

## Light requirements of seedlings: a method for selecting tropical trees for plantation forestry

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### Abstract

A greenhouse experiment was conducted on seedlings of three native trees from the Ecuadorian Amazon: *Pollalesta discolor*, *Inga densiflora*, and *Platymiscium pinnatum*. We studied their growth and photosynthetic performances in contrasting light environments, in order to assess the potential of these seedlings for future silvicultural use as well as to characterize their optimal light requirements. Seedlings were grown for 3.5 months in a greenhouse under three light intensities, full light (100%), partial shade (15%), and full shade (2.5%). Survival, growth, biomass allocation, leaf turnover and plant morphology were determined for all seedlings and gas exchange measurements were measured on a sub-sample of each species. Results showed that *Pollalesta discolor* had a high growth rate, a rapid leaf turnover, a large total leaf area and a high specific leaf area (SLA), coupled with high photosynthetic rates, when grown in a full-light environment. These traits confirm that it is shade intolerant, requiring a high-light environment for establishment as a seedling, characteristic of an early-successional species. *Inga densiflora* appeared to require some shade during its seedling stage, as shown by highest photosynthetic rates in partial shade. The full light treatment caused photoinhibition, impairing photosynthetic rates, and the full shade treatment was linked to high mortality, indicating that this species could not persist in a forest understory. *Platymiscium pinnatum* thrived equally well under both shade treatments, and had lower photosynthetic rates under the full light treatment. It was definitely a shade-tolerant species, displaying characteristics of a late-successional species. Increased growth performances with increased light intensity would indicate that this species could eventually benefit from higher light conditions. This experimental characterization of light requirements for seedlings of lesser known native species, through growth and photosynthetic performances under contrasting light environments, provided valuable information on their early establishment requirements, which could be used in selecting the proper light regime in nurseries and plantation models.

Ein Gewächshausexperiment wurde mit drei einheimischen Bäumen des ecuadorianischen Amazonasgebietes *Pollalesta discolor*, *Inga densiflora* und *Platymiscium pinnatum* durchgeführt. Wir untersuchten ihre Wachstums- und Photosyntheseleistung bei unterschiedlichen Lichtbedingungen, um das Potential dieser Keimlinge für zukünftige forstwirtschaftliche Nutzung abzuschätzen und ihre optimalen Lichtansprüche zu charakterisieren. Die Keimlinge wurden für 3.5 Monate bei drei verschiedenen Lichtintensitäten kultiviert: volles Licht (100%), teilweiser Schatten (15%) und voller Schatten (2,5%). Für alle Keimlinge wurde die Überlebensrate, das Wachstum, die Biomassen-Allokation, der Blattwechsel und die Pflanzenmorphologie bestimmt. Der Gasaustausch wurde für eine Teilprobe jeder Art gemessen. Die Ergebnisse zeigten, dass *Pollalesta discolor* eine

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hohe Wachstumsrate, einen schnellen Blattwechsel, eine große Gesamtblattfläche und eine hohe spezifische Blattfläche (SLA) in Verbindung mit hohen Photosyntheseraten besaß, wenn sie in einer Umgebung mit voller Lichtintensität wuchs. Diese Eigenschaften bestätigen, dass sie schattenintolerant ist, eine lichtintensive Umwelt für die Etablierung als Keimling benötigt und charakteristisch für eine Art der frühen Sukzession ist. *Inga densiflora* schien ein wenig Schatten im Keimlingsstadium zu benötigen, was durch die höchsten Photosyntheseraten im Teilschatten gezeigt wurde. Volles Licht verursachte Photoinhibition und beeinträchtigte die Photosyntheserate. Voller Schatten war mit einer hohen Mortalität verbunden, die anzeigte, dass diese Art im Unterholz nicht bestehen könnte. *Platymiscium pinnatum* gedieh unter den beiden Schatten-Bedingungen gleich gut und hatte bei vollem Licht geringere Photosyntheseraten. Sie war definitiv eine schattentolerante Art und zeigte Eigenschaften einer Pflanze später Sukzession. Steigende Wachstumsleistung mit zunehmender Lichtintensität würde anzeigen, dass diese Art letztlich von höheren Lichtintensitäten profitieren könnte. Diese experimentelle Charakterisierung der Lichtansprüche bei Keimlingen wenig bekannter, einheimischer Arten durch Wachstums- und Photosyntheseleistung bei unterschiedlichen Lichtbedingungen lieferte wertvolle Informationen über ihre frühen Etablierungsansprüche. Das könnte für die Auswahl eines geeigneten Lichtregimes in Baumschulen und Plantagenmodellen genutzt werden.

**Key words:** Light environment – seedling establishment – photosynthesis – tropical tree seedlings – growth – ecophysiology – tropical forestry

## Introduction

Tree diversity of the Ecuadorian Amazon is among the highest reported in the world for tropical rain forests (Valencia et al. 1994). The high deforestation rate of Ecuador (FAO 1993) is threatening this diversity. Considering the silvicultural potential of many native timber tree species for reforestation, either for forestry or agroforestry purposes, research is urgently needed to establish their requirements, which are generally unknown (Sawyer 1993). This silvicultural potential is likely to be related to the successional status, because early- and late-successional species have different physiological and growth traits (Bazzaz & Pickett 1980), enabling them to adapt and perform in different light environments.

Tropical plant ecophysiology, as a discipline, has increased our knowledge on the relationships existing between the physiological and morphological traits of studied species. Early-successional species have high inherent growth rates (Kitajima 1996), which have been linked to a shorter leaf life-span, a high leaf N content (expressed on a mass basis), a high specific leaf area (SLA) and high maximum photosynthetic rates on a mass basis (Reich et al. 1992). These species are shade-intolerant, or light-demanding, since they are rarely found to persist in the understory, whereby they lack resources and are subjected to pathogens and herbivores (Strauss-Debenedetti & Bazzaz 1996), because of their low investments to defense compounds and structures (Kitajima 1996). Conversely, late-suc-

cessional species have lower relative growth rates (Kitajima 1996), attributed to their adaptation to shaded environments, because seedlings must increase allocation to defensive traits against herbivores (Coley 1988). Their maximum photosynthetic rates are lower, and rapidly saturate even at high light intensities (Strauss-Debenedetti & Bazzaz 1996).

Although the successional status is useful to describe and understand species ecology in the context of the dynamic processes characterizing the tropical forest, it is difficult to predict the physiological requirements of a species based solely upon its status. Moreover, these requirements are likely to vary among ontogenetic stages for a given species. The seedling stage being critical for establishment purposes, the characterization of the ecological requirements during this phase becomes particularly important.

The few studies conducted to improve the characterization of lesser-known native tropical species with a forestry or agroforestry potential have been completed using screening trial plantations. However, the determination of the ecophysiological requirements of selected seedlings, such as growth and photosynthetic assimilation characteristics in relation to various light environments, would permit to rapidly assess their proper light regime and their silvicultural potential. Therefore, the objective of this study is to infer the light requirements of three tropical tree species native to the Ecuadorian Amazon, at the seedling stage, based on their growth and photosynthetic performances in contrasting light environments.

