vary depending on the response variable analysed, as well as the environmental variation (Valladares et al. 2002; Gratani 2014). Of particular importance is adjustment of the carbon balance in response to shade through physiological traits such as maximum photosynthetic rate, light compensation point and stomatal conductance (Valladares et al. 2016). These are traits that must be studied in order to elucidate the combined effects of elevation gradients and shade on plant performance. Another opportunity would be to analyse wider variation in the light environment in order to better represent the plastic response of species to this factor, and its influence on seedling survival, as well as to use a larger number of mother trees, which may help to obtain a better estimate of phenotypic plasticity in natural populations of cloud forest trees and analyse the responses of locally adapted ecotypes.

Changes in abiotic factors such as temperature and radiation can have differential direct and indirect effects among species, and anticipating how species and functional groups will respond to new climatic conditions is therefore of increasing interest. While tropical forest tree species are arrayed along a continuum of shade tolerance (Wright et al. 2003), shade tolerant species can

represent more than 80% of tropical tree species saplings (Brokaw 1985; Uhl et al. 1988). Despite its limitations, this study demonstrates the utility of elevational gradients as model systems to help understand the relationship between phenotypic plasticity in leaf functional traits and the ability of species to respond to variations in climate. Overall, our results provide evidence that LMA, rather than its plasticity, plays an important role in cloud forest tree seedling performance. In addition, our results show that the low phenotypic plasticity of leaf structural traits displayed by the group of shade tolerant species studied does not seem to impede the seedlings in overcoming variation in environmental conditions and thus highlights the important role that the capacity to tolerate stress could play in the face of global climate change.

Acknowledgements Instituto de Ecología A.C. provided all the facilities. We thank V. Vásquez, C. Gallardo, M. Peralta, J. Tolome, M. SanGabriel, C. Pinto and M. Bautista for their help in the field and G. Sánchez for processing hemispherical photographs. We are grateful to R. Landgrave for writing the script and performing the analysis for estimating the RDPI. K. Macmillan revised the English text. We thank the two anonymous reviewers for their very helpful criticisms.

Funding information Consejo Nacional de Ciencia y Tecnología (CONACYT CB-2014-01 238831)

Data availability The datasets generated and/or analyzed during the current study are available in the TRY Plant Trait Database (Toledo-Aceves and García-Hernández 2019) at <https://doi.org/10.17871/TRY.50>

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix

Table 6 Soil characteristics of forest plots along an elevation gradient in Veracruz, Mexico. Total soil carbon (tot-C), total soil nitrogen (tot-N), and total soil phosphorus (tot-P)

Plot	Elevation (m a.s.l.)	pH	Soil density (g cm ⁻²)	Tot-C (%)	Tot-N (%)	Tot-P (%)
1	1250	4.5	0.90	5.8	0.66	0.03
2	1520	4.7	0.82	9.81	0.95	0.05
3	1600	4.2	0.43	16.90	1.33	0.07
4	1680	5.4	0.47	13.24	1.17	0.07
5	1845	4.4	0.60	16.34	1.14	0.03
6	1984	4.2	0.32	18.63	1.10	0.02
7	2290	4.20	0.38	22.44	1.91	0.05
8	2498	3.60	0.42	27.57	2.38	0.05
9	2517	4.36	0.41	18.06	1.36	0.03

Table 7 Species ranking based on probability of survival at the sites with lowest mean temperatures (− 1.0 °C) and highest mean temperatures (17.7 °C). *N* = 30

Species	Lower temperature	Higher temperature
MA	0.867	0.862
MV	0.600	0.967
UM	0.700	0.767
PR	0.867	0.867
OD	0.900	0.967
OM	0.900	0.900
CT	0.867	0.967
SC	0.900	1.000
JP	0.933	0.600
QS	0.867	0.967
CM	0.933	1.000
FU	0.933	0.800
QG	1.000	1.000

