

FROM SEEDLING TO SAPLING: TREE SPECIES RESPONSES TO SPATIAL AND TEMPORAL UNDERSTORY LIGHT HETEROGENEITY IN DISTURBED TROPICAL MONTANE FORESTS

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Abstract: Difficulties in measuring small-scale light heterogeneity in forest understories is reflected in the classification of species, conventionally based on their responses to gaps or shade, rarely present in uniform conditions in space and time. Spatial and temporal heterogeneity expressed as a contrast between direct vertical light and light coming from the surroundings allows for a better assessment of the understory light environment and thus of the effect of its variation on species performance. Using repeated measures, we evaluated the effect of vertical light, contrast, and distance to the gap center on the performance of transplanted seedlings of *Alnus acuminata*, *Cornus excelsa*, *Liquidambar styraciflua*, *Quercus laurina* and *Persea americana*. Highlands of Chiapas between 1999 and 2005 in eight plots of pine-oak forest, each one with a small gap in the middle. Illumination was evaluated with hemispherical photographs at the beginning and the end of the study. We measured stem slenderness and survival after one, two, four, and six years following transplantation. Distance had an effect on survival of *Alnus* and *Liquidambar*. Vertical light only had an effect on *Liquidambar* slenderness. Contrast explained slenderness of *Liquidambar*, *Cornus* and *Quercus*, and survival of *Liquidambar*, *Quercus* and *Persea* conditional on plant age. Initial light contrast predicted the final condition well, which vertical light did not. Contrast between two gradients of the same resource produced a remarkable improvement in the predictive power of light over the performance of the studied species describing the small variations of light in forest understory.

Key words: disturbance, light contrast, shade tolerance, sunflecks, temporal elasticity.

Resumen: Las dificultades para medir a pequeña escala la heterogeneidad de luz en el sotobosque se refleja en la clasificación de especies, convencionalmente basada en su respuesta al claro o a la sombra, condiciones rara vez uniformes en el espacio y el tiempo. La heterogeneidad espacial y temporal expresada por el contraste entre la luz directa sobre un área (luz vertical) y la luz sobre sus alrededores, permitirá mejorar la estimación del ambiente de luz del sotobosque y de la respuesta de las especies a sus variaciones. Analizamos con medidas repetidas el efecto de luz vertical, contraste y distancia al claro sobre el desempeño de plántulas trasplantadas de *Alnus acuminata*, *Cornus excelsa*, *Liquidambar styraciflua*, *Quercus laurina* y *Persea americana*. Los Altos de Chiapas entre 1999 y 2005, en ocho parcelas de bosque de pino-encino, cada una con un claro central pequeño. Evaluamos la iluminación mediante fotografías hemisféricas al principio y al final del estudio. Se midió esbeltez y supervivencia a uno, dos, cuatro y seis años del trasplante. Distancia afectó la supervivencia de *Alnus* y *Liquidambar*. Luz vertical explicó esbeltez de *Liquidambar*. Contraste explicó esbeltez de *Liquidambar*, *Cornus* y *Quercus* y supervivencia de *Liquidambar*, *Quercus* y *Persea*, condicionada a la edad de la planta. La condición inicial de contraste inicial predijo la final, no así la luz vertical. El contraste entre dos gradientes del mismo recurso aumentó notablemente su poder predictivo sobre el desempeño de las especies al describir las pequeñas variaciones de luz en el sotobosque.

Palabras clave: contraste de luz, disturbio, sunflecks, elasticidad temporal, tolerancia a la sombra.

Spatial heterogeneity is an ever-present characteristic of ecosystems. In the forest understory light intensity and direction varies constantly depending on openings in the canopy and on the angle of incidence at different time, season, latitude, and slope aspect (Hutchison and Matt, 1977).

Gap formation is a major source of local heterogeneity in forests involving, among other things, light, creating contrasting conditions within and around the gap where the forest physical structure acts as a light filter. The resulting sunflecks as well as their complementary shadeflecks vary

in size, duration and intensity according to different temporal and spatial scales, and represent local light variation that may influence the growth of the herbaceous layer, young trees, and seedling abundance (Denslow, 1987; Chazdon, 1988; Smith *et al.*, 1989; Canham, 1989; Way and Percy, 2012; Smith and Berry, 2013).

Measuring heterogeneity of light availability in forest understory remains as a challenging task. Although there is extensive literature on gap dynamics and sunflecks it is often hard for managers to interpret results due to inconsistent variability in methods which still are to a large extent arbitrary (Schliemann and Bockheim, 2011; Way and Percy, 2012). These difficulties are implicit in forest dynamic models that do not take small-scale variations into account (Deutschman *et al.*, 1999; Baraloto and Couteron, 2010) inducing a kind of Simpson's paradox leading to a potentially important misleading interpretations of plant-environment interactions under dynamic irradiance regimes (Leakey *et al.*, 2005) and hindering the understanding of the effects of heterogeneous light availability on plant performance. Plant individuals should exhibit phenotypic plasticity that allows them to cope with environmental heterogeneity which may directly affect the persistence of their populations facing long term changes (Gianoli, 2004; Nicotra, *et al.*, 2010). Depending on how much of a specialist or a generalist the organism may be (Kolasa and Rollo, 1991) this responsiveness to changes in light intensity could be driven by relative trade-offs between water loss and carbon absorption (Knapp and Smith, 1990; Naumburg and Ellsworth, 2000). These trade-offs that might affect different performance parameters (*e.g.* growth pattern and eventually survival). For intolerant species survival the escape strategies include the production of tall and slender stems, with a minimum investment in diameter growth and leaves (Kohyama and Hotta, 1990; Gilbert *et al.*, 2001; Coutand *et al.*, 2010). Plant ability to tolerate shade in the forest understory depends on its efficient use of limiting resources as light, soil nutrients and water (Coomes and Grubb, 2000; Nilsen *et al.*, 2009). This partitioning of resources for plants might vary not only along microhabitat gradients (Tilman, 1990; Suding and Goldberg, 2001) but also through their ontogeny (Coleman *et al.*, 1994; Parrish and Bazzaz, 1985; Coomes and Grubb, 2000; Sultan, 2000; Wright and McCaughey, 2002; Lusk, 2004). However it remains unclear to what extent the transient nature of sunflecks and shade-flecks in the understory may affect plant survival and growth (Naumburg and Ellsworth, 2000; Leakey *et al.*, 2005). In addition, the time lags between changes in the light environment and plant responses further thwarts attempts to understand the effect of light on plant responses (Smith *et al.*, 1992). The underlying mechanisms supporting functional classifications of plant response to light remain both scarce and controversial (Poorter and Garnier, 2007). This is partly because plant responses to light has been mainly studied only for short periods at early stages of