## Materials and methods

### Plant material

Three tropical tree species native to the area of Macas (2°12'S, 78°05'W), in the southern part of the Ecuadorian Amazon, were selected. They corresponded to different assumed successional stages, known *a priori* from anecdotal local knowledge, and through observation of their natural habitat. These species represented a subset among 15 species previously chosen for a screening trial experiment conducted in the Amazonian Ecuador, for which the criteria of selection were described in Davidson et al. (1998). Among early-successional species, seeds of *Inga densiflora* Bentham were collected from two parent trees and left in their pods to avoid desiccation. They were unshelled the day before being transported by plane to Montreal and most were already producing roots in the pod. Seedlings of *Pollalesta discolor* (Kunth) Aris-Reguieta were collected along a small road near Macas and protected from desiccation. Because this species is wind dispersed, these seedlings probably originated from many parent trees. The time elapsed between collection in the field and sowing or transplantation in our greenhouse facilities in Montreal was less than two weeks for *Inga densiflora* and one week for *Pollalesta discolor*. The late-successional species *Platymiscium pinnatum* (Jacquin) Dugand was collected as seeds from a single parent tree. The time elapsed between collection in the field and sowing in the greenhouses was two weeks. This species has a seed viability of approximately two months.

In Montreal, all plant material was sown or planted in a rooting medium made of 50% peat moss and 50% sand, and placed in a propagation area with heating cables and a mist system under ambient light. Seedlings of the three species were transplanted into 3.5 L pots approximately three weeks later, using PRO-MIX BX (Premier, Canada), which is a soil mix containing 75–85% sphagnum peat moss by volume, perlite, vermiculite, macronutrients, micronutrients, dolomitic and calcitic limestone and a wetting agent. They were grown for 4 weeks in the full light environment of the greenhouse and were then set in contrasting light environments after that period.

### Experimental design and growing conditions

The experiment was conducted in a glass ridge-and-furrow Dutch-type greenhouse, with environmental variables computer controlled. A complete randomized block design was used. It consisted of three blocks, each one subdivided in three plots measuring 1.80 m × 1.80 m each. In each plot, 7 seedlings of each species were used, for a total of 21 plants per plot.

Three contrasting light treatments were created, on the basis of one per plot: a full light treatment (FL), a partial shade treatment (PS), and a full shade treatment (FS). The shade treatments were achieved by fastening a shade cloth on a wooden frame box 1.80 m long × 1.80 m wide × 1.80 m high. The Agrinet shade cloth (Novatex, Italy) was made of black polyethylene and screened 83% of the light intensity. One layer was used for the partial light treatment, and two layers were superimposed for the full shade treatment. The experiment lasted 14 weeks, from July 11 to October 17. A 24-8-16 water-soluble fertilizer (Peters, PA) was applied every two weeks, at a low dosage, delivering 50 ppm of N (20 ppm of N-NO<sub>3</sub>, 15 ppm of N-NH<sub>4</sub>, 15 ppm Urea), 27.7 ppm of K, and 7.3 ppm of P. Bendiocarb (Trumpet 80WP, NORAMCO, Wilmington, DE) was sprayed every two weeks to control western flower thrips and greenhouse whitefly, and Dienochlor (Pentac 50WP, Sandoz Agro Canada, Canada) was sprayed once to control the two-spotted mite.

The photosynthetic photon flux density (PPFD) was measured simultaneously within each treatment using quantum sensors LI-190SA (Li-Cor Inc., Lincoln, NE), one block per day. Air temperature was recorded at the same time, using sensors 1000-16 (Li-Cor Inc., Lincoln, NE). All sensors were connected to a DataLogger LI-1000 (Li-Cor Inc., Lincoln, NE). The average light intensity was recorded every minute of the day, whereas air temperature was recorded every minute for a 24-hr period to estimate day and night temperatures. The R:FR ratio was estimated once, in the full light treatment and below the shading cloth, using a SKR 110 660/730nm sensor (Skye Instruments LTD, UK). Greenhouse measurements showed that for both instantaneous and integrated light intensities, the partial shade treatment and the full shade treatment represented respectively about 15% and 2.5% of the full light treatment (Tab. 1). The R:FR ratio was similar with or without the shading cloth, averaging 2.25, which was quite high, possibly because the glass covering of the greenhouse removed part of the FR wavelength. Normally, the R:FR ratio diminishes with increasing shade, from the canopy to the understory (Chazdon et al. 1996). The shade cloth we used did not modify this ratio. Consequently, the two shade treatments reproduced a decrease in the light intensity, but did not take into account the decrease of R:FR occurring in natural shade. The air temperature was similar among light treatments, being about 3.5 °C cooler at night.

Finally, the average daily integrated PPFD was also measured on the site of a screening trial experiment conducted in the Ecuadorian Amazon to allow for a characterization of the light intensity of the region where the three studied species occur naturally. Mea-

**Table 1.** Means and standard deviation of the *PPFD* and air temperature of the light treatments in the greenhouse facilities (August and September 1994;  $n = 4$ ). Davidson, R., Mauffette, Y., Gagnon, D.

Light treatment	<i>PPFD</i>		Air temperature	
	Instantaneous ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Integrated ( $\text{mol m}^{-2} \text{d}^{-1}$ )	Day ( $^{\circ}\text{C}$ )	Night ( $^{\circ}\text{C}$ )
Full light (FL)	234.9 $\pm$ 135.6	12.0 $\pm$ 8.0	26.1 $\pm$ 2.9	22.7 $\pm$ 1.1
Partial shade (PS)	35.5 $\pm$ 16.3	1.7 $\pm$ 0.9	26.5 $\pm$ 3.2	22.7 $\pm$ 1.0
Full shade (FS)	5.7 $\pm$ 2.5	0.3 $\pm$ 0.1	26.0 $\pm$ 2.9	22.7 $\pm$ 1.1

measurements taken for 5 days in the open, on a 8 m tower, showed that the average daily integrated *PPFD* was  $24.7 \text{ mol m}^{-2} \text{ d}^{-1}$ , which was similar to measurements conducted in the clearing of a tropical rain forest site in Costa Rica (Chazdon & Fetcher 1984). Based on these data, the integrated *PPFD* of the greenhouse FL treatment was about half the values of these two open sites. It was similar to the average maximum integrated *PPFD* measured in a  $400 \text{ m}^2$  gap in the tropical rain forest of Costa Rica (Chazdon & Fetcher 1984), and to a  $100 \text{ m}^2$  gap of a Malaysian tropical forest (Raich 1989). The integrated *PPFD* of the PS treatment and of the FS treatment were respectively similar to the minimum integrated *PPFD* of a smaller gap of  $200 \text{ m}^2$  and to the average value of the understory of the tropical rain forest of Costa Rica (Chazdon & Fetcher 1984).