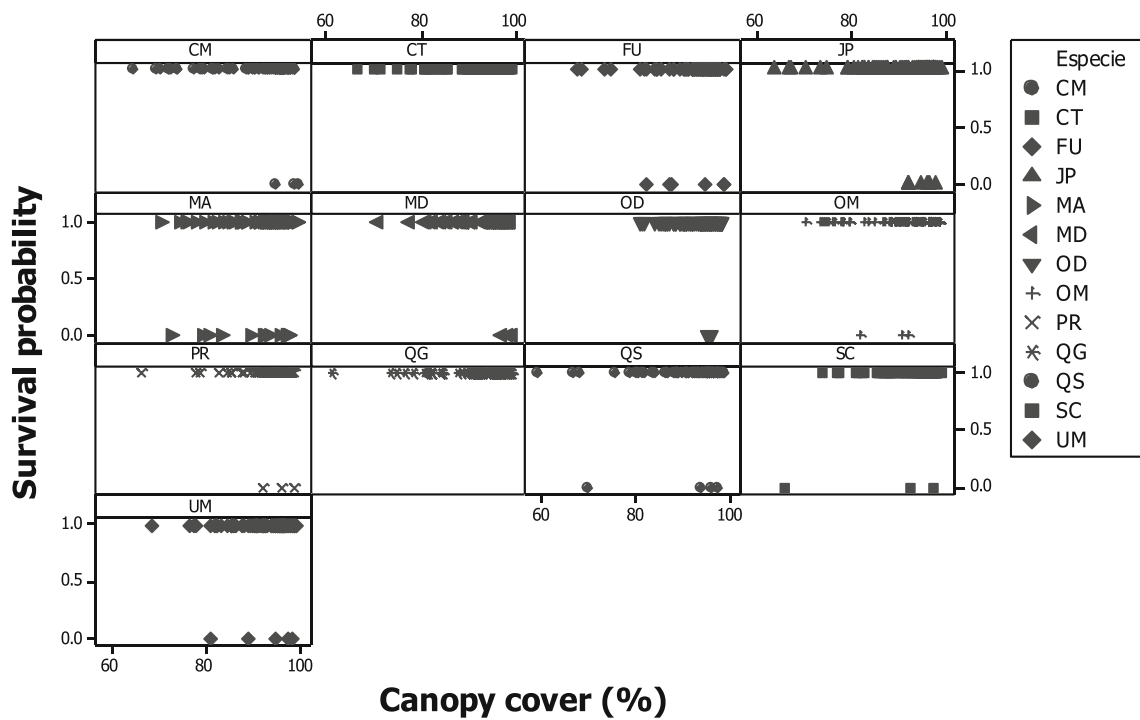


Fig. 3 Probability of seedling survival in tropical montane cloud forest tree species and canopy cover in the forest understorey along an elevation gradient. CM *Clethra macrophylla*, CT *Carpinus tropicalis*, FU *Fraxinus uhdei*, JP *Juglans pyriformis*, MA *Meliosma alba*, MV *Magnolia*

vovidesii, OD *Ocotea disjuncta*, OM *Oreomunnea mexicana*, PR *Prunus rhamnoides*, QG *Quercus germana*, QS *Quercus sartorii*, SC *Sideroxylon contrerasii*, UM *Ulmus mexicana*

Table 8 Parameters of the generalized linear models to evaluate the effects of mean values of functional traits (LMA and LDMC), temperature, canopy cover and initial seedling height, and their interactions, on seedling survival in 13 cloud forest tree species along an elevational gradient

	F	P
LMA	30.681	< 0.001
Canopy cover	30.808	< 0.001
Temperature	0.140	0.708
Initial height	1.045	0.308
LMA:canopy cover	0.121	0.727
LMA:temperature	3.242	0.074
Canopy:temperature	0.089	0.765
LMA:canopy cover:temperature	1.362	0.245
LDMC	18.922	< 0.001
Canopy cover	13.136	< 0.001
Temperature	1.603	0.208
Initial height	2.524	0.115
LDMC:canopy cover	0.674	0.413
LDMC:temperature	0.814	0.368
Canopy:temperature	0.248	0.619
LDMC:canopy cover:temperature	1.128	0.290

Table 9 Seedling leaf mass area (LMA) and leaf dry matter content (LDMC) of 13 cloud forest tree species at 2 years after transplantation in a forest understorey in Veracruz, Mexico (mean \pm SE)

Species	LMA (g cm ⁻²)	LDMC (g g ⁻¹)
<i>Carpinus tropicalis</i> Walter	0.00307 \pm 8.6e-5	0.38557 \pm 7.97e-3
<i>Clethra macrophylla</i> M. Martens & Galeotti	0.00534 \pm 2.62e-4	0.26249 \pm 4.24e-3
<i>Fraxinus uhdei</i> (Wenz.) Lingelsh.	0.00277 \pm 1.28e-4	0.23604 \pm 4.91e-3
<i>Juglans pyriformis</i> Liebm.	0.00276 \pm 9.5e-5	0.24404 \pm 5.38e-3
<i>Magnolia vovidesii</i>	0.00265 \pm 7.3e-5	0.18635 \pm 3.21e-3
<i>Meliosma alba</i> (Schltdl.) Walp.	0.002438 \pm 8.0e-5	0.20345 \pm 4.05e-3
<i>Ocotea disjuncta</i> Lorea-Hern.	0.00490 \pm 1.4e-4	0.29970 \pm 6.7e-3
<i>Oreomunnea mexicana</i> J.F. Leroy	0.00470 \pm 1.12e-4	0.35980 \pm 6.07e-3
<i>Prunus rhamnoides</i> Koehne	0.00439 \pm 1.37e-4	0.34141 \pm 7.69e-3
<i>Quercus germana</i> Schltdl. & Cham.	0.00601 \pm 1.66e-4	0.41594 \pm 5.75e-3
<i>Quercus sartorii</i> Liebm.	0.00563 \pm 1.58e-4	0.40873 \pm 6.24e-3
<i>Sideroxylon contrerasii</i> (Lundell) T.D.Penn.	0.00458 \pm 1.3e-4	0.29149 \pm 4.92e-3
<i>Ulmus mexicana</i> (Liebm.) Planch.	0.00380 \pm 1.46e-4	0.32482 \pm 8.86e-3