plant development in the field (Ishida and Peters, 1999), and partly because plant responses to light variation has been mostly studied under controlled conditions in the laboratory (*e.g.* Sims and Pearcy, 1993; Watling *et al.*, 1997; Huante *et al.*, 1998; Stevens and Carson, 2002; Bloor and Grubb, 2004) with coarse grain excluding settings (light *vs.* shade) or in field gap *vs.* understory conditions, as if they were the more common conditions spatially and temporally speaking. Successional and seasonal variation, plus the complex effects of tree falls on the light environment show that a dichotomy between gap and understory or likewise between sun and shade, may be too simplistic for many purposes (Smith *et al.*, 1992). Recent studies have demonstrated that the homogeneity in both gaps and understory conditions is the less frequent condition (Méndez-Dewar *et al.*, 2014).

In this paper, we evaluate six years of plant response to the light heterogeneity under field conditions. We followed the framework proposed in Méndez-Dewar *et al.* (2014) which is a bidimensional scheme developed to describe plot heterogeneity to a fine scale by placing vertical light on growth area (*Vertical light*) as the y-axis, and the background light (*Sidelight*) in the horizontal axes. In such light map many understory conditions may be pinpointed with far more precision than the one-dimensional approaches may so far. Those authors have shown that this representation, estimated with measurements made at one point in time, allowed to accurately describe relationships between light spatial heterogeneity and seedling performance. In this contribution we test the time frame elasticity of such contrasts. We hypothesize that besides of the balancing effects of contrasting patches which may increase the performance of seedlings under homogeneously high or low light conditions, the span of such effects will be longer than the effects between *Vertical light* conditions and plant performance. We take that spatial and temporal variation of light may influence differentially plant performance depending on the initial light heterogeneity and on the shade-tolerance of each species. To this aim we studied the spatial and temporal light patch structure as a factor influencing interspecific differences in plant performance (stem slenderness and survival) in a number of field plots where gaps had been recently created and later regenerated naturally during six years of forest succession. For this study we evaluated transplanted seedlings growth of five native tree species (*Alnus acuminata*, *Cornus excelsa*, *Liquidambar styraciflua*, *Persea americana*, and *Quercus laurina*) over a period of six years in the field as a function of three gradients: distance to the center of the gap, direct light at growth area, and contrast between light at growth area with its neighboring area along the first six years of secondary succession following small gap phase regeneration in montane cloud forests of Chiapas, Mexico. These species differ in their shade-tolerance as judge by expert opinions. Hence, they offer a range of plant responses to

explore a number of light heterogeneity metrics (Ramírez-Marcial *et al.*, 2008).

Materials and methods

The study area, species, experimental designs, light measurements, light environment heterogeneity as well as the measurements on seedling performance are described briefly below, but a more detailed description can be found in Méndez-Dewar *et al.* (2014).

Study site. We conducted the study at Rancho Merced-Bazom, in the central highlands of Chiapas, Mexico (2,300–2,450 m, 16° 44' N, 92° 29' W). We collected field data in eight pine-oak forest plots each corresponding to a small, recent, naturally created gap (< 2 years old; E-W diameter, $d = 7.5\text{--}15.0$ m, Table 1). Plots were protected against grazing and trampling. In each plot, we established N-S transects 3 m apart and points every 2.5 m along each transect (E-W).

Transplanted species and plant performance measurements. In March 1999, we transplanted one-year old seedlings produced in a nursery of *Alnus acuminata* Kunth (N = 92), *Liquidambar styraciflua* L. (N = 124), *Cornus excelsa* Kunth (N = 124), *Quercus laurina* Bonpl. (N = 131), and *Persea americana* Mill. (N = 125) (from now onwards *Alnus*, *Liquidambar*, *Cornus*, *Quercus*, or *Persea*). We defined the spot or microsite where each transplanted seedling grows as the “growth area” (GA) obtaining a total of 596 growth areas. We evaluated stem height (SH, cm) and basal stem diameter (BSD, mm \times 10) within two, four and six years after transplantation. They were combined in an allometric shape ratio aimed to describe stem slenderness (*Slenderness*): This variable is unitless (cm/cm) and were used to assess plant performance.

$$\text{Slenderness} = SH \times BSD^{-1} \quad (\text{eq. 1})$$

Light environment. In year 2005 we shot a series of 982 hemispheric photographs that followed the design of a similar sampling made in 1999 when the plots were initially established and the seedlings planted in the understory (Méndez-Dewar *et al.*, 2014). Both samples were taken between 0700 and 1100 hours, under cloud overcast sunshine light along five consecutive days. Pictures were taken at 1.2 m, above ground and analysed with Hemiphot (version 5, ter Steege, 1994). For the second series we used a digital camera Nikon Coolpix 995 equipped with a fish-eye lens Nikon (Fc-E8). We estimated the Direct Site Factor (DSF) from each photograph. This DSF corresponds to the *Vertical light* source for the growth area where each seedling was planted for the experiment.