### Gas exchange measurements

Gas exchange measurements were made after completion of the experiment on the remaining seedlings after the destructive measurements completed at week 14. There were 3 plants per species per treatment remaining (except for *Platymiscium pinnatum* where this number was reduced to 2 specimens). An open gas exchange measurement system was used. It included in the absolute mode, a LI 6250  $\text{CO}_2$  gas analyzer (Licor Inc., Lincoln, NE), and in the differential mode, a LI-6262  $\text{CO}_2/\text{H}_2\text{O}$  gas analyzer and a dew point generator LI-610. For each plant, measurements were conducted on the first or second fully expanded leaf. Gas exchange measurements were first conducted in the dark to measure the respiration rate. Then, the light intensity was successively increased to: 150, 250, 500, 1000 and  $1500 \text{ mol m}^{-2} \text{ s}^{-1}$ . The light source, a slide projector lamp, was filtered with various neutral plexiglass filters to attain the desired intensity. For each level of light intensity, leaves were left to adjust until a stable photosynthetic rate was obtained, 5 to 20 minutes depending on species and light intensity. Then, an average value of seven measurements 10 s apart was used as the net photosynthetic rate. The cup

air temperature range varied from 17 to  $21^{\circ}\text{C}$ . Measurements were not done after mid-afternoon, because photosynthetic rates would begin to decrease due to decreasing natural light intensity.

### Growth measurements

Destructive measures were made at week 10 (September) and 14 (October) to allow for *RGR* calculations for that period, on a sampling of nine seedlings per light treatment each time (except for *Inga densiflora* under the FS treatment where this number was reduced to 4 specimens). Biomass allocation, root:shoot ratio and plant morphology were estimated only on the sampling made at week 14. Seedlings were divided into leaves (petioles were considered as stems parts), stems, and roots. Roots were washed to remove soil medium. Branches, when present, were numbered, and measured. All plant material was then dried at  $60^{\circ}\text{C}$  and weighed to measure biomass. The total leaf area was measured on the separated and dried leaves (dried flat in a plant press) using the MacFolia software (Régent Instruments Inc., Qué, Canada). Height and basal diameter of seedlings remaining after the destructive measures made at week 10, which totaled 12 seedlings per species per light treatment (except for *Inga densiflora* under the FS treatment where this number was reduced to 7 specimens), were measured on week 10 and again at week 14, to allow for *RGRH* and *RGRD* calculations for that period. At week 14 only, leaves present were numbered, and the total count of fallen leaves during the course of the experiment was made.

### Growth analysis

Relative growth rates were calculated for the total biomass between week 10 ( $t_1$ ) and week 14 ( $t_2$ ), using the formula from Hunt (1990):  $RGR = (\text{Ln } W_2 - \text{Ln } W_1) / (t_2 - t_1)$ , and was expressed in  $\text{g g}^{-1} \text{ wk}^{-1}$ . The formula was adapted to calculate a *RGR* for height (*RGRH*) expressed in  $\text{cm cm}^{-1} \text{ wk}^{-1}$  and for the basal diameter (*RGRD*) expressed in  $\text{mm mm}^{-1} \text{ wk}^{-1}$ . Final root:shoot ratio was calculated as  $RW_2 / (SW_2 + LW_2)$ ,

where  $RW$  = root weight,  $SW$  = stem weight and  $LW$  = leaf weight. The final leaf mass per area ( $LMA_2$ ) was calculated from  $LW_2 / LA_2$ , where  $LA$  = total leaf area. The final specific leaf area ( $SLA_2$ ) was calculated from  $LA_2 / LW_2$ . A final leaf turnover (%) was calculated from  $LFI / (LFI + LPS) \times 100$ , where  $LFI$  = total number of leaves fallen between week 1 and week 14, and  $LPS$  = total leaves present at week 14.

### Statistical analyses

Growth ( $RGRH$  and  $RGRD$ ), biomass allocation ( $LW$ ,  $SW$ ,  $RW$ ,  $W$ ,  $RGR$  and root:shoot), leaf turnover (leaves present, leaves fallen, turnover) and plant morphology (nb of branches, average branch length,  $LA$ ,  $SLA$  and  $LMA$ ) were analyzed using ANOVA, followed by a Tukey means comparison test. The full shade treatment was excluded from the analysis of variance for  $SLA$  and  $LMA$  because of too small sample size, due to some leafless *Pollalesta discolor* plants in the partial shade treatment. SAS software was used for all statistical analyses (SAS Institute 1997).

## Results

### Gas exchange measurements

*Pollalesta discolor* had the highest maximum photosynthetic assimilation rate under the full light (FL) treatment, and it reached saturation at a higher light intensity than both other species (Tab. 2). Under the partial shade (PS) treatment, trends were similar for the  $A_{mass}$ , although the saturation light intensity was lower. A comparison between the light treatments showed that the  $A_{area}$  of *Pollalesta discolor* was reduced by half in the PS treatment, but less so for the  $A_{mass}$ , and that the respiration rate was similar among the light treatments. *Inga densiflora* had  $A_{area}$  values

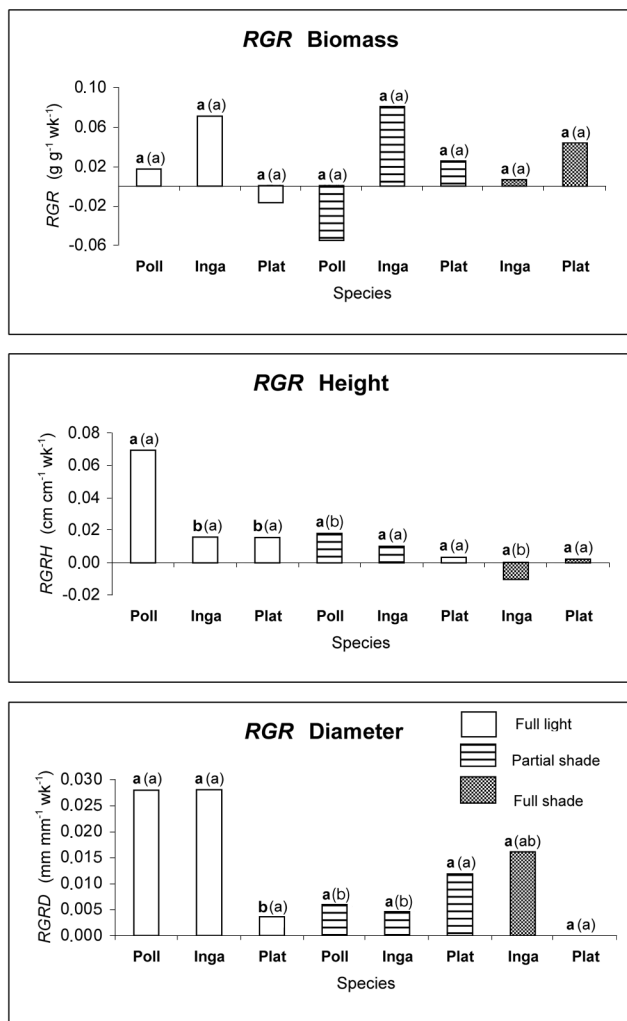
about twice as high as those of *Platymiscium pinnatum* under the FL and the PS treatment. The same trend occurred for  $A_{mass}$  values but only under the FL treatment. As for the light treatment effect, the highest values of  $A_{area}$  and  $A_{mass}$  for *Inga densiflora* were measured under the PS treatment. *Platymiscium pinnatum* had similar  $A_{area}$  and  $A_{mass}$  values across shade treatments, but a reduction was observed under the FL treatment. The saturation light intensity of *Inga densiflora* was the same across the light treatments, and was always superior to that of *Platymiscium pinnatum*, this species saturating at a relatively low light intensity. Both *Inga densiflora* and *Platymiscium pinnatum* had similar respiration rates within the same light treatment, and both exhibited higher values under the FL treatment than under the shade treatments.

