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ORIGINAL ARTICLE - Silviculture

Quality of *Lecythis tuyrana* Pittier Seedlings Using Controlled-Release Fertilizer, Volumes of Container and Light Acclimatation

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Abstract

Lecythis tuyrana is an endemic tree in the Magdalena River basin in Colombia with unexplored forestry, nutraceutical, medicinal and nutritional potential. In the nursery, two experiments on the production of *L. tuyrana* seedling were evaluated. In the first experiment, three container volumes and the absence or presence (3 g L^{-1}) of a controlled-release fertilizer (CRF) were evaluated. The use of tube trays (700 cm^3) and CRF significantly increased the height, biomass, and Dickson quality index of the seedlings (between 28 to 61 %) compared to those not fertilized. In the second experiment the light acclimation of seedlings was evaluated in two environments: full sun at 50% and 100%. There were no changes in photosynthetic rates when the seedlings were kept in the shade for longer, but there was a lesser accumulation of biomass. A light intensity of approximately 1 600 µmol m^{-2} s^{-1} is considered optimal for *L. tuyrana* seedling.

Keywords: Monkey pot, forest nursery, photosynthesis, Lecythidaceae, reforestation.

1. INTRODUCTION AND OBJECTIVES

Among the vast biodiversity of flora and fauna in the Magdalena Medio valley (Andean region), which includes the lowlands (40 to 200 m altitude) between the Central and Eastern Mountain ranges of the Magdalena River (Restrepo & Escobar, 2018), is the forest species *Lecythis tuyrana* Pittier (fam. Lecythidaceae). The seeds extracted from the fruit are used as antidiarrheal medicine by the Guna indigenous people (Panama and Colombia), and the oil has interesting nutraceutical properties that could be used as an ingredient for conventional frying, vacuum frying, and baking processes (Alzate et al. 2018). Although the international conservation status is Least Concern, the species is in the Vulnerable category in Colombia, which is why its use is restricted or banned in some municipalities of department Antioquia and Santander (Celis, 2015; CORNARE, 2020; López-Gallego & Morales, 2022).

Commercial programs of reforestation and recovery of degraded areas with native forest species, such as the Magdalena River basin, whose forest cover estimated at 66 % in 1980 barely decreased by 13 % by 2010 (Restrepo & Escobar, 2018), demand a constant supply of seedlings. Among the factors that affect the quality of the seedlings produced in the nursery, the container volume or size and the application of fertilizers to the substrate are the most relevant (Mendoça et al., 2020; Santos et al., 2020). Compared with conventional fertilizers, controlled-release fertilizers (CRF) continuously provide nutrients to seedlings for a prolonged period, reducing their loss due to volatilization and leaching (Cunha et al., 2021). Even though it is a more environmentally friendly technology and has proven effective in several forest species (Dias et al., 2018; Cunha et al., 2021), the marketing values continue to be high and exhibit low efficiency in releasing nutrients (Vejan et al., 2021). The ideal dose of CRF is related to the type of container and, from a commercial perspective, its volume is to be reduced without limiting the root and aerial morphological quality of the seedlings produced (Chu et al., 2020).

Another essential factor in the production of seedlings is the environment, that is, the light supply. The intensity, duration, and interval of sunlight on seedlings directly

influence photosynthesis and, therefore, the production of photoassimilates that can generate biomass accumulation in their organs (Coopman et al., 2008). A strategy to improve the quality indices and acclimation of seedlings is the prior combination of exposure periods in the shaded nursery and full sun, thus increasing their chances of successful establishment in the field (Marana et al., 2015). This early induction or hardening of seedlings under contrasting light and temperature conditions may cause morphological, physiological, and anatomical changes (Coopman et al., 2008).

Due to the absence of a basic protocol for producing *L. tuyrana* seedlings and its potential as a native forest species to generate income for the local producer, this study evaluated 1) the presence of CRF in different container volumes and 2) acclimation periods in full sun on the morphological quality parameters.

2. MATERIALS AND METHODS

2.1. Seedling production

This study included two independent experiments conducted in the municipality of Rionegro, Santander, Colombia (7°22'10"N, 73°10'39"W; 550 m of altitude). Initially, the ripe fruit from trees in the municipalities of Cimitarra and Puerto Parra, Santander, a Magdalena Medio valley subregion, were collected in October and December 2021 to produce *L. tuyrana* seedlings. The species was identified and an exsiccate was deposited in the Herbarium at Universidad Industrial de Santander under identification number 22225. According to the Köeppen classification, the two municipalities involved had a tropical rainforest climate (Af) similar to that of Rionegro, with historical averages (1991-2020) of 27.5 °C and 2 822 mm year^{-1} with a bimodal rainfall regime. The two rainy periods of the year occur from March to April and September to November (IDEAM, 2022).

After manually extracting the seeds from the fruit, they were sown individually in 700 cm^3 plastic trays containing river sand arranged in a nursery with anti-thermal low-density polyethylene film (LDPE) and photoselective to U.V radiation at 50% shading, and automated micro-sprinkler irrigation. After 50 days of sowing (DAS), the seedlings were transplanted to the respective container for the experiment. A formulation of the local substrate was used to produce seedlings, made up of the proportion (v/v) of 60 % soil collected at 0-30 cm depth in a forest reserve adjacent to the experimental area: 20 % commercial vermicompost and 20 % river sand. The soil and sand were previously sifted through a sieve mesh of 5 mm. This substrate formulation is the most common in local nurseries. A substrate sample was sent to the laboratory to classify physical and chemical properties according to the Colombian Technical Standard NTC 5167 (ICONTEC, 2011). The apparent density was determined following the Brazil methodology (2007) (Table 1).