Spatial light heterogeneity. The spatial distribution of DSF was described with three heterogeneity components (Méndez-Dewar *et al.*, 2014): (1) *Vertical light*, which represents

the highest spatial resolution in this study (7.5 m^2) and by definition is internally homogeneous; (2) *sidelight*, obtained by clustering and averaging eight immediately adjacent neighboring patches (total of 60 m^2), and (3) Spatial light *Contrast* for each of the 596 growth areas or microsites with the following equation:

$$\text{Contrast} = (\text{Vertical light} - \text{Sidelight}) \times (\text{Vertical light} + \text{Sidelight})^{-1} \quad (\text{eq.2}).$$

Background light levels for each growth area were defined by three factors: (1) distance from a given GA to the center of the gap. Three distance (D) classes were defined: (i) if $D \leq \text{radius } (r)$ of the gap, then the growth area was considered to be within the gap; (ii) if $r < D \leq 2r$ then the GA was taken as at the “edge” of the gap; finally, (iii) if $D > 3r$ then the GA was recorded as located inside the forest understory. (2) *Vertical light* classified in three levels: low (*Vertical light* < 15%), medium (*Vertical light* < 25 %), and high (*Vertical light* > 25 %). (3) *Contrast*: negative (C^- has values between -1 and -0.05), null (C^0 between -0.049 a 0.049) and positive (C^+ between 0.05 and 1).

Analysis. Seedling height and diameter were measured at the time of transplant (1999), and one, two, four, and six years later. Stem slenderness ratio of each species (SS) was analyzed for all plants alive six years after transplantation, to determine the long-term effects (regarded as fixed effects) of the three distance to the center of the gap (D) classes (Gap, Edge and Understory), of three *Vertical light* levels (low, medium and high), and of the three types of light *Contrast* (C^- , C^0 , C^+). Predictive power of initial DSF over what was measured six years later was compared with what happened with the light contrast using a linear regression. Stem slenderness was analyzed using a repeated measures two-way ANOVA along years (Y) and final DSF (2005) as random effects, allowing for the particular successional development effects at each growth area. The significance of differences in stem allometry was assessed with Tukey's posterior test. We contrasted two ANOVA models, with the initial heterogeneity components *Vertical light* and *Contrast* as factors not in the same model as they represent two light heterogeneity gradients (one-dimensional and bi-dimensional, respectively) whose temporal elasticity we intend to analyze separately. Plant survival was analyzed for each species with binary logistic regression (backwards procedure) as a function of D , SS_{t-1} , VL , and C . The SS ratio entered was that of the previous time to the one at which death was recorded. All statistical analyses were performed using IBM-SPSS version 19 (2010).

Results

Spatial and temporal light variation. The equality of *Vertical light* and *Sidelight* corresponds to a “null contrast” or

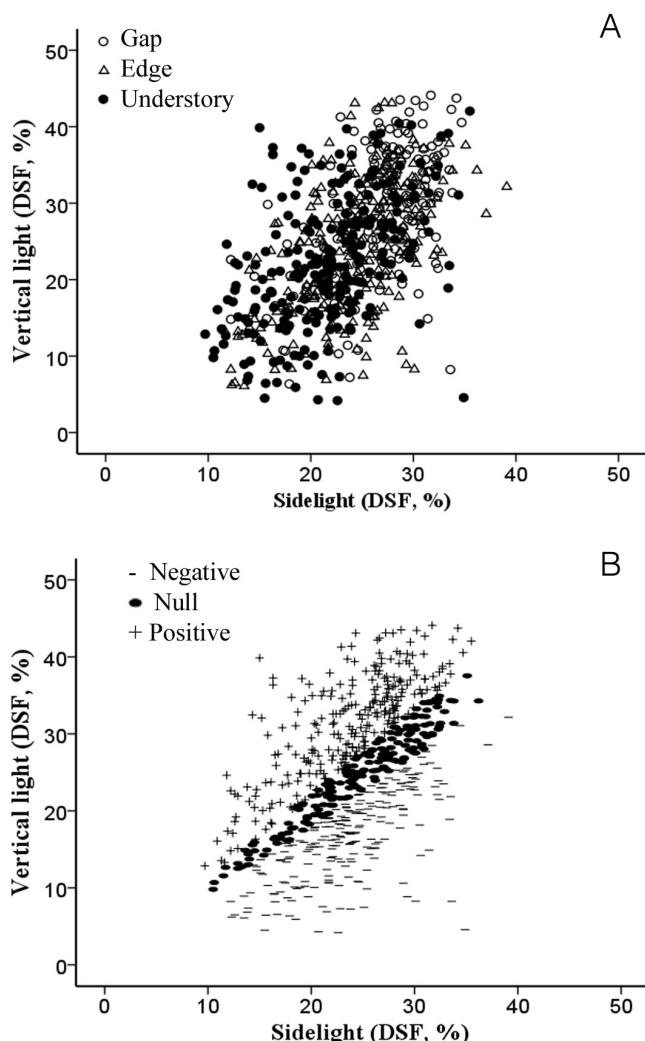


Figure 1. A) Fine grained heterogeneity observed in gaps (open circles), edge (triangles) and understory (solid circles) ($N = 680$). B) Intersection of Vertical light and Sidelight values recorded in the forest understory and spatial light contrast of 680 points within eight plots with a small central gap. Positive contrasts (C^+): VL > SL; negative contrasts (C^-): VL < SL; null contrasts (C^0).