To determine LMA and LDMC, each leaf was placed inside a sealed plastic bag in a cooler and transported to the laboratory in the Functional Ecology Department at INECOL within 3 h of collection, where they were rehydrated by placing them in a tray with the petiole submerged in water for ~ 12 h. After this rehydration period, excess water was removed with a cloth and the remnant petiole was cut. The fresh weight was recorded, the leaf scanned with an Epson Expression 11000XL and leaf area measured with the program WinFolia version Pro (Regent Instruments Inc.). Following the scan, all leaves were dried in an oven at 80 °C for 48 h, after which the weight of each leaf was measured with an analytical balance.

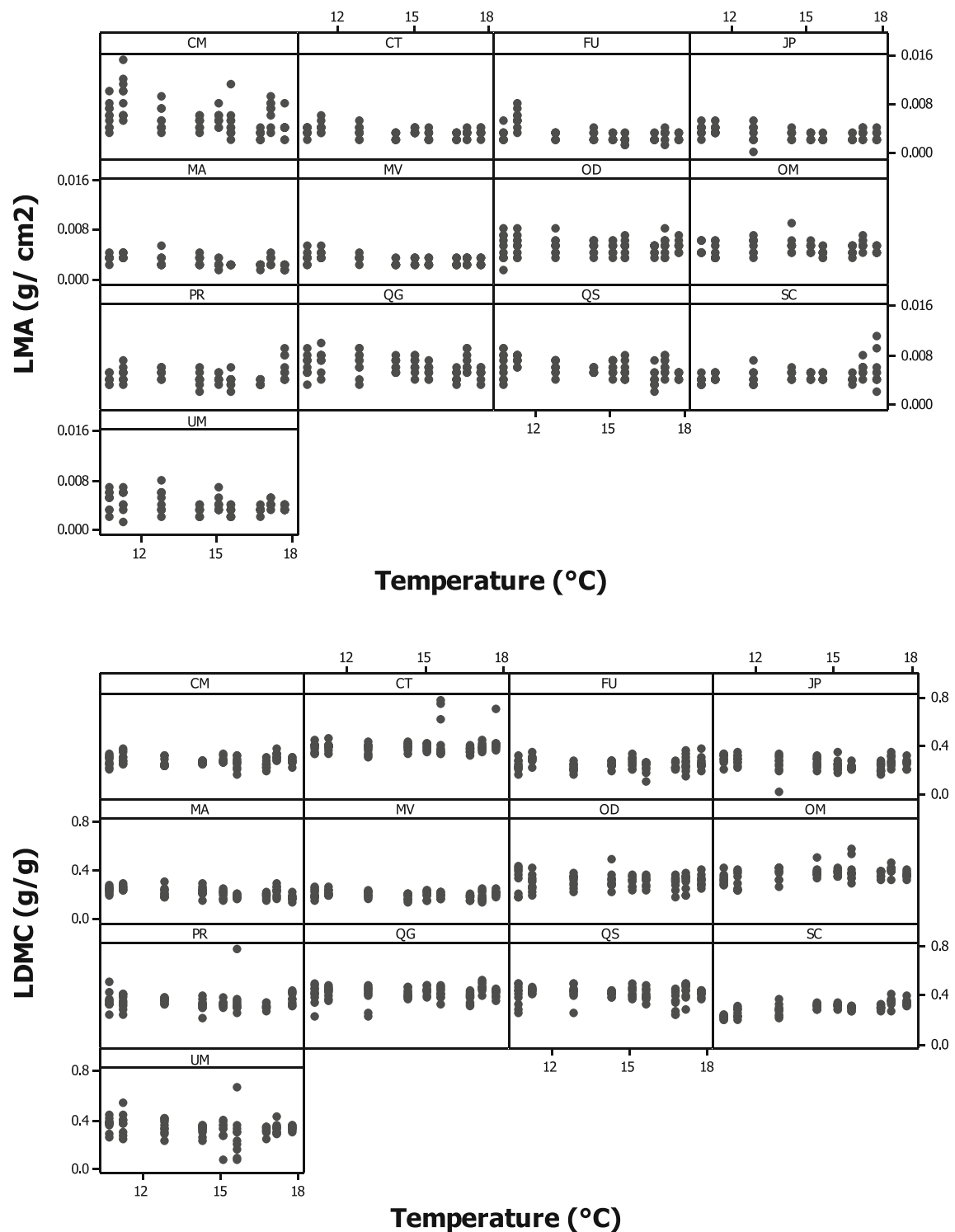


Fig. 4 Leaf mass area (LMA; top) and leaf dry mass content (LDMC; bottom) of cloud forest tree seedlings along a temperature gradient. CM *Clethra macrophylla*, CT *Carpinus tropicalis*, FU *Fraxinus uhdei*, JP *Juglans pyriformis*, MA *Meliosma alba*, MV *Magnolia vovidesii*, OD

Ocotea disjuncta, OM *Oreomunnea mexicana*, PR *Prunus rhamnoides*, QG *Quercus germana*, QS *Quercus sartorii*, SC *Sideroxylon contrerasii*, UM *Ulmus mexicana*

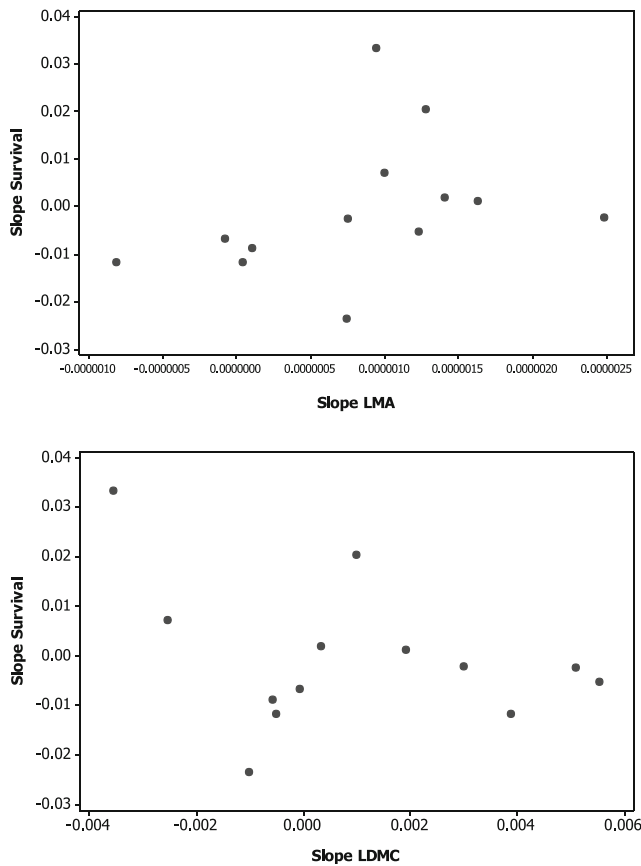


