

Growth and photosynthetic performance of five tree seedlings species in response to natural light regimes from the Central Pacific of Costa Rica

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Abstract: Crecimiento y desempeño fotosintético de cinco plántulas de especies arbóreas en respuesta a regímenes lumínicos naturales del Pacífico Central de Costa Rica. Environmental heterogeneity mostly dominated by differing light regimes affects the expression of phenotypic plasticity, which is important for plant growth and survival, especially in the forest understory. The knowledge about these responses to this heterogeneity is a key factor for forest restoration initiatives. In this study, we determine several phenotypic responses to contrasting light conditions in five native tree seedling species of La Cangreja National Park, Central Pacific of Costa Rica, four of them with threatened or relict populations. After 14 weeks at a medium gap condition (24% of full sun), seedlings were transferred and acclimated for 11 weeks to three different natural light regimes: large gap (LG), medium gap (MG) and small gap (SG), corresponding to 52%, 24%, 9% of the mean direct and indirect radiation at each site from full sun. Growth, biomass allocation and leaf gas exchange were measured after the acclimation period. Four species strongly reduced relative growth rate (*RGR*) in the lower light condition. Total biomass (*TB*) and *RGR* were different in *Hymenaea courbaril* and *Platymiscium curiense*. *H. courbaril* and *Astronium graveolens* had significant changes in the maximum assimilation rate, with a mean value in the LG of 11.02 and 7.70 $\mu\text{molCO}_2/\text{m}^2\text{s}$, respectively. *P. curiense* showed the same trend and significant changes in *RGR* and biomass allocation. *Aspidosperma myrsiticifolium* and *Plinia puriscalensis* showed no adjustments to the light regimes in any of the measured variables. This study remarks the importance of determining the growth and physiological performance of these tree native species. It also demonstrates that the most threatened species are those with the less plastic responses to the light regimes, which stresses the difficult situation of their natural populations. This study highlights an urgent definition of the conservation and restoration needs of the degraded forests of the Costa Rican Central Pacific area, where these species dwell. *Rev. Biol. Trop.* 61 (3): 1433-1444. Epub 2013 September 01.

Key words: assimilation rate, biomass allocation, relative growth rate, light curve responses, phenotypic plasticity, native tree species.

Tropical forests present great variability in light regimes (Chazdon & Fetcher 1984, Chazdon & Pearcy 1991), which have influenced the growth and development patterns of many seedlings (Théry 2001), which has been considered a potentially important mechanism to promote local plant biodiversity (Kitajima & Pooter 2008). As sessile organisms, plants have developed a series of morphological and physiological adaptations to cope with environmental light heterogeneity. Changes in these traits may possess a diversity of

plastic phenotypic responses in each species (Valladares *et al.* 2007, Lambers *et al.* 2008), enabling them to survive in different environments according to their light requirements. Many researchers have looked at the response of native trees in Costa Rica to changes in the light environment (Fournier 1985, Fetcher *et al.* 1987, Torres & Luján 1999). However, we still have large gaps in scientific and technical knowledge of the light preferences of many species, especially those species with restricted distributional ranges or affected by



anthropogenic changes in the original habitats. This information is required, because the recovery of native forests must concentrate on the restoration through an accurate knowledge of the micro-environmental needs and tree performance for the use in forestry.

Some authors have classified plants according to their light requirements (Bazzaz & Pickett 1980, Lambers *et al.* 2008) as shade tolerant or intolerant (Reich *et al.* 2003, Valladares & Niinemets 2008). Functional groups studies show that shade intolerant have high phenotypic plasticity (Valladares *et al.* 2000) than shade tolerant plants in response to the different light regimes. In addition, phenotypic responses in intolerant plants have often been linked to physiological and leaf morphological changes, while tolerant plants seems to respond mostly with architectural traits (e.i. in the branch bifurcation ratio) (Valladares & Niinemets 2008).

This study aims to characterize the growth, biomass allocation and carbon assimilation of seedlings of five tree species native to the Central Pacific area of Costa Rica. This region is dominated by wet forests with a significant dry season which has been severely degraded since last century. Because the selected species have actually reduced populations in their native habitats, our data will facilitate the definition of alternatives to choose better management practices for their reforestation success.

MATERIAL AND METHODOS

Study site: The study was conducted from May through November 2010 at La Cangreja National Park (PNLC), Puriscal, Costa Rica (9°42'10.77"N-84°23'52.47"W). This park contains the last remaining patches of tropical wet and premontane wet forest in the Central Pacific region of Costa Rica (Holdridge 1967). The PNLC has a high average annual precipitation (4 000mm), with a rainy season from April to December, high humidity, nutrient-poor soils and variable topography, resulting in great diversity and plant endemism, representing about 7.25% of the country endemic plants (Acosta 1998, Bermúdez 2005).