homogeneity and is represented in figure 1A by the identity line of these variables. At the spatial scale of this study, none of the three habitat types (Gap, Edge, or Understory) could

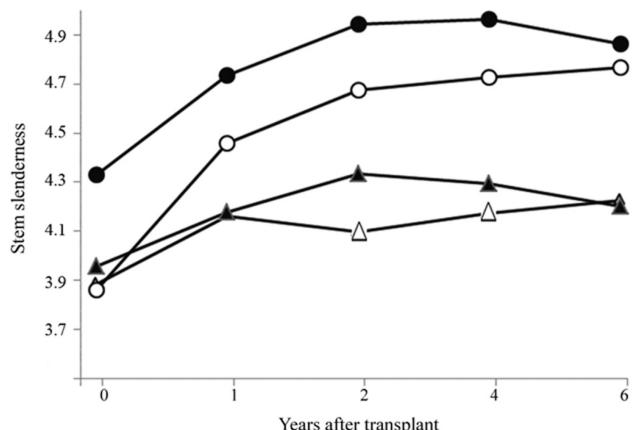


Figure 2. Change in stem slenderness ratio (cm/cm) of seedlings of four native tree species observed at different times along a six-year period after transplant into the understory of cloud forests in Chiapas, Mexico. *Liquidambar* (open circles), *Cornus* (solid circles), *Quercus* (solid triangles) and *Persea* (open triangles).

be described either by *Vertical light*, *Sidelight*, or *Contrast* alone (Figure 1B). The level of light reaching the understory as expected was much reduced after six years of forest succession (Table 1). *Vertical light* did not predict the final amount of light in the same point ($F_{1,653} = 0.845, P = 0.358$), but the relationship between light contrast was much stronger ($F_{1,653} = 514.826, P < 0.001, r^2 = 0.43$).

Seedling performance along six years in forest understory. Stem slenderness (SS) was different among species since the beginning of the study ($F_{3,261} = 93.81; P < 0.0001$; Figure 2). The maximum observed value of SS ratio was attained at different times. The most shade-intolerant species (*Liquidambar*) and *Quercus* attained relatively taller stems before *Cornus* or *Quercus*. Only *Cornus* shifted from low to high SS ratio from one year after transplantation onwards, and *Persea* showed a relatively consistent height/diameter ratios through time (Figure 2). Data on *Alnus* were not included in this analysis because of the small number of plants surviving until the end of the study.

Vertical light values in growth area did not explain stem slenderness ratio changes along time for any species but

Table 1. Size of forest gaps (m^2), total plot size (m^2), initial (1999) and final (2005) mean direct site factor (DSF \pm SE) in each plot. DSF values with the same letter are not different with $P < 0.05$. Frequency of negative, null and positive contrasts by plot (C^- , C^0 y C^+ respectively).

Plot	1	2	3	4	5	6	7	8
Gap area (m^2)	89.5	63.8	174	78.3	168	67.5	63	72
Plot area (m^2)	682.5	450	945	577	892.5	472.5	577.5	375
$DSF_{initial}$ (%)	20.9(0.67 ^b)	17.7(0.86 ^a)	21.7(0.81 ^b)	23.7(1.05 ^b)	25.8(0.63 ^c)	22.7(0.62 ^b)	27.1(0.59 ^c)	26.0(0.89 ^c)
DSF_{final} (%)	18.02(0.21 ^{b,c})	17.02(0.28 ^{a,b})	18.64(0.18 ^c)	17.01(0.20 ^{a,b})	16.61(0.30 ^{b,c})	15.49(0.21 ^a)	15.49(0.21 ^a)	16.22(0.29 ^a)
Contrast								
(C; C ⁰ ; C ⁺)	34,33,37	22,13,35	49,25,52	24,14,39	47,40,32	26,21,16	17,28,30	12,12,26