### Height, basal diameter and survival

*Pollalesta discolor* obtained the best relative growth rate expressed in terms of height between week 10 and 14 ( $RGRH$ ) under the FL treatment, but failed to do so under the PS treatment (Fig. 1). The relative growth rate expressed in terms of basal diameter between week 10 and 14 ( $RGRD$ ) under the FL treatment was also high, although almost identical to that of *Inga densiflora*, but it was not different from the other two species under the PS treatment. Finally, *Pollalesta discolor* was strongly stimulated by an increased light intensity, as  $RGRH$  and  $RGRD$  were significantly higher under the FL treatment compared to the PS treatment. All specimens under the FS treatment died, whereas survival under the FL and the PS treatment was 100%. *Inga densiflora* and *Platymiscium pinnatum* had similar low  $RGRH$  values between week 10 and 14 under all light treatments. Under the FS treatment, *Inga densiflora* had a negative  $RGRH$  value. The  $RGRD$  of *Inga densiflora* between week 10 and

**Table 2.** Means and standard deviation of gas exchange measurements of seedlings of three tropical tree species under contrasting light intensities, after 14 weeks of growth. Davidson, R., Mauffette, Y., Gagnon, D.

Light Species	n	Maximum photosynthetic assimilation rate		Saturation light intensity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Dark respiration rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ )
		$A_{area}$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ )	$A_{mass}$ ( $\text{nmol CO}_2 \text{ g}^{-1} \text{s}^{-1}$ )		
<b>Full light</b>					
<i>Pollalesta discolor</i>	3	10.53 $\pm$ 2.78	303.6 $\pm$ 80.1	1000–1500	-0.40 $\pm$ 0.07
<i>Inga densiflora</i>	3	4.43 $\pm$ 1.94	62.1 $\pm$ 27.2	500–1000	-0.53 $\pm$ 0.06
<i>Platymiscium pinnatum</i>	3	1.88 $\pm$ 1.96	35.8 $\pm$ 37.3	150–500	-0.58 $\pm$ 0.11
<b>Partial shade</b>					
<i>Pollalesta discolor</i>	3	4.66 $\pm$ 0.71	212.0 $\pm$ 32.1	500–1000	-0.37 $\pm$ 0.06
<i>Inga densiflora</i>	3	7.10 $\pm$ 1.11	144.6 $\pm$ 22.7	500–1000	-0.35 $\pm$ 0.09
<i>Platymiscium pinnatum</i>	3	3.73 $\pm$ 1.36	130.5 $\pm$ 47.5	150–500	-0.27 $\pm$ 0.05
<b>Full shade</b>					
<i>Inga densiflora</i>	3	4.30 $\pm$ 1.65	88.8 $\pm$ 34.0	500–1000	-0.30 $\pm$ 0.14
<i>Platymiscium pinnatum</i>	2	3.55 $\pm$ 0.21	128.4 $\pm$ 15.1	150	-0.20 $\pm$ 0.00



**Figure 1.** Relative growth rates expressed in terms of total biomass, height and basal diameter between week 10 and 14, for seedlings of three tropical tree species under contrasting light intensities. Letters indicate significant differences from a Tukey grouping ( $p < 0.05$ ), bold letters are for comparisons between species within the same light treatment, and letters in parentheses are for comparisons between light treatments within the same species (Poll = *Pollalesta discolor*; Inga = *Inga densiflora*; Plat = *Platymiscium pinnatum*). Davidson, R., Mauffette, Y., Gagnon, D.

14 was high and superior to that of *Platymiscium pinnatum* under the FL treatment, and it was stimulated by an increased light intensity. The survival of *Inga densiflora* and *Platymiscium pinnatum* was 100% under all light treatments, except for *Inga densiflora* under the FS treatment where it was reduced to 54%.

### Biomass

*Pollalesta discolor* had the highest total biomass under the FL treatment after 14 weeks (Tab. 3). This was reflected in a larger leaf, stem and root biomass. Under

the PS treatment, its total biomass was significantly higher than that of *Platymiscium pinnatum* and its stem biomass was again the highest. The RGR between week 10 and 14 (Fig. 1) and the root:shoot ratio (Tab. 3) were not statistically different among species within the same light treatment. Still, the RGR of *Pollalesta discolor* was negative under the PS treatment and positive under the FL treatment. Finally, a decreased light intensity reduced the total biomass of that species, as well as that of its separate structures. For all light treatments, *Inga densiflora* tended to have a higher total biomass than that of *Platymiscium pinnatum* after 14 weeks. An increased light intensity tended to stimulate the total biomass and the RGR of *Inga densiflora* and this trend was significant for the total biomass of *Platymiscium pinnatum*. Conversely, both species had a lower root:shoot ratio under the PS treatment, as compared to the FL treatment, but only for *Platymiscium pinnatum* was this statistically significant.

### Leaf turnover

*Pollalesta discolor* had a higher leaf turnover after 14 weeks than the other two species under both the FL and PS treatments, as well as more leaves present at week 14 and a much higher number of total leaves fallen between week 1 and 14 (Tab. 4). *Inga densiflora* and *Platymiscium pinnatum* had similar leaf turnover patterns under the FS and the PS treatments. They had few leaves present and lost almost nothing during 14 weeks, resulting in a low leaf turnover. However, the FL treatment increased the leaf turnover of both species.

### Plant morphology

*Pollalesta discolor* tended to produce more branches, which were longer than those of *Inga densiflora* and *Platymiscium pinnatum* under the FL and the PS treatment (Tab. 5). Within each light treatment, both *Inga densiflora* and *Platymiscium pinnatum* had few branches, which were characterized by a short length. However, *Platymiscium pinnatum* did increase its branching habit under the full light treatment compared to the shade treatments, whereas the branching habit of *Inga densiflora* was rather insensitive to the light treatments. *Pollalesta discolor* had the largest total leaf area under both the FL and the PS treatments, and its leaves were also the largest and the thinnest ones among the three species. An increased light intensity tended to stimulate its total leaf area and did favor the production of smaller and thicker leaves. *Inga densiflora* had a somewhat larger total leaf area than that of *Platymiscium pinnatum*, but

**Table 3.** Biomass and root:shoot ratio after 14 weeks of growth of seedlings of three tropical tree species under contrasting light intensities. Davidson, R., Mauffette, Y., Gagnon, D.