Study species: We selected three shade-intolerant and two shade-tolerant species native to the Costa Rican Central Pacific region. The Instituto Costarricense de Electricidad (ICE) has a reforestation program in this area and maintains a nursery in the PNLC, and our tree species were obtained from the available stock, reason why chosen plants were in different developmental stage (Table 1). Seedlings of *Astronium graveolens*, *Hymenaea courbaril* and *Platymiscium curuense* were three, four, and six months old, respectively, and were transplanted from the sand beds in the ICE nursery were they germinated. *Aspidosperma*

TABLE 1
Natural distribution in Costa Rica, habitat and seedling light preferences of studied species

Species	Family	Distribution	Habitat preferences	Light preferences
<i>Hymenaea courbaril</i>	Fabaceae	Both coasts, most often in the Central Pacific region ^{1,6}	Dry forests, deciduous ¹	Shade intolerant ²
<i>Platymiscium curuense</i> *	Fabaceae	Central and South Pacific region ¹	Rainforests ¹	Shade intolerant ¹
<i>Astronium graveolens</i>	Anacardiaceae	Across the Pacific region ¹	Dry forests, deciduous ¹	Shade intolerant ³
<i>Aspidosperma myristicifolium</i>	Apocynaceae	Central and South Pacific region ⁵	Primary and secondary forests, deciduous ⁴	---
<i>Plinia puriscalensis</i> **	Myrtaceae	Only within the PNLC ⁷	Gallery forest and secondary forest ⁶	---

*Species endemic at Costa Rican Pacific region, **Species endemic at La Cangreja National Park, --- no information.

¹Jiménez *et al.* 2011, ²Cordero & Boshier 2003, ³Martin & Flores 2002, ⁴Morales 2001, ⁵Zamora *et al.* 2000, ⁶Jiménez *et al.* 1986, ⁷Sánchez & Jiménez 1989.

myristicifolium and *Plinia puriscalensis* were 12 months old, and were growing in 3-liter pots with soil taken from field sites. These plants were germinated in small pots at conditions similar to our MG light regime. Detailed knowledge about their specific growth and photosynthetic traits is little, but their habitats preferences and distribution is well documented (Table 1). The small number of seedlings obtained from the highly threatened species *P. puriscalensis* did not allowed us to quantify its biomass allocation, and only gas exchange data are presented for this species. There was no need to artificially watering the seedlings during the experiment because the entire growing period was developed during the rainy season.

Experimental design: We used 30 to 40 seedlings per species and transplanted them to 3.5-liter pots containing a 3:1 mixture of forest topsoil and river sand. Afterwards, seedlings were put under a natural understory light condition, where they were maintained for 14 weeks (first growth period). We harvest 10 plants at the end of the first period which data were only used to calculate the relative growth rate (as explained below). After that first growth period at low light conditions, six to 10 remaining plants per species were transferred to the following three contrasting natural light conditions: large gap (LG), medium gap (MG) and small gap (SG) (Table 2), for a second growth period of 11 weeks. Seedlings were fertilized with 100mL of a complete commercial mineral nutrient formula in the middle of each growing period. The natural light regime of the three sites was characterized

by taking eight hemispherical photographs per site, positioned at one meter above the ground using a digital camera (Sigma Inc) in a horizontal position with a 180° fisheye lens (Sigma Inc) coupled with a tripod. These photographs were analyzed with the software *HemiView 2.1* (Delta-T Devices Ltd Inc, USA), which considers the location with respect to the magnetic pole, magnetic declination, geographic location and elevation of the site for calculating among others. The following parameters were considered: the direct site factor (*DSF*), the diffuse site factor (*ISF*), global site factor (*GSF*) and leaf area index (*LAI*), *DSF* and *ISF* reflect the proportion of direct and diffuse light, *GSF* reflects the proportion of canopy gaps and the *LAI* is an estimation of the leaf area by square meter of ground (Pierce & Running 1988).

Growth and biomass allocation: After each growing period, six to 10 plants per species were harvested to measure total (*TB*), root (*R*) and shoot (*S*) dry biomass, total leaf fresh area (*LA*), total leaf biomass (*LB*). Root to shoot ratio (*R/S*) and specific leaf area (*SLA*, as *LA/LB*) were calculated following Beadle (1985). *LA* was measured with a leaf area meter (Li-3100, LICOR Inc., USA). Total plant biomass of the second growth period and the average value of the total biomass of 10 plants of the first growing period were used to calculate relative growth rate (*RGR*) per plant according to Villar *et al.* (2004). No root constriction was observed during plant harvest.

Gas exchange measurements: Two open portable photosynthesis systems (LI-6400XT, LICOR, Inc USA and ADC, Inc. London,

TABLE 2

Mean (\pm SD) of the direct side factor (*DSF*), indirect side factor (*ISF*), global side factor (*GSF*) and leaf area index (*LAI*) on the sites with light regime to grow estimated from hemispherical photographs

Condition	<i>DSF</i> (mol/m ² yr)	<i>ISF</i> (mol/m ² yr)	<i>GSF</i> (mol/m ² yr)	<i>LAI</i> (m ² /m ²)
LG	0.541 \pm 0.04	0.339 \pm 0.03	0.521 \pm 0.03	1.902 \pm 0.23
MG	0.254 \pm 0.09	0.215 \pm 0.07	0.249 \pm 0.09	1.847 \pm 0.39
SG	0.099 \pm 0.04	0.089 \pm 0.03	0.098 \pm 0.04	2.628 \pm 0.33

Large gap (LG), medium gap (MG) and small gap (SG).