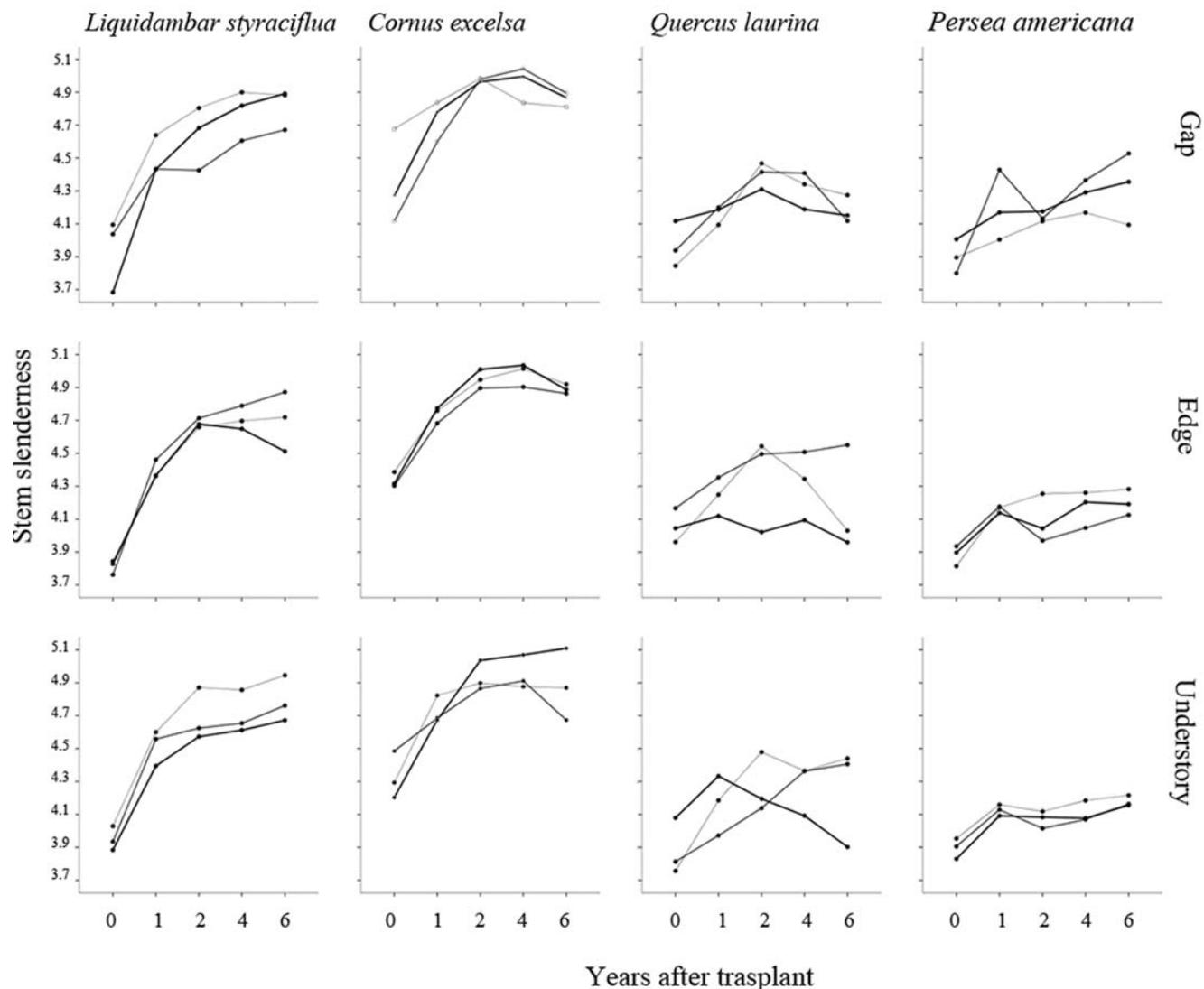


Figure 3. Changes in stem slenderness (height/basal diameter) of four native tree species arranged from left to right according to their increased shade tolerance, along a six-year period after their transplant into three habitat conditions (Gap, Edge, and Understory) in cloud forests in Chiapas, Mexico. Spatial light contrast is indicated by the thickness of the line: negative (thin), null (medium), and positive (thick).

Liquidambar, whose stem allometry was related to *Vertical light* (between subjects $F_{2,77} = 4.495$; $P = 0.014$). On the other hand, *Contrast* as a within subject effect, was found to be significant in all species in this study. *Contrast* was also the only factor with significant effects in interaction with *Year (Y)* for *Cornus* and *Quercus* ($F_{2,94} = 3.91$; $P = 0.024$ and $F_{2,94} = 3.48$; $P = 0.040$), and with both *Y* and *Distance* in the shade-intolerant species (*Cornus*: $F_{4,94} = 4.09$; $P = 0.004$; *Liquidambar*: $F_{4,77} = 2.67$; $P = 0.038$) (Figure 3). Changes in *SS* ratio of shade-intolerant species in the Gap and Edge habitat types were relatively similar (Figure 3), and it was in the understory habitat type where the response to either positive or negative contrasts became more evident. The effect of heterogeneity on *Liquidambar*, expressed as spatial light contrasts, was invariant through time. This could be

explained by the between subjects effect of *Contrast*, independently of development stage ($F_{1,77} = 5.47$; $P = 0.006$). *Liquidambar* developed more slender stems in Understory habitat with *C*. Growth curves of *Quercus* (a shade-tolerant species) show an antagonistic effect between *C*⁺ and *C*⁻ on *SS* ratio both in the Edge and Understory habitat types.

Seedling mortality in heterogeneous understory. A total of 280 individuals died six years after transplantation (44%). Survival was highest for *Cornus* (80%), *Persea* (70%) and *Liquidambar* (68%), and lowest for *Quercus* (38%) and *Alnus* (12%, Figure 4). Survival differences between species was significant since the first evaluation, and kept increasing afterwards (Wilcoxon statistic > 12.79 ; $df = 4$; $P \leq 0.012$). The effect of previous *SS* ratio on plant survival was

Table 2. Backward logistic regression of seedling survival at two, four and six years after transplant in forest understory as a function of *Distance* (D) to the center of the gap (m), stem slenderness ratio at previous evaluation (SS_{t-1}), *Vertical light* (VL), and spatial light *Contrast* at growth area (C). The table shows the estimated model parameter (B), its standard error (SE) and the significance (P) of Wald's test. The estimate of the model fit is based on Nagelkerke's R^2 (Norusis, 1997).