Light Species	n	LW (g)	SW (g)	RW (g)	W (g)	Root:shoot
<b>Full light</b>						
<i>P. discolor</i>	9	8.34 ± 2.03 <b>a</b> (a)	12.79 ± 1.76 <b>a</b> (a)	10.22 ± 2.64 <b>a</b> (a)	31.34 ± 4.70 <b>a</b> (a)	0.50 ± 0.14 <b>a</b> (a)
<i>I. densiflora</i>	9	4.81 ± 1.99 <b>a</b> (a)	2.08 ± 0.54 <b>b</b> (a)	2.93 ± 0.44 <b>b</b> (a)	9.83 ± 2.65 <b>b</b> (a)	0.46 ± 0.08 <b>a</b> (a)
<i>P. pinnatum</i>	9	0.82 ± 0.08 <b>b</b> (a)	0.84 ± 0.30 <b>b</b> (a)	0.75 ± 0.25 <b>b</b> (a)	2.41 ± 0.61 <b>b</b> (a)	0.44 ± 0.07 <b>a</b> (a)
<b>Partial shade</b>						
<i>P. discolor</i>	9	3.64 ± 2.10 <b>a</b> (a)	2.90 ± 0.99 <b>a</b> (b)	1.74 ± 0.57 <b>a</b> (b)	8.28 ± 3.40 <b>a</b> (b)	0.34 ± 0.07 <b>a</b> (a)
<i>I. densiflora</i>	9	3.63 ± 0.76 <b>a</b> (a)	1.02 ± 0.24 <b>b</b> (ab)	1.31 ± 0.26 <b>a</b> (b)	5.96 ± 1.21 <b>ab</b> (a)	0.29 ± 0.01 <b>a</b> (a)
<i>P. pinnatum</i>	9	0.84 ± 0.13 <b>a</b> (a)	0.34 ± 0.09 <b>b</b> (b)	0.29 ± 0.06 <b>b</b> (b)	1.47 ± 0.27 <b>b</b> (b)	0.25 ± 0.02 <b>a</b> (b)
<b>Full shade</b>						
<i>I. densiflora</i>	4	1.73 ± 0.18 <b>a</b> (a)	0.52 ± 0.03 <b>a</b> (b)	0.70 ± 0.00 <b>a</b> (b)	2.94 ± 0.21 <b>a</b> (a)	0.32 ± 0.04 <b>a</b> (a)
<i>P. pinnatum</i>	9	0.38 ± 0.04 <b>a</b> (b)	0.16 ± 0.03 <b>a</b> (b)	0.12 ± 0.02 <b>b</b> (b)	0.66 ± 0.09 <b>a</b> (b)	0.23 ± 0.03 <b>a</b> (b)

Letters indicate significant differences from a Tukey grouping ( $p < 0.05$ ), bold letters are for comparisons between species within the same light treatment, and letters in parentheses are for comparisons between light treatments within the same species.

Biomass: LW = Leaf weight, SW = Stem weight, RW = Root weight, W = Total biomass, root:shoot ratio = RW / (LW + SW). All specimens of *Pollalesta discolor* died under the full shade treatment.

**Table 4.** Leaf turnover of seedlings of three tropical tree species under contrasting light intensities, after 14 weeks of growth. Davidson, R., Mauffette, Y., Gagnon, D.

Light Species	n	Leaves present <sup>(1)</sup> nb	Leaves fallen <sup>(2)</sup> nb	Turnover <sup>(3)</sup> (%)
<b>Full light</b>				
<i>P. discolor</i>	12	52.8 ± 23.4 <b>a</b> (a)	88.8 ± 61.0 <b>a</b> (a)	59.6 ± 16.3 <b>a</b> (a)
<i>I. densiflora</i>	12	11.1 ± 4.4 <b>b</b> (a)	1.8 ± 1.9 <b>b</b> (a)	15.0 ± 15.0 <b>c</b> (a)
<i>P. pinnatum</i>	12	8.3 ± 1.9 <b>b</b> (a)	4.9 ± 2.3 <b>b</b> (a)	36.6 ± 12.7 <b>b</b> (a)
<b>Partial shade</b>				
<i>P. discolor</i>	12	28.7 ± 17.9 <b>a</b> (a)	34.9 ± 17.0 <b>a</b> (a)	56.2 ± 22.9 <b>a</b> (a)
<i>I. densiflora</i>	12	10.3 ± 3.8 <b>b</b> (a)	0.1 ± 0.3 <b>b</b> (b)	0.6 ± 1.9 <b>b</b> (b)
<i>P. pinnatum</i>	12	7.3 ± 1.3 <b>b</b> (a)	0.0 ± 0.0 <b>b</b> (b)	0.0 ± 0.0 <b>b</b> (b)
<b>Full shade</b>				
<i>I. densiflora</i>	7	7.1 ± 2.3 <b>a</b> (a)	0.4 ± 0.5 <b>a</b> (b)	4.7 ± 6.1 <b>a</b> (b)
<i>P. pinnatum</i>	12	4.6 ± 0.8 <b>a</b> (b)	0.1 ± 0.3 <b>a</b> (b)	2.1 ± 7.2 <b>a</b> (b)

Letters indicate significant differences from a Tukey grouping ( $p < 0.05$ ), bold letters are for comparisons between species within the same light treatment, and letters in parentheses are for comparisons between light treatments within the same species.

All specimens of *Pollalesta discolor* died under the full shade treatment.

<sup>(1)</sup> Leaves present at week 14 ; <sup>(2)</sup> Total leaves fallen between week 1 and 14 ; <sup>(3)</sup> Leaves fallen / (leaves fallen + leaves present) × 100

**Table 5.** Plant morphology after 14 weeks of growth, for seedlings of three tropical tree species under contrasting light intensities. Davidson, R., Mauffette, Y., Gagnon, D.

Light Species	n	Branching characteristics		Leaf characteristics		
		Nb	Av. length (cm)	LA (m <sup>2</sup> )	SLA (m <sup>2</sup> g <sup>-1</sup> )	LMA (g m <sup>-2</sup> )
<b>Full light</b>						
<i>P. discolor</i>	9	8.4 ± 3.4 <b>a</b> (a)	17.9 ± 3.7 <b>a</b> (a)	0.259 ± 0.164 <b>a</b> (a)	0.030 ± 0.006 <b>a</b> (b)	34.70 ± 7.33 <b>c</b> (a)
<i>I. densiflora</i>	9	2.2 ± 0.8 <b>a</b> (a)	5.9 ± 0.5 <b>b</b> (a)	0.071 ± 0.044 <b>b</b> (a)	0.014 ± 0.002 <b>b</b> (b)	71.38 ± 8.99 <b>a</b> (a)
<i>P. pinnatum</i>	9	3.1 ± 0.8 <b>a</b> (a)	7.6 ± 3.5 <b>b</b> (a)	0.016 ± 0.005 <b>b</b> (b)	0.020 ± 0.004 <b>b</b> (b)	52.63 ± 10.92 <b>b</b> (a)
<b>Partial shade</b>						
<i>P. discolor</i>	9	3.7 ± 1.8 <b>a</b> (a)	13.0 ± 2.1 <b>a</b> (a)	0.184 ± 0.142 <b>a</b> (a)	0.046 ± 0.005 <b>a</b> (a)	21.96 ± 2.43 <b>c</b> (b)
<i>I. densiflora</i>	9	1.4 ± 1.3 <b>a</b> (a)	4.4 ± 3.2 <b>b</b> (a)	0.074 ± 0.020 <b>b</b> (a)	0.021 ± 0.002 <b>c</b> (a)	49.05 ± 5.62 <b>a</b> (b)
<i>P. pinnatum</i>	9	0.7 ± 0.7 <b>a</b> (b)	1.1 ± 1.0 <b>b</b> (b)	0.029 ± 0.007 <b>b</b> (a)	0.035 ± 0.002 <b>b</b> (a)	28.59 ± 1.83 <b>b</b> (b)
<b>Full shade</b>						
<i>I. densiflora</i>	4	1.8 ± 0.2 <b>a</b> (a)	6.2 ± 3.3 <b>a</b> (a)	0.034 ± 0.008 <b>a</b> (a)	0.021 ± 0.002	48.44 ± 3.56
<i>P. pinnatum</i>	9	0.2 ± 0.4 <b>a</b> (b)	0.5 ± 0.9 <b>a</b> (b)	0.014 ± 0.003 <b>b</b> (b)	0.037 ± 0.004	27.59 ± 2.54