England) were used to build photosynthetic light response curves for three plants in the second growth, using the following standard conditions. The CO₂ ambient concentration was constant during each measurement, but ambient concentration varied from 360 to 390 between measurements. Leaf temperature and relative humidity were maintained around site mean values (25°C and 60-80%, respectively). We used fully developed and recently expanded leaves produced during the second period, that were pre-illuminated at 1 000-1 200 μmol/m²s of photon flux density (PDF) for at least 2min. However, each plant remained 20-60min at ambient light under the mild shade of a plastic canopy before introducing the leaf into the leaf chamber. Carbon assimilation was measured at several PDF values ranging from 1 500 to 0 μmol/m²s from a red light source (LICOR Part 6400-02 LED, 660-675nm wavelength range and the ADC Light units LED's, 660nm wavelength and between 5-10% of blue light) attached to the leaf chamber. Assimilation rates versus photosynthetic active radiation data were fitted to the following empirical model (Küppers & Schulze 1985):

$$A = A_{max} [1 - e^{-\theta(I-I_c)}]$$

where A is the rate of carbon assimilation, A_{max} is light-saturated rate of photosynthesis, θ is a parameter that describes the shape of the light response curve apparent quantum yield, I is irradiance and corresponds to the incident PDF (μmol/m²s) and I_c is the light compensation point. The light response curves were fitted by SigmaPlot 11.0 curve fitting (Systat Software, Inc., California) to obtain the parameters A_{max} and θ . Independently, the slope of a linear regression of A values between 0 and 50 μmol/m²s of PDF was used to calculate the apparent quantum yield (Q_{app}). Dark respiration (R_d) was calculated from the intersection on the "y" axis, and the intersection of "x" axis was used to obtain I_c .

All parameters measured at the end of the second period were compared using a one way ANOVA and *a posteriori* Tukey tests mean

comparison with the goal of evidence differences between exposure treatments. A principal components analysis (PCA) per species was done on growth and biomass allocation parameters to show what combination of parameters explains most of the total variance. The component scores extracted from the first two principal components were tested by an analysis of variance comparing them by exposure treatments. All analysis were made following Quinn & Keough (2002), using the software JMP 7 (SAS).

RESULTS

Light environments: Based on the GSF our three sites represented conditions of light gaps of approximately 50, 25 and 10% of full sunlight (Table 2). *LAI* was similar between the large (LG) and the medium light gap (MG), but both of these places had a significant low *LAI* respect to the small light gap (SG) condition. The LG condition received 25 and 40% more of the ISF and DSF than the MG and SG conditions, respectively. These results show that the sites used for the light treatment acclimation were significantly contrasting between them, and represent a diversity of light regimes naturally found in the present conditions of the forested areas of the Central Pacific zone.

Growth and biomass allocation: The four species presented a gradient of mean SLA in the following order: *P. curuense*, *A. graveolens*, *H. courbaril* and *A. myristicifolium*. None of the species showed significant changes in *SLA* between light conditions (Table 3). Root to shoot ratio was larger in *H. courbaril* and *A. myristicifolium* (0.517 and 0.496 respectably) and smaller in *A. graveolens* (0.238), but none of this species adjusted the *R/S* according to the prevailing light treatment. Only *P. curuense* showed a significant lower mean of *R/S* in the LG treatment compared to the other two light growing conditions. However, this is contrary to our expectations. Total biomass was significantly lower in the SG treatment for both *H. courbaril* and *P. curuense*, and the

TABLE 3
Biomass allocation of four tree seedling species on three contrasting light regimes
at La Cangreja National Park, Costa Rica

Parameter	Condition	Species			
		<i>H. courbaril</i> (<i>df</i> =2/23)	<i>P. curuense</i> (<i>df</i> =2/23)	<i>A. graveolens</i> (<i>df</i> =2/21)	<i>A. myrasticifolium</i> (<i>df</i> =2/18)
<i>SLA</i>	LG	188.63±25.56	279.25±30.69	267.53±56.71	147.28±35.47
	MG	193.01±36.49	309.14±57.83	306.54±72.85	146.87±20.40
	SG	187.12±29.79	297.66±56.96	238.41±65.31	155.33±9.25
	<i>F</i> -ratio	0.08	0.67	2.11	0.61
	<i>P</i> -value	0.92	0.52	0.14	0.55
<i>R/S</i>	LG	0.551±0.19	0.374±0.06 ^A	0.204±0.04	0.516±0.15
	MG	0.545±0.07	1.162±1.44 ^B	0.279±0.13	0.526±0.09
	SG	0.455±0.06	0.573±0.30 ^{AB}	0.231±0.07	0.445±0.07
	<i>F</i> -ratio	1.26	3.55	0.75	0.93
	<i>P</i> -value	0.30	0.04	0.48	0.41
<i>TB</i>	LG	5.13±0.52 ^A	15.27±5.83 ^A	0.63±0.28	8.10±2.74
	MG	4.84±1.58 ^A	15.55±12.55 ^{AB}	0.53±0.18	7.61±2.61
	SG	2.82±0.82 ^B	8.30±7.66 ^B	0.57±0.21	5.62±1.48
	<i>F</i> -ratio	10.51	3.51	2.60	1.94
	<i>P</i> -value	<0.001	0.04	0.09	0.17