Species	Years	Independent	B	SE	Wald	df	P	Exp(B)	R^2
<i>Alnus</i>	2	D	-0.12	0.06	3.70	1	0.054	0.89	0.07
	4	D \times VL	-0.01	0.00	6.98	1	0.008	0.99	0.20
<i>Liquidambar</i>	1	C	4.00	1.75	5.22	1	0.022	54.61	0.11
	2	SS_{t-1}	2.04	0.76	7.17	1	0.007	7.66	0.10
	4	D \times C	0.33	0.14	5.29	1	0.021	1.40	0.16
		SS_{t-1}	1.69	0.83	4.20	1	0.040	5.43	
	6	D	-0.12	0.06	3.98	1	0.046	0.89	0.13
		D \times C	0.27	0.13	3.93	1	0.047	1.31	
<i>Cornus</i>	2	SS_{t-1}	2.99	1.15	6.80	1	0.009	19.89	0.19
	4	D	-0.18	0.08	5.82	1	0.016	0.83	0.11
<i>Quercus</i>	1	D \times VL	-0.01	0.00	4.56	1	0.033	0.99	0.11
	2	D \times C	0.40	0.17	5.75	1	0.017	1.49	0.08
	4	SS_{t-1}	1.12	0.56	3.98	1	0.046	3.06	0.05
	6	D \times VL	-0.04	0.02	8.27	1	0.004	0.96	0.64
		C	-50.78	19.71	6.64	1	0.010	0.00	
		VL	0.28	0.11	6.11	1	0.013	1.32	
		D \times C	7.91	3.03	6.81	1	0.009	2,717.43	
	4	SS_{t-1}	3.45	1.07	10.40	1	0.001	31.59	0.18
<i>Persea</i>		C	2.82	1.44	3.84	1	0.05	16.77	

positive and significant for all species (but *Alnus*) with different times along their ontogeny: earlier for *Liquidambar* and *Cornus* ($P = 0.007$ and $P = 0.009$, respectively), than for *Quercus* and *Persea* ($P = 0.046$ and $P = 0.001$, respectively; Table 2). Distance to the center of the gap enhanced the probability of death of all species (but *Persea*): *Quercus* responded to *Distance* in every survival evaluation, *Alnus* responded to *Distance* two and four years after transplant ($P = 0.054$), and *Cornus* only four years after transplant (P

$= 0.016$) and *Liquidambar* only after six years ($P = 0.046$). Light contrast enhanced the probability of survival of *Liquidambar* one year after transplant ($P = 0.022$), as it did for *Persea* and *Quercus* four and six years after transplant, respectively ($P = 0.050$ and $P = 0.010$, respectively). A significant effect of *Vertical light* on survival of *Quercus* was also detected when the whole observation time was considered ($P = 0.013$).

The interaction between *Distance* and *Contrast* had a significant effect on survival of *Liquidambar* at four and six years after the transplant into the forest ($P = 0.021$ and $P = 0.047$, respectively). This interaction was also significant to explain the survival of *Quercus* at two and six years after the transplant ($P = 0.017$ and $P = 0.009$, respectively). The interaction between *Distance* and *Vertical light* was significant in *Alnus* four years after transplant (Wald statistic = 6.98; $P = 0.008$) and one and six years after *Quercus* ($P = 0.033$ and $P = 0.004$, respectively; Table 2). A higher mortality of *Liquidambar* and *Quercus* was observed with the intensifying effect of *C* and the Understory habitat type (Figure 5).

Discussion

In order to improve current understanding of plant-environment interactions under dynamic irradiance regimes typically found in field conditions, sunfleck assessment should recognize the importance of then levels context light (Liefers *et al.*, 1999; Leakey *et al.*, 2005). Our results, obtained

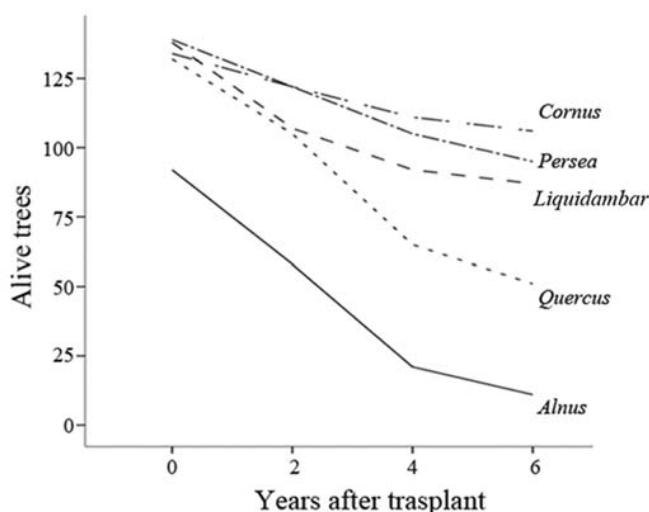


Figure 4. Mortality of one-year seedlings of five native tree species along a period of six years after being transplanted into cloud forests in Chiapas, México.