Letters indicate significant differences from a Tukey grouping ( $p < 0.05$ ), bold letters are for comparisons between species within the same light treatment, and letters in parentheses are for comparisons between light treatments within the same species.

All specimens of *Pollalesta discolor* died under the full shade treatment.

The full shade treatment has been excluded from the Tukey means comparison test for SLA and LMA due to some leafless specimens.

only under the FS treatment was this statistically significant. Its leaves were the thickest among the three species. The total leaf area of *Inga densiflora* was stimulated by an increased light intensity, whereas that of *Platymiscium pinnatum* was superior under the PS treatment only. Both *Inga densiflora* and *Platymiscium pinnatum* produced larger and thinner leaves under the two shade treatments, compared to the FL treatment.

## Discussion

### *Pollalesta discolor*

Photosynthetic performance of *Pollalesta discolor* seedlings was highest under the full light treatment, whilst its impairment under the shade treatments was indicative of shade intolerance. The high value of the maximum photosynthetic rate attained by *Pollalesta discolor* on an area basis ( $A_{area}$ ) is typical of pioneer species (Strauss-DeBenedetti & Bazzaz 1996). When the average value was expressed on a mass basis ( $A_{mass}$ ), it was still high due to a high *SLA*. An  $A_{mass}$  value above  $300 \text{ nmol g}^{-1} \text{ s}^{-1}$  has been shown to be characteristic of species with short leaf life-span (Reich et al. 1992), this trait being linked to an early-successional status (Ackerly 1996). The high light saturation intensity of that species is indicative of its light requirements. Oberbauer & Strain (1984) have shown that species found in clearings saturated at a light intensity above  $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . A two-fold decrease in  $A_{area}$  was measured under the PS treatment. Although this trend has been explained by a high level of physiological plasticity for early-successional species (Bazzaz & Pickett 1980), it was not accompanied by a significant decrease in dark respiration rates, suggesting that *Pollalesta discolor* could have problems maintaining a positive carbon balance in the shade, and argues for a limited physiological acclimation to lower light levels, in spite of some morphological change expressed by an increased *SLA*.

Growth performances of *Pollalesta discolor* under the FL treatment were superior from that of the other two species, in accordance to its high photosynthetic assimilation rates, and also pointed to its high-light requirements. This could be caused by the fact that *Pollalesta discolor* was brought from Ecuador as seedlings, whereas the other two species were brought as seeds. It is rather difficult to estimate if this fact influenced positively or negatively our results, because seedlings were also more likely to suffer from a transplantation shock. Moreover, seeds of the other two species, especially those of *Inga densiflora*, contained large reserves, which could have stimulated their growth at the start of the experiment. The higher

growth rate measured for *Pollalesta discolor* in a field experiment (Davidson et al. 1998) supports our contention that performance in the greenhouse is more likely to be related to this species' characteristics than to the type of plant material (seedling vs seed).

Relative growth rates expressed in terms of height (*RGRH*) and basal diameter (*RGRD*) between weeks 10 and 14 were a better parameter to characterize the vigorous growth of *Pollalesta discolor* than when expressed in terms of its biomass (*RGR*). This could be attributed to the high leaf turnover of *Pollalesta discolor*, which lowered the increase in biomass between weeks 10 and 14, mainly through a greater number of leaves fallen than number of leaves produced during this period. This underestimated the *RGR*, because fallen leaves had been produced but were excluded from *RGR* calculations. Comparisons of *RGR* between species were therefore difficult to make for all light treatments, as shown by the lack of statistically significant differences, as the three species had different leaf turnover rates within and across light treatments. Consequently, values of *RGR* for *Pollalesta discolor* under the FL treatment were much lower than what is commonly found in the literature for early-successional species (Oberbauer & Donnelly 1986, Ramos & Grace 1990, Kitajima 1996, Veenendaal et al. 1996).

The high final biomass of *Pollalesta discolor* under the FL treatment reflected its ability to develop in a high-light environment. When stem and leaf biomasses were expressed in percentage of the total biomass, this species showed a higher investment in its stem biomass and a lower allocation to its leaf biomass. The larger investment in stem biomass was reflected in a greater number of branches, which were also longer on average. This highly branched structure is assumed to be characteristic of gap and pioneer species (Bazzaz 1984), although some early-successional species have a sparse branch framework (Bazzaz & Pickett 1980). *Pollalesta discolor* has single leaves and depends on branch production for its leaf display. The lower investment in its leaf biomass simply reflected the fact that its leaves were thinner. The large number of leaves, which had a high *SLA*, totaled the largest total leaf area among the three species under the FL treatment. The investment in a large leaf area, which maximized light interception, was probably more relevant in terms of growth performance, than the percentage of biomass allocation to leaves. In other words, the leaf area, with its relationship to the *SLA*, seemed to be a better correlate of growth than the leaf biomass itself. The *SLA* of *Pollalesta discolor* was similar to that of an other early-successional species, *Cedrela odorata* (Ramos & Grace 1990), and to various early-successional species in a successional ranking experi-

ment by Oberbauer & Donnelly (1986). The *SLA* of early-successional species is assumed to be higher than that of late-successional species, a trait linked to their higher growth rates and shorter leaf life-span (Reich et al. 1992, 1994).