Large gap (LG), medium gap (MG) and small gap (SG). Values are mean ± standard deviation. Significant differences ANOVA ($p < 0.05$) and Tukey test orientations are indicated by the letter code. Degrees of freedom (*df*) for each species are presented within parentheses.

same trend was observed in *A. myrasticifolium*. However, this species and *A. graveolens* did not change significantly in biomass between light treatments.

P. curuense and *A. graveolens* showed the larger variation in *RGR* (Fig. 1), being the species with the larger and smaller plants, respectively at the beginning of the experiment. These species were significantly affected by the light regime (*H. courbaril*: $F_{2/23} = 12.52$, $p < 0.001$, and *P. curuense*: $F_{2/23} = 4.01$, $p = 0.03$). The species *A. graveolens* had the higher *RGR* value, and it was the only species with a positive *RGR* in the forest understory conditions. *A. myrasticifolium* presented lower *RGR* values across the three light regimes, and they did not differ between them (Fig. 1).

The PCA's for the growth and biomass allocation variables per species (Fig. 2) show that the first and the second component explained in all species more than 50 and 22% of the variation, respectively. In all case (except

A. graveolens) the first component is influenced largely by *RGR* and *TB*, while the second was mostly influenced by *SLA* and *R/S* (Table 4). Analyses of variance of the score values extracted from the PCA's showed a significant difference between treatments of the first components for *H. courbaril* and *P. curuense* ($F_{2/23} = 12.06$, $p < 0.001$; $F_{2/23} = 4.77$, $p < 0.01$, respectively) (Fig. 2). The other components of these and the other species did not show differences ($p > 0.05$).

Gas exchange measurements: In general, the light response curve of all species shows a maximum light saturation just above 600 $\mu\text{mol}/\text{m}^2\text{s}$ (Fig. 3). A_{max} comparisons between species were made at 1 000 $\mu\text{mol}/\text{m}^2\text{s}$ values to ensure the maximum leaf photosynthetic activity. The light response curves clearly changed in the shade intolerant species and remained similar between light treatments in the two shade tolerant species (Fig. 3).

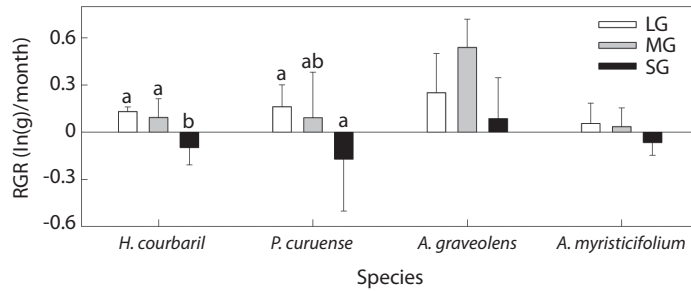


Fig. 1. Relative growth rate (*RGR*) of four tree seedling species across three natural light regimes at La Cangreja National Park, Costa Rica. Large gap (LG), medium gap (MG) and small gap (MG). Values are means \pm standard deviation bars. Significant differences from the ANOVA ($p < 0.05$) and Tukey tests are indicated by the letter code.

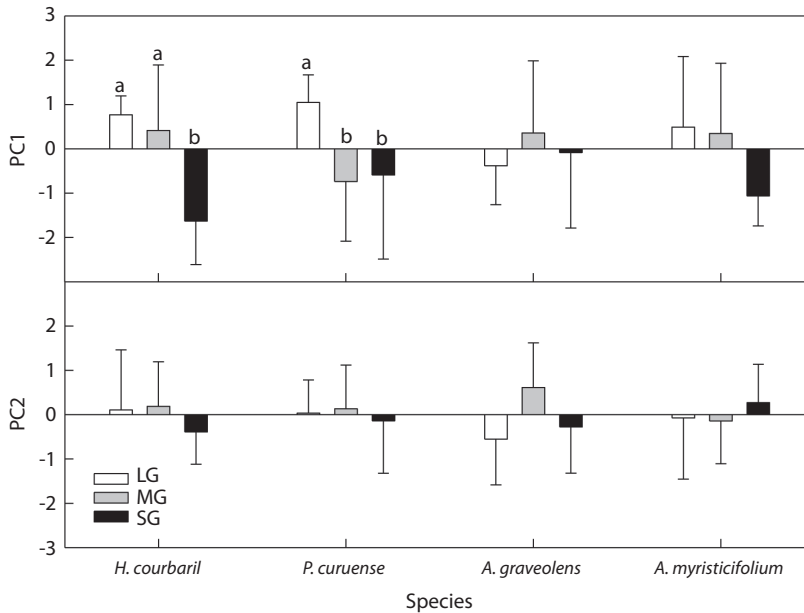


Fig. 2. Scores of first two principal components of the PCA on biomass allocation parameters of four tree seedling species in three natural light regimes at La Cangreja National Park, Puriscal, Costa Rica. Large gap (LG), medium gap (MG) and small gap (MG). Values are means \pm standard deviation bars. Significant differences ANOVA ($p < 0.05$) and Tukey test orientations are indicated by the letter code.