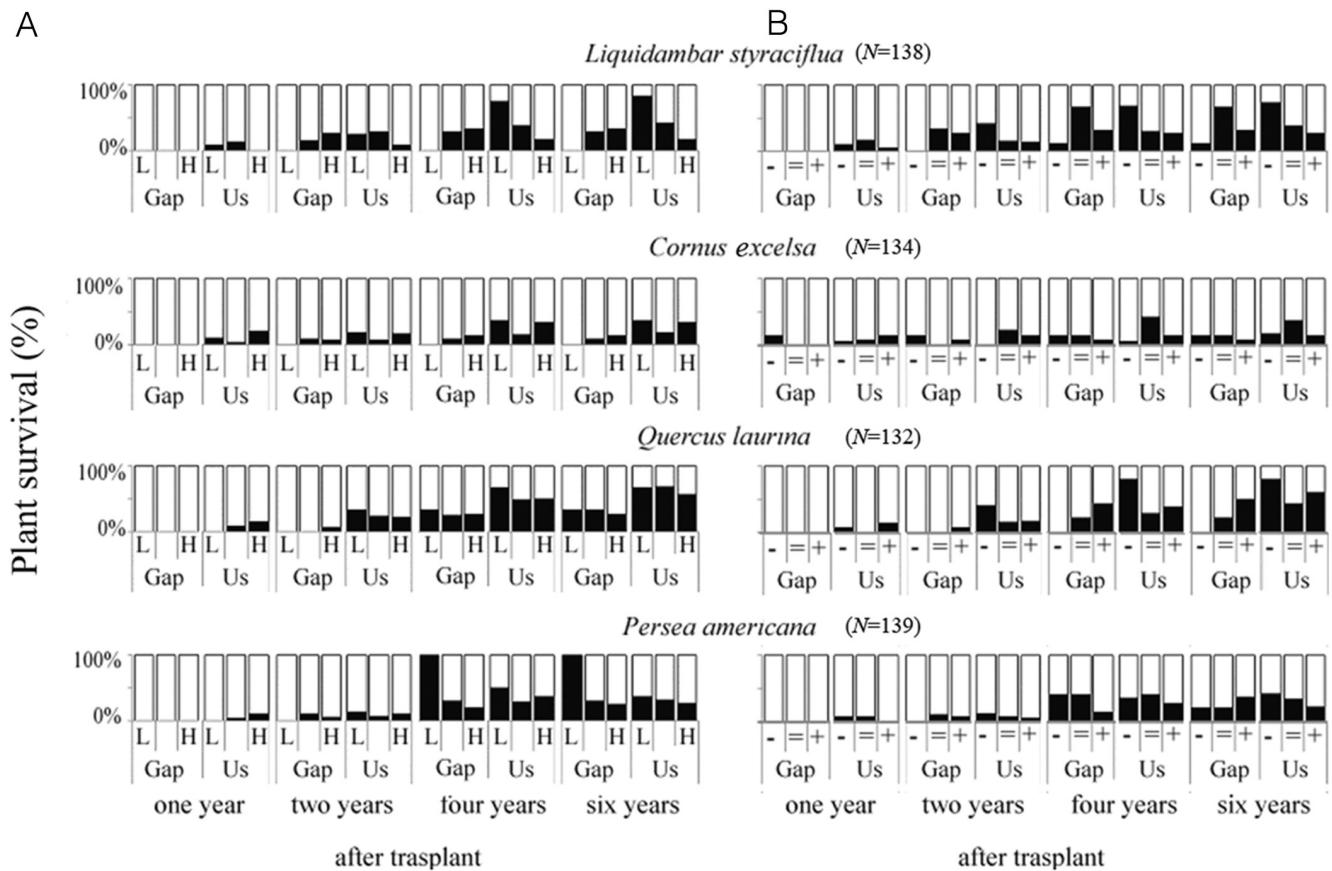


Figure 5. Relative survival of four native tree species along a period of six years in two contrasting habitat conditions, Gap and Understory (Us), in cloud forests in Chiapas, Mexico. Proportion of dead individuals is shown in black. A) Response to three light levels: Low (L), Medium (M), and High (H). The letter M is not shown between L and H because of space restrictions. B) Response to three different types of spatial light contrast: negative (-), null (=) and positive (+).

under field conditions, provide evidence that thresholds for sunflecks should be related to the light demands of the understory species either within a habitat mosaic or along a successional path.

Light heterogeneity and successional changes in montane forests. At the spatial scale of this study none of the three habitat types (Gap, Edge, or Understory) could be explained by *Vertical light*, *Sidelight*, or *Contrast* alone, suggesting the existence of a potential large number of fine-scale microhabitats variables in moderately disturbed forests. During secondary succession, as a stand undergoes crown closure, light transmission to the understory may decline sharply (Horn, 1971; Kane *et al.*, 2011). Light intensity, as experienced by the plants at the beginning of the study, were not correlated with that prevailing after six years. The information used to determine the light contrast allows for a reconstruction of the microenvironment along a hypothetical successional routes, with more predictive power. The light contrasts consider a number of structural attributes at the canopy and understory levels (*e.g.* stem density, basal area) that collectively determine the forest light filter (Méndez-

Dewar *et al.*, 2014). In this regard, we consider that after six years microsites initially classified as C^+ , for example, will share more coincidences among themselves. In them it was more likely that the cover of plants located in neighboring shaded points would continue over the illuminated area. A less likely process is one where the vegetation of the neighboring area could lose cover.