The *RGRH* and *RGRD* of *Pollalesta discolor* reflected the species' reaction to a shaded environment because these ratios expressed the growth in the last month of the experiment. The significantly lower values under the PS treatment, together with the lack of statistically significant differences between that species and *Inga densiflora* and *Platymiscium pinnatum*, were indicative of an impaired growth performance. It is possible that the higher R:FR than that occurring in natural shade prevented a stimulation of the stem growth of *Pollalesta discolor* under the PS treatment. A lower R:FR could have caused higher values than those of *Inga densiflora* and *Platymiscium pinnatum*. Although a modification of light spectral quality does not influence photosynthetic rates of tropical plants (Chazdon et al. 1996), it could have an effect on the morphology of light-demanding species grown in the shade (Kwesiga & Grace 1986), such as a shift in allocation to stem growth (Tinoco-Ojanguren & Pearcy 1995, Lee 1996). The much lower total biomass after 14 weeks of growth was also indicative of an impaired growth performance. Although the total biomass was still allocated in a relatively high stem biomass, which seems to be typical of this species, the shift toward a lower allocation to root and higher allocation to leaf was observed for all three species, which explains the lack of statistically significant differences for the root:shoot ratios. Finally, in spite of a lower number of leaves in the PS treatment compared to the FL treatment, *Pollalesta discolor* did not lower its leaf turnover, and still maintained the highest total leaf area.

*Pollalesta discolor* seedlings are clearly advantaged by a high-light environment and their light requirements could be inferred from the assumed early-successional status. Their performances were impaired by partial shade and it proved to be completely intolerant to the light conditions of a forest understory, as all specimens died under the FS treatment. Being shade-intolerant, it could not persist nor regenerate in the later stages of succession as shade increases. This species would thus be able to exploit an open environment both morphologically and physiologically, arguing for its use in deforested areas within the edaphic and climatic range where it grows naturally. In addition, the growth performance of the seedlings was indicative of their silvicultural potential, as this species was among the best in height and diameter growth in a field trial experiment carried out in the Ecuadorian Amazon (Davidson et al. 1998).

### *Inga densiflora*

The lower  $A_{rea}$  and  $A_{mass}$  under the FL treatment compared to the PS treatment are in the range of values reported for late-successional species (Strauss-DeBenedetti & Bazzaz 1996), which would indicate that the photosynthetic system of *Inga densiflora* was damaged, to a certain degree, when grown in full light. This reduced performance was probably related to species' characteristics linked to this growing stage, and do not represent a temporary shock similar to the sudden creation of a gap, since these plants were subjected to the high-light treatment from the start of the experiment. Indeed, we have previously observed leaf burns upon transplantation in open field conditions, as well as a delayed growth (Davidson et al. 1998).

But in spite of *SLA* and *RGR* values similar to that of late-successional species when compared with the literature (Oberbauer & Donnelly 1986, Ramos & Grace 1990, Kitajima 1996), an increased light intensity did stimulate the *RGR*, which was more than 10 times that of the FS treatment, indicating that *Inga densiflora* would tend to increase its biomass in both a gap environment and in an open site. The *RGR* should be a more accurate tool to characterize the growth of *Inga densiflora* than it was for *Pollalesta discolor*, because almost no loss in leaf biomass occurred between weeks 10 and 14. This fact did not reflect in its plant morphology though, which was characterized by a weak branching habit, probably because *Inga densiflora* has large compound leaves. *RGRD* values were also stimulated by an increase in light intensity, being almost the same as the shade-intolerant *Pollalesta discolor* under the FL treatment. Interestingly, diameter measurements would suggest a preference for a higher light environment, which could not be detected from height parameters alone. Indeed, the *RGRH* of *Inga densiflora* was not indicative of a clear preference for a high-light environment. This parameter was relatively insensitive to an increase in light intensity and was not significantly different from the more shade-tolerant *Platymiscium pinnatum*. Its value was inferior to that of the late-successional species *Brosimum alicastrum*, achieved under both the sun and the shade treatments of a light contrasting experiment (Ramos & Grace 1990). Thus, this species seems to invest more into its diameter. Different species can have different growth strategies, and using only one growth indicator could lead to a misinterpretation of the growth potential. Dawkins (1963) suggested that diameter increment was related to the crown diameter, after a study on allometry of forestry plantation species. Indeed, in the field, *Inga densiflora* develops a wide crown relative to its height. (R. Davidson, pers. obs.). Growth performances in this open environment showed that they

began to accelerate after 1.0 yr, becoming similar to other studied early-successional species, although not as high as *Pollalesta discolor*, which suggests that morphological and physiological acclimation could occur across ontogenetic stages (Strauss-Debenedetti & Bazzaz 1996).

A negative *RGRH* for *Inga densiflora* seedlings subjected to the FS treatment, related to some dying back of the apical shoot, a strong reduction of  $A_{area}$  and  $A_{mass}$  values combined with a limited reduction of their dark respiration rates, and the fact that they did not increase their *SLA* beyond what was achieved in the PS treatment, points towards a lack of adaptation to the light environment of a forest understory, which was suspected from the death of almost half of the seedlings in these conditions.

Thus, on the whole, light requirements deduced from photosynthesis and growth performances of seedlings of *Inga densiflora* could not be inferred easily from its assumed early-successional status. This species seems to perform better under the medium light environment, both morphologically and physiologically, at least at this stage. The better photosynthetic performance in the PS treatment, which was accompanied by a significant decrease of the dark respiration rate, points toward a requirement for some shade during the seedling stage, and would suggest that it can maintain a positive carbon gain under conditions similar to a gap environment. Although birds and mammals (Janzen 1983) could disperse seeds of *Inga* species, they may also germinate on the ground, under the shade of the parent tree, which could explain why this species might have the capacity to tolerate shade. These facts suggest that seedlings of *Inga densiflora* should be protected from high-light conditions, whether through growing them in a semi-shaded nursery for up to a year, or through integrating them in a more complex plantation model which could provide some shade during its initial growing stage.

### **Platymiscium pinnatum**

*Platymiscium pinnatum* definitely displayed characteristics of a shade-tolerant species, performing similarly in both shade treatments, whether morphologically or physiologically. This species was able to maintain similar  $A_{area}$  and  $A_{mass}$  in PS and FS treatments. This was linked to a strong increase of its *SLA* and to a physiological acclimation achieved through a significant reduction of its dark respiration rates. A large reduction of the dark respiration rate of seedlings of a shade-tolerant tree species was also observed when grown in the understory (García-Núñez et al. 1995). Growth performances of *Platymiscium pinnatum* were relatively modest and most parameters also pointed to a

tolerance to a shade environment, indicative of a later-successional stage (Augsburger 1984). This species clearly displayed morphological plasticity enabling it to adapt to a shaded environment. The *RGRH* was inferior to that of a late-successional species in an experiment by Ramos & Grace (1990). Shade tolerance, which was also inferred from its high survival under the FS treatment, could be related to the maintenance of positive *RGRH* and *RGR* under the FS treatment, and to a very low leaf turnover (Coley 1988) under the two shaded environments. Kitajima (1996) suggested that shade-tolerant species should have greater allocation to defense in a low-light environment, at the expense of their inherent growth rates. Indeed, *Platymiscium pinnatum* was characterized by a low *RGR* under both shade treatments. It was also the only species in this experiment to significantly lower its root:shoot ratio under both shaded environments. This was due to a shift toward a proportionally higher allocation to leaf biomass, and a reduction of biomass allocation to roots and shoots. An increased allocation to leaf biomass as a consequence of shading, which was paralleled by an increased *SLA*, is an indication of a species' capacity to increase its photosynthetic versus non-photosynthetic tissue (Björkman 1981).