The shade-intolerant species had maximum assimilation rates in agreement with the present light environments in which they developed (Fig. 4), that is, higher A_{max} in the LG treatment than in the SG treatment. These trends among treatments were only significantly different in *H. courbaril* ($F_{2/6} = 5.89$, $p = 0.02$) and *A. graveolens* ($F_{2/4} = 7.84$, $p = 0.04$). The other two shade-tolerant species did not

change their maximum photosynthetic response to the prevailing light regimes, but they both showed a much lower A_{max} compared with the shade intolerant species. Of the other variables extracted from light curves response only stomatal conductance in *H. courbaril* was significantly lower in the SG environment (Table 5). This trend was followed by *P. curuense* and *A. myristicifolium*. Mean dark respiration was

TABLE 4

Eigenvalues and *eigenvectors* of first two principal components (1, 2) of the PCA on biomass allocation parameters of four tree seedling species in three contrasting light regimes at La Cangreja National Park, Puriscal, Costa Rica

	Species							
	<i>H. courbaril</i>		<i>P. curuense</i>		<i>A. graveolens</i>		<i>A. myristicifolium</i>	
	1	2	1	2	1	2	1	2
Eigenvalues	2.04 (50.90)	1.17 (29.26)	2.45 (61.13)	0.90 (22.43)	2.01 (50.25)	1.25 (31.26)	2.24 (55.89)	1.16 (29.08)
Eigenvectos								
RGR	0.69	-0.01	0.55	0.15	0.70	0.06	-0.63	-0.23
SLA	-0.13	0.72	-0.27	0.95	-0.10	0.70	-0.10	0.83
R/S	0.15	0.70	-0.51	-0.26	0.70	0.06	0.41	-0.47
TB	0.69	-0.01	0.60	0.07	0.01	-0.71	0.65	0.19

Values in parentheses represent the percentage of variance explained by each component.

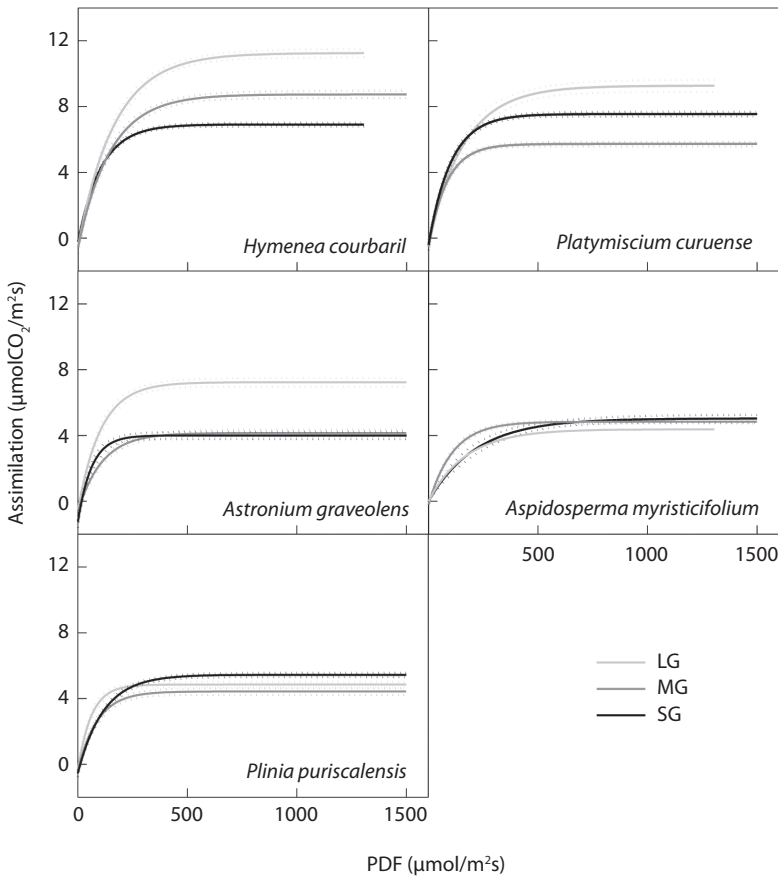


Fig. 3. Leaf photosynthetic light curve response of five tree seedling species on three natural light regimes at La Cangreja National Park, Costa Rica. Large gap (LG), medium gap (MG) and small gap (MG). Line represents the best curve fitting from all light curve points in each light condition and points the confidence intervals for each curve at 95%.