Fig. 5 Relationship between slopes of (top) leaf mass area (LMA) and (bottom) leaf dry mass content (LDMC) and slopes of seedling survival in relation to temperature, where each data point represent one species. The correlation coefficients were non-significant ($P = 0.234$ and $P = 0.267$)

Table 10 Summary of the fitted models to evaluate the effects of canopy cover and temperature on LMA. Explained variance and Akaike Information Criterion (AIC) per model and contribution of each predictive variable and corresponding AIC

Species	Explained variance per model		Explained variance by canopy cover		Explained variance by temperature	
	R^2	AIC	R^2	AIC	R^2	AIC
<i>Carpinus tropicalis</i>	0.385	- 543.91	0.298	- 534.03	0.087	- 9.88
<i>Clethra macrophylla</i>	0.439	- 435.90	0.370	- 427.47	0.0690	- 8.43
<i>Fraxinus uhdei</i>	0.579	- 505.74	0.503	- 492.94	0.076	- 12.8
<i>Juglans pyriformis</i>	0.323	- 461.23	0.323	- 461.23	0	0
<i>Magnolia vovidesii</i>	0.485	- 577.10	0.392	- 564.42	0.093	- 12.68
<i>Meliosma alba</i>	0.579	- 542.82	0.368	- 508.63	0.211	- 34.19
<i>Prunus rhamnoides</i>	0.078	- 421.69	0.078	- 421.69	0	0
<i>Quercus germana</i>	0.245	- 491.66	0.196	- 488.08	0.049	- 3.58
<i>Quercus sartorii</i>	0.309	- 492.41	0.246	- 486.46	0.063	- 5.95
<i>Sideroxylon contrerasii</i>	0.124	- 509.19	0.030	- 501.98	0.083	- 7.21
<i>Ulmus mexicana</i>	0.165	- 407.47	0.112	- 403.89	0.053	- 3.58

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