Seedling responses to light heterogeneity in montane forests. In our six year study we found evidence supporting the idea that microenvironmental heterogeneity, evaluated with light contrasts, influenced SS seedling survival. In consistency with findings on resource allocation (Canham, 1989; Bloor and Grubb, 2004; Coutand *et al.*, 2010), shade-intolerant species developed longer and slender stems than the shade-tolerant ones. The curves of SS ratio changes of shade-intolerant species through time are parallel in the Gap and Edge habitat types, but not in the Understory habitat, as shade-intolerant traits show the most plastic responses to an increase in light at the lower end of the gradient (*e.g.* Veenendaal *et al.*, 1996; Poorter, 1998). However, the shade-tolerant *Persea* showed more similar responses in the Understory than in

the Gap or Edge habitat types. It has been suggested that the phenotypic plasticity could induce greater competitive capacity under irregularly changing environments (Givnish, 2002). There is mounting evidence suggesting that plants have epigenetic mechanisms in their cells that provide them with the capacity to memorize a history of exposition to stressors and specifically to “sun footprints” in terms of UV and light stress (Müller-Xing *et al.*, 2014). Notwithstanding that we did not find a significant effect of *Vertical light* on the performance of all species we studied (but *Liquidambar*), its effect is clearly implicit and better described in our light contrasts, as we observed intraspecific differences in the norm of reaction under different types of contrast. Survival was affected by distance to the center of the gap and was higher in the Gap than in the Understory habitat type (with the exception of the shade-tolerant *Persea*).

Light heterogeneity: intensifying vs. balancing effects. The ecological interpretation of the light contrasts is focused on the supplement effects (Parish and Bazzaz, 1985; Stuefer *et al.*, 1994; Stuefer, 1996; Hutchings and Wijesinghe, 1997) suggesting that increase survival depends on the habitat context: a C^- may have a soothing effect in gaps and hardens conditions within a shade continuum in the understory. On the contrary, a C^+ may have an intensifying effect in the gap and a balancing one in the understory (Méndez-Dewar *et al.*, 2014). In a Gap open habitat C^- may have complementary effects on *Liquidambar* and *Quercus* as they had lower mortality under those conditions and responded to surrounding shade with longer and slender stems, which may help to avoid or at least reduce competitive suppression (Smith, 1982; Holbrook and Putz, 1989; Schwinnig and Weiner, 1998). On the other hand, in Gap habitat the light intensifying effects (C^+ , $C^=$), reduced *Liquidambar* survival. This results striking cause *Liquidambar* is regarded as a typical heliophile shade-intolerant species (Herrick and Thomas, 1999). Some species cannot fully use periods of extremely bright light (Sims and Pearcy, 1993), because of low relative humidity, and (or) high leaf temperature load or UV damaging exposition as likely mechanisms underlying this reaction (Weis and Berry, 1988; Niinemets, 1998; McDonald and Urban, 2004; Brenes-Arguedas *et al.*, 2011), or photoinhibition (Powles, 1984; Kitao *et al.*, 2006). This suggest that analysis of its performance in Gap habitat as a function of some of the proposed light heterogeneity metrics allows us to gain insight into its more complex responses to spatially and temporally varying environments. In Understory habitat, increasing *DSF* values in C^+ produced stem elongation of *Cornus*. Under these relatively shaded conditions, high light availability is relatively small (only when the sun is close to the zenith) and possibly limiting. Therefore, only species with a highly responsive photosynthetic machinery would benefit from the balancing effects of a C^+ as intermittent intense light flashes the spot (Pearcy *et al.*, 1994).

On the other hand, the effect of shade intensification in the Understory habitat type may reduce net carbon gain and plant growth (Katahata *et al.*, 2005). The results showed a negative effect of C^- where stem height of *Liquidambar* was lowest (even with high *SS* ratio), and the largest number of dead plants of this species was recorded. Although a higher survival was expected in shade-tolerant species in the Understory habitat type, the survival of *Liquidambar* and *Cornus* was higher than it was in the shade-tolerant *Quercus*.

Ontogeny in heterogeneous understory. This study presents an approach to quantify, at the stand level, the idea of balancing patches that represent likely temporal and spatial shifts in the complementarity of positive and negative effects of microsites. Spatial heterogeneity may affect performance at any age of the plant, but as we observed in *Liquidambar* and *Cornus*, its consequences may be more severe in early stages of the life cycle (Strauss-Debenedetti and Bazzaz, 1991; Gómez, 2003). Shade-tolerant species responded to light heterogeneity at all evaluated conditions, which is consistent with previous studies (*e.g.* Pearcy, 1987; Rozendaal *et al.*, 2006). This suggests that shade-tolerant climax species may exhibit a wider plasticity because of large ontogenetic latitude through their life cycle. The trade-off could be as extreme as not growing at all but surviving under low light and then grow quickly under high light conditions (Kitajima, 1994; Kitajima and Bolker, 2003). So, if homogeneity is the less frequent habitat condition in forest understory it could be expected that only a few species specialized in using homogeneous environments could be able to occupy any of the two extremes of the light gradient in our bi-dimensional plane and also that most plant species (including those followed in this study) might be subjected to selection on this bi-dimensional light intensity and heterogeneity gradient where subtle balancing effects are well depicted.

Different forest scenarios that could be useful to rank the shade-tolerance dichotomy can be envisaged within the light contrast framework. In this sense, we evaluate the responses of seedlings and saplings under a wider but also more precise range of light contrasts than are conventionally included in old-growth forests, when only gap or non-gap areas are visualized. This study provides spatially explicit information about six years of forest regeneration. We ascertain that, with this sample, the spatial light contrast clearly is a good sensor of stand development related to other attributes of forest structure. These structural attributes jointly determine the quantity and quality of light that filters down onto the forest floor, with effects that enhances availability of other resources at both above and below ground levels (Coomes and Grubb, 2000). We are convinced that spatial light contrasts are useful in developing more complex functional and successional schemes with adequate elasticity to span forest recovery needed in the development of improved functional

classification of forest species that could better support the management of highly species-rich forests.

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