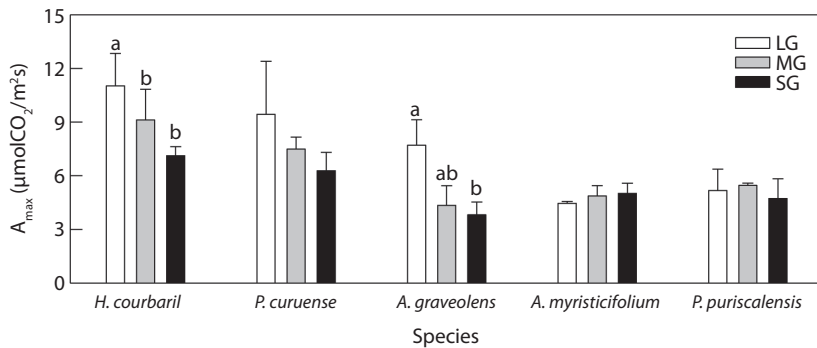


Fig. 4. Maximum photosynthetic rate (A_{max}) of five tree species of seedling on three natural light regimes at La Cangreja National Park, Costa Rica. Large gap (LG), medium gap (MG) and small gap (MG). Values are the mean \pm standard deviation bars. Significant differences of the ANOVA ($p < 0.05$) and Tukey tests are indicated by the letter code.

always higher than $-0.88 \mu\text{molCO}_2/\text{m}^2\text{s}$ across species and treatments. There were no significant changes in mean transpiration or water use efficiency between treatments or species (Table 5). There were no changes in apparent quantum yield, which varied between 0.04 and 0.08. Similarly, light compensation points were as low as $4 \mu\text{mol}/\text{m}^2\text{s}$ in *H. courbaril* at SG, and as high as $16.7 \mu\text{mol}/\text{m}^2\text{s}$ in *A. graveolens* in the MG treatment.

DISCUSSION

The plasticity to light acclimation is directly related to physiological, morphological and growth traits (Bazzaz & Carlson 1982, King 1991). In this connection, our species can be separated into two groups: (1) high plasticity species (*H. courbaril*, *P. curuense* and *A. graveolens*) and (2) low plasticity species (*A. myrasticifolium* and *P. puriscalensis*). The species of these two groups can certainly be categorized as shade intolerant and shade tolerant species according to their light habitat preferences, where the first group is differentiated by the faster growth, greater biomass accumulation, and a clear acclimation response in maximum assimilation rate according to light conditions.

Several studies show shade-tolerant species as usually having low phenotypic plasticity

against the light regimes (Poorter 1999, Valladares *et al.* 2000, Portsmouth & Niinemets 2007), which has been considered a functional trait for the survival and development in environments where the resource is low (Valladares *et al.* 2007, Valladares & Niinemets 2008). Other traits normally ascribed to shade-tolerant species include lower respiration values, lower maximum assimilation and lower *SLA* than intolerant species (Kitajima 1994, Reich *et al.* 2003, Lusk *et al.* 2011). However, none of these traits showed clear trends between our five studied species.

Depending on the magnitude of the light radiation, the shade-intolerant species may exhibit a number of physiological and morphological adaptations of greater plasticity when they are in low radiation (Rice & Bazzaz 1989, Lambers *et al.* 2008), such as bifurcations of the branches and horizontal angles in the leaves (Lambers *et al.* 2008, Valladares & Niinemets 2008). These variables were not measured in this study, although it is possible that they could be key parameters in the acclimation regimes. In general, the five species are a very idiosyncratic selection. For example, if we consider *RGR* as the only parameter to classify species performance, we must classify *A. myrasticifolium* and *H. courbaril* as shade-intolerant species, giving its negative *RGR* at the lower light regime. However, only *H. courbaril*

TABLE 5
Gas exchange parameters of five tree seedling species on three contrasting light regimes at La Cangreja National Park, Costa Rica