The lower photosynthetic rates measured under the FL treatment would argue for some damage of the photosynthetic system in this light environment. Indeed, the specimens used for gas exchange measurements all showed leaf chlorosis. The strong standard deviations measured on both  $A_{area}$  and  $A_{mass}$  under the FL treatment would suggest that plants were not equally impaired, in spite of visual symptoms, and that acclimation to a higher light regime may eventually be possible for this species. In fact, seedlings of *Platymiscium pinnatum* were sensitive to an increased light intensity, which stimulated, although modestly, the total biomass after 14 weeks, as well as favored a more branched structure. This implies that they would benefit from a gap opening, as suggested for primary species in a gap-phase regeneration study by Brokaw (1985). The consequence of an increased light intensity seemed to be an investment in a high *RGRH*, rather than in a high *RGRD*, suggesting that forest seedlings would maximize their growth in stem height towards light, at the expense of stem diameter increments. The stimulated branching pattern could be advantageous for light foraging in a gap opening. Results from an experimental plantation established in the Ecuadorian Amazon showed that this species, which was growing in an open field, began to accelerate its growth after 1.0 yr., similarly to *Inga densiflora*, and that its growth performances were the best among the late-successional species tested, although high variability was observed (Davidson et al. 1998). The fact that the

leaf turnover was faster under the FL treatment is probably not that conclusive since species from different successional status also experienced an increased leaf turnover with an increased light intensity (Bongers & Popma 1990). Thus, valuable information on the light requirements of *Platymiscium pinnatum* was gained from this experiment that was not associated to the late-successional status of this species.

However, at the seedling stage, this species would be better adapted to a silvicultural model able to provide some shade. The results of this study suggest that it could be used for forest enrichment, through planting in the light environment of a small gap. It could also be integrated in a multi-species plantation, under the shade of early-successional species during the earlier stage of its development.

## Conclusion

As a common generalization, early- and late-successional species are respectively described as being shade intolerant and shade tolerant, both traits linked to the environment where they typically establish themselves. This experiment showed that light requirements of their seedling phase cannot be inferred so easily for species for which the successional status is already thought to be known, and that it can sometimes differ from their later requirements as young trees, as shown when comparisons are made with field growth measurements of the same species (Davidson et al. 1998). Thus, a careful characterization of growth and photosynthetic performances in contrasting light environments appear to provide important information on light requirements for the studied species during their seedling stage, providing an opportunity to choose an optimal light environment for their establishment in the nursery, in plantation models or for forest enrichment.

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## References

- Ackerly DD (1996) Canopy structure and dynamics: integration of growth processes in tropical pioneer trees. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman and Hall, New York, pp 619–658.
- Augspurger CK (1984) Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72: 777–795.
- Bazzaz FA (1984) Dynamics of wet tropical forests and their species strategies. In: Medina E, Mooney HA, Vazquez-Yanes C (eds) Physiological ecology of plants of the wet tropics. Dr W Junk Publishers, The Hague, pp 233–243.
- Bazzaz FA, Pickett STA (1980) Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* 11: 287–310.
- Björkman O (1981) Responses to different quantum flux densities. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology, New series vol. 12A, Physiological plant ecology I. Springer-Verlag, New York, pp 57–107.
- Bongers F, Popma J (1990) Leaf dynamics of seedlings of rain forest species in relation to canopy gaps. *Oecologia* 82: 122–127.
- Brokaw NVL (1985) Gap-phase regeneration in a tropical forest. *Ecology* 66: 682–687.
- Chazdon RL, Fetcher N (1984) Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72: 553–564.
- Chazdon RL, Pearcy RW, Lee DW, Fetcher N (1996) Photosynthetic responses of tropical forest plants to contrasting light environments. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman and Hall, New York, pp 5–55.
- Coley PD (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74: 531–536.
- Davidson R, Gagnon D, Mauffette Y, Hernandez H (1998) Early survival, growth and foliar nutrients in native Ecuadorian trees planted on degraded volcanic soil. *Forest Ecology and Management* 105: 1–19.
- Dawkins HC (1963) Crown diameters, their relation to bole diameter in tropical forest trees. *Commonwealth Forestry Review* 42: 318–337.
- FAO (1993) Forest resources assessment 1990. Tropical countries. Publications Division, FAO, FAO Forestry Paper 112, Rome.
- García-Núñez C, Azócar A, Rada F (1995) Photosynthetic acclimation to light in juveniles of two cloud forest tree species. *Trees* 10: 114–124.
- Janzen DH (ed) (1983) Costa Rican natural history. The University of Chicago Press, Chicago.
- Hunt R (1990) Basic growth analysis. Unwin Hyman Ltd, London.
- Kitajima K (1996) Ecophysiology of tropical tree seedlings. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman and Hall, New York, pp 559–596.

- Kwesiga F, Grace J (1986) The role of the red/far-red ratio in the response of tropical tree seedlings to shade. *Annals of Botany* 57: 283–290.
- Lee DW (1996) Irradiance and spectral quality affect Asian tropical rain forest tree seedling development. *Ecology* 77: 568–580.
- Oberbauer SF, Donnelly MA (1986) Growth analysis and successional status of Costa Rican rain forest trees. *The New Phytologist* 104: 517–521.
- Oberbauer SF, Strain BR (1984) Photosynthesis and successional status of Costa Rican rain forest trees. *Photosynthesis Research* 5: 227–232.
- Raich JW (1989) Seasonal and spatial variation in the light environment in a tropical Dipterocarp forest and gaps. *Biotropica* 21: 299–302.
- Ramos J, Grace J (1990) The effects of shade on the gas exchange of seedlings of four tropical trees from Mexico. *Functional Ecology* 4: 667–677.
- Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* 62: 365–392.
- Reich PB, Walters MB, Ellsworth DS, Uhl C (1994) Photosynthesis-nitrogen relations in Amazonian tree species. 1. Patterns among species and communities. *Oecologia* 97: 62–72.
- SAS Institute (1997) SAS/STAT user's guide, Release 6.11, Edition SAS Inst., Cary.
- Sawyer J (1993) Plantations in the tropics: environmental concerns. IUCN, Gland and Cambridge.
- Strauss-Debenedetti S, Bazzaz FA (1996) Photosynthetic characteristics of tropical trees along successional gradients. In: Mulkey SS, Chazdon RL, Smith AP (eds) *Tropical forest plant ecophysiology*. Chapman and Hall, New York, pp 162–186.
- Tinoco-Ojanguren C, Pearcy RW (1995) A comparison of light quality and quantity effects on the growth and steady-state and dynamic photosynthetic characteristics of three tropical tree species. *Functional Ecology* 9: 222–230.
- Valencia R, Balslev H, Paz y Miño G (1994) High tree alpha-diversity in Amazonian Ecuador. *Biodiversity and Conservation* 3: 21–28.
- Veenendaal EM, Swaine MD, Lecha RT, Walsh MF, Abbrese IK, Owusu-Afriyie K (1996) Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology* 10: 501–511.