Parameter	Condition	Species				
		<i>H. courbaril</i> (df= 2/6)	<i>P. curuense</i> (df= 2/6)	<i>A. graveolens</i> (df= 2/4)	<i>A. myristicifolium</i> (df= 2/5)	<i>P. puriscalensis</i> (df= 2/5)
A_{max} ($\mu\text{mol CO}_2/\text{m}^2\text{s}$)	LG	11.02±1.82 ^A	9.43±2.96	7.70±1.43 ^A	4.46±0.10	5.17±1.20
	MG	9.12±1.71 ^A	7.49±0.67	4.34±1.10 ^{AB}	4.87±0.58	5.46±0.13
	SG	7.12±0.50 ^B	6.28±1.03	3.81±0.72 ^B	5.01±0.57	4.73±1.10
	<i>F-ratio</i>	5.29*	2.21	7.84*	0.78	0.31
R_d ($\mu\text{mol CO}_2/\text{m}^2\text{s}$)	LG	-0.38±0.12	-0.37±0.06	-0.66±0.13	-0.45±0.01	-0.31±0.12
	MG	-0.56±0.60	-0.36±0.10	-1.14±0.29	-0.31±0.09	-0.88±0.63
	SG	-0.23±0.01	-0.42±0.13	-0.87±0.58	-0.36±0.11	-0.46±0.20
	<i>F-ratio</i>	0.62	0.27	1.27	1.70	1.87
g ($\text{mol}/\text{m}^2\text{s}$)	LG	0.41±0.07 ^A	0.24±0.17	0.16±0.16	0.15±0.14	0.03±0.02
	MG	0.22±0.02 ^B	0.12±0.07	0.18±0.01	0.11±0.07	0.20±0.05
	SG	0.10±0.03 ^C	0.12±0.08	0.33±0.18	0.07±0.05	0.17±0.16
	<i>F-ratio</i>	36.86***	0.40	0.84	0.52	2.05
T ($\text{mol}/\text{m}^2\text{s}$)	LG	1.95±0.47	2.82±1.81	2.42±1.59	2.27±1.18	1.03±0.70
	MG	2.80±1.81	1.99±0.76	1.82±0.37	1.79±0.81	2.41±0.37
	SG	2.16±0.41	1.48±0.08	2.95±1.54	1.25±0.18	1.43±0.92
	<i>F-ratio</i>	0.48	1.18	0.30	1.01	1.81
WUE ($\mu\text{mol CO}_2 / \text{mmol H}_2\text{O}$)	LG	5.77±0.81	3.87±1.65	4.04±2.35	2.28±1.23	5.41±2.65
	MG	4.85±4.19	4.13±1.53	2.37±0.11	3.07±1.28	2.28±0.29
	SG	3.36±0.62	4.22±0.51	1.42±0.49	4.11±0.99	1.72±1.51
	<i>F-ratio</i>	0.71	0.05	3.44	1.54	1.95
Q_{app} (10^{-2})	LG	5.89±0.26	5.15±0.88	7.71±0.16	5.03±0.83	8.13±0.03
	MG	6.26±1.04	4.5±3.6	8.08±3.7	5.22±0.19	6.79±3.82
	SG	5.73±0.80	5.34±0.46	5.40±0.35	5.61±1.31	6.30±0.02
	<i>F-ratio</i>	0.36	3.14	0.58	0.26	1.32
I_c ($\mu\text{mol}/\text{m}^2\text{s}$)	LG	6.54±2.31	7.23±1.45	8.53±1.81	9.07±1.27	5.08±2.82
	MG	8.86±9.40	2.04±2.44	16.75±11.30	6.05±1.80	12.67±8.58
	SG	4.02±0.80	8.03±3.30	15.78±0.88	6.42±0.48	8.68±6.92
	<i>F-ratio</i>	0.82	5.01	1.53	3.59	1.83
$A_{max(M)}$	LG	11.11±1.39 ^A	9.36±2.97	7.58±1.72	4.34±0.16	4.12
	MG	9.00±1.37 ^{AB}	7.57±0.62	4.56±1.42	4.89±0.66	5.48±0.21
	SG	6.85±0.70 ^B	5.70±0.61	4.07±1.28	5.32±0.16	4.72±1.18
	<i>F-ratio</i>	6.88*	3.13	3.86	---	---
$\Theta_{(M)}$ (10^{-3})	LG	6.43±1.06	7.33±3.71	9.71±3.16	7.5±3.25	22.3
	MG	6.33±1.86	9.60±1.87	15.35±1.77	9.33±2.74	8.90±3.68
	SG	9.50±1.35	11.07±2.27	10.01±1.98	10.55±5.59	11.13±0.31
	<i>F-ratio</i>	4.55	1.42	3.24	---	---
$I_{c(M)}$	LG	6.69±2.64	6.08±2.58	7.51±2.09	6.52	6.01
	MG	9.75±13.68	5.03±0.96	15.83±10.54	4.23±3.61	9.20±12.54
	SG	3.85±0.47	7.35±2.02	16.22±1.02	5.29±1.45	6.76±5.79
	<i>F-ratio</i>	---	1.03	2.06	---	---
$R_{d(M)}$	LG	-0.49±0.22	-0.39±0.23	-0.56±0.22	-0.28	-0.59
	MG	-0.56±0.79	-0.38±0.13	-1.09±0.43	-0.21±0.17	-0.62±0.86
	SG	-0.26±0.06	-0.47±0.09	-0.75±0.43	-0.33±0.24	-0.33±0.24
	<i>F-ratio</i>	---	0.21	1.41	---	---

Large gap (LG), medium gap (MG) and small gap (SG). Stomatal conductance (g), transpiration rate (T), water-use efficiency (WUE) were obtained from the original data sets. Dark respiration rate (R_d), apparent quantum yield (Q_{app}) and light compensation point (I_c) were calculated from linear regression of the initial part of the light curve response. Maximum assimilation rate model ($A_{max(M)}$), dark respiration rate model ($R_{d(M)}$), the curvature ($\Theta_{(M)}$) and light compensation point model ($I_{c(M)}$) were obtained from curve fitting following the model used by Küppers and Schulze (1985). Values are the mean ± SD. Significant differences from ANOVA and Tukey tests are indicated by the letter code. Differences significant at $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***). Degrees of freedom (df) for each species are presented within parentheses.

responded with significant changes of their maximum assimilation rates to the prevailing light conditions. This example explains why it is important to study various parameters for the characterization of performance of the species to its environment and their changes. It is noteworthy to consider that normal understory conditions are about 2-3% of full sun in tropical primary forests (Chazdon & Fetcher 1984), which is significantly lower compared with our low light regime of about 9% of full sunlight. For this reason, we cannot discard that this not so low light condition could reduce the differences obtained. For example, the SLA is a variable that commonly shows large variation in low and high light levels sites, in temperate and tropical environments (Valladares *et al.* 2000, Lambers *et al.* 2008). In this sense, SLA can almost be used as a good indicator of subtle plastic changes in light regimes for many species. This situation confirms that our low light treatment was a little above average for a forest understory.

By reducing resource allocation to biomass in general (Poorter 1999, Lambers & Poorter 2004), shade-intolerant plants may experience rapid adaptation to the site where they are (Montgomery & Chazdon 2002). These functional features are probably responsible for differences in *RGR*, *TB* and maximum assimilation rates in the shade-intolerant species than shade-tolerant species.

It is clear that the less plastic species, *A. myrasticifolium* and *P. puriscalensis*, are the two shade tolerant species with the smaller growth rates and the ones with the most critical conditions in their remnant populations. *P. puriscalensis* has a reduced population distribution, known only in the PNLC (Jiménez 2001), and *A. myrasticifolium* has restricted distributions in primary and secondary forest (Morales 2001), aspects that should probably put both as endangered species. The present growth and physiological results are intended to help in the decision making about the use of these species, and all other species in similar situation, in restoration and conservation projects, either through the selection of sites with suitable light

conditions for the growth and establishment of species or in the selection of environments to protect the natural forest where these species still dwell. We recommend for future reforestation programs to avoid high light regime sites for *A. myrasticifolium* and *P. puriscalensis*, and to keep its distribution within their natural range (Table 1). *H. courbaril*, *P. curuense* and *A. graveolens* are species that can be planted in open areas after a short acclimation to high light in nurseries when seedlings. Larger sizes can be used directly into reforestation trails along the Pacific slopes. Any effort in this sense will help reduce the speed of biodiversity loss if our degraded tropical areas.

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RESUMEN

La heterogeneidad ambiental dominada mayormente por diferencias en los regímenes lumínicos afecta la expresión de la plasticidad fenotípica, la cual es importante para el crecimiento y la supervivencia de las plantas, especialmente en el sotobosque. Conocer dichas respuestas ante la heterogeneidad es un factor clave para las iniciativas de restauración forestal. En este estudio, determinamos varias respuestas fenotípicas ante condiciones lumínicas contrastantes de cinco especies de plántulas de árboles nativos del Pacífico Central de Costa Rica, algunos de ellos con poblaciones amenazadas. El crecimiento, la asignación de biomasa y el intercambio gaseoso a nivel foliar se midieron al final de once semanas de aclimatación en tres regímenes con diferente radiación: claro grande (LG), claro mediano (MG) y claro pequeño (SG) que corresponden al 54, 24 y

9% de la media del factor de radiación indirecta e indirecta en cada sitio a pleno sol, respectivamente. Cuatro especies presentan fuertes disminuciones en la tasa de crecimiento relativo (*RGR*) en la condición de poca luz. La biomasa total, *RGR* y la relación raíz/tallo fueron diferentes para todas las especies. *Hymenaea courbaril* y *Astronium graveolens* respondieron significativamente en la tasa de asimilación máxima, con un valor promedio en el LG de 11.02 y 7.70 $\mu\text{molCO}_2/\text{m}^2\text{s}^1$ respectivamente. *Platymiscium curuense* mostró tendencias similares y cambios significativos en la *RGR* y la asignación de biomasa. *Aspidosperma myrsiticifolium* y *Plinia puriscalensis* mostraron una plasticidad muy baja debido que no expresaron ajustes en ninguna de las variables medidas ante los regímenes de luz. Este estudio resalta la importancia de determinar el crecimiento y el rendimiento fisiológico de estas especies de árboles nativos. También demuestra que las especies más amenazadas son aquellas con las respuestas con menor plasticidad ante los regímenes luz, lo que acentúa la difícil situación de sus poblaciones naturales. Este estudio destaca una urgente definición de las necesidades de conservación y restauración de los bosques degradados de zona del Pacífico Central costarricense, donde estas especies habitan.

Palabras clave: tasa de asimilación, asignación de biomasa, tasa de crecimiento relativo, curva de respuesta a la luz, plasticidad fenotípica, árboles nativos.

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