Table 1. Physical and chemical properties of the substrate prepared in the two experiments before adding controlled-release fertilizer Basacote ® Plus 6M.

pH	E.C[1]	N	P	K	C[2]	CEC[3]	Bd[4]	WHC[5]
	dS m^{-1}			%		cmol$_c$ kg^{-1}	g cm^{-3}	%
7.4	1.1	0.18	0.21	0.09	0.82	7.61	1.39	41.3

[1] electrical conductivity (E.C), [2] carbon (C), [3] cation exchange capacity (CEC), [3] bulk density (Bd) and water holding capacity (WHC).

2.2. Experiment 1: controlled-release fertilizer x volume container

A randomized complete block experimental design was adopted with four repetitions in a 3 x 2 factorial arrangement and an experimental unit of eight seedlings. In factor A, three container volumes were evaluated: tube trays with 24 conical cavities of 700 cm^3 (8 cm largest diameter x 1.8 cm smallest diameter x 25 cm height), with the occupation reduced to 50 % after two months of transplantation; a small bag of 1 250 cm^3 (10 cm diameter x 27 cm height), the size of container most used locally with other forest species, and a big bag of 2 300 cm^3 (10 cm diameter x 41 cm height). In factor B, the presence of CRF Basacote® Plus 6M was evaluated: absence and presence with a dose of 3 g L^{-1} substrate. For better homogenization, 180 g of CRF was added for every 60 liters of substrate until the required quantity was finished. According to the manufacturer, the CRF has a formulation of 16 % N, 8 % P_2O_5, 12 % K_2O, 2 % MgO, 5 % S, 0.2 % B, 0.05 % Cu, 0.4 % Fe, 0.06 % Mn, 0.015 % Mo, and 0.02 % Zn, with a granule size from 2.5 to 3.5 mm and a release time of nutrients of five to six

months, after application at a constant 21 °C. Production of seedlings was in a nursery with black monofilament screens and mesh to offer 50% shading, and daily irrigation by automated micro-sprinkler twice a day, comprising a water blade of 10 mm day^{-1}.

2.3. Experiment 2: light acclimatation

Three light acclimation treatments (light hardening) combining exposure to two light environments were implemented until the seedling reached a production cycle of 180 DAS. The light environments were 1) full sun at 50% shade and daily irrigation by automated micro-sprinkler (as Experiment 1) and 2) full sun at 100% (not shaded) with manual watering every other day twice a day, except on rainy days. In the three light acclimation treatments (H1, H2 and H3), initially, the seedlings were produced in a full sun at 50% environment and later transferred to full sun at 100% environment (Table 2). A randomized complete block experimental design was adopted with three repetitions and an experimental unit of ten seedlings.

The seedlings were produced in bags (1 250 cm^3), substrate (3:1:1/v:v:v) and dose (3 g L^{-1} substrate) of CRF Basacote ® Plus 6M as Experiment 1.

Table 2. Exposure time (days) within different light environments where the *Lecythis tuyrana* seedlings remained according to the light hardening treatments.

Hardening	full sun at 50%		full sun at 100%	total cycle
	days	height (cm)*	days	
H1	65	22.5 ± 0.5	115	180
H2	105	35.1 ± 0.7	75	180
H3	145	38.5 ± 1.3	35	180

*Values (mean ± standard error) of the height of the *Lecythis tuyrana* seedling upon leaving the full sun at 50 % environment.

2.4. Morphological and physiological variables

At 180 DAS the following morphological variables were determined: stem diameter (SD) measured at the epicotyl scar with a digital caliper (0.1 mm), seedling height (H) measured from the level of the substrate to the apical bud with a metric tape (0.1 cm), and robustness index (RI) calculated as the H/SD ratio. As destructive variables, the shoot dry mass (SDM) and root dry mass (RDM) were calculated by drying the plant material in an oven at 65 °C up to constant weight. With these values, the SDM/RDM ratio and the Dickson quality index (DQI) were determined (Dickson, Leaf, & Hosner, 1960) according to Equation 1:

$$DQI = (SDM + RDM) / ((H / SD) + (SDM / RDM)) \quad (1)$$

Where height (H [cm]), stem diameter (SD [mm]), shoot dry mass (SDM [g]) and root dry mass (RDM [g]).}

In Experiment 2, the physiological variables were determined with a portable Infrared Gas Analyzer - IRGA (Licor 6800). The measurements were made in three periods: 95, 130, and 180 DAS on the third expanded leaf, counting from the last leaf inserted at the apex, between 8:00 and 13:00 on a sunny day, on six randomly selected seedlings for each treatment and period. In the first measurement, at 95 DAS, six seedlings were taken randomly from both treatments considering that H2 and H3 remained in full sun at 50 %. For light photosynthetic response curves (A-PPFD), CO_2 partial pressure and temperature inside the leaf chamber were maintained at 40 Pa and 28 °C, respectively, and PPFD was changed from 2 000 to 0 μmol m^{-2} s^{-1} according to Calzadilla et al. (2022). The A-PPFD fitting model was performed using a non-rectangular hyperbola according to Lieth and Reynolds (1987). Additionally, the photosynthetic quantum efficiency (LUE), maximum light-limited net photosynthesis (Pnmax), dark respiration rate (Rdark), stomatal conductance (gSw), water use efficiency (WUE = net photosynthesis / transpiration rate), saturation light onset (IK), and light compensation point (LCP) of light required for 90% of maximum photosynthesis (LSP90 %) were calculated.

During the experimental period, the mean temperature ± standard deviation recorded every 30 min inside the nursery in Experiment 1 was 26.1 ± 5.6 °C. In Experiment 2, in the full sun at 50 % environment, it was 26.1 ± 1.0 °C, and in full sun at 100 %, it was 28.3 ± 0.6 °C (Figure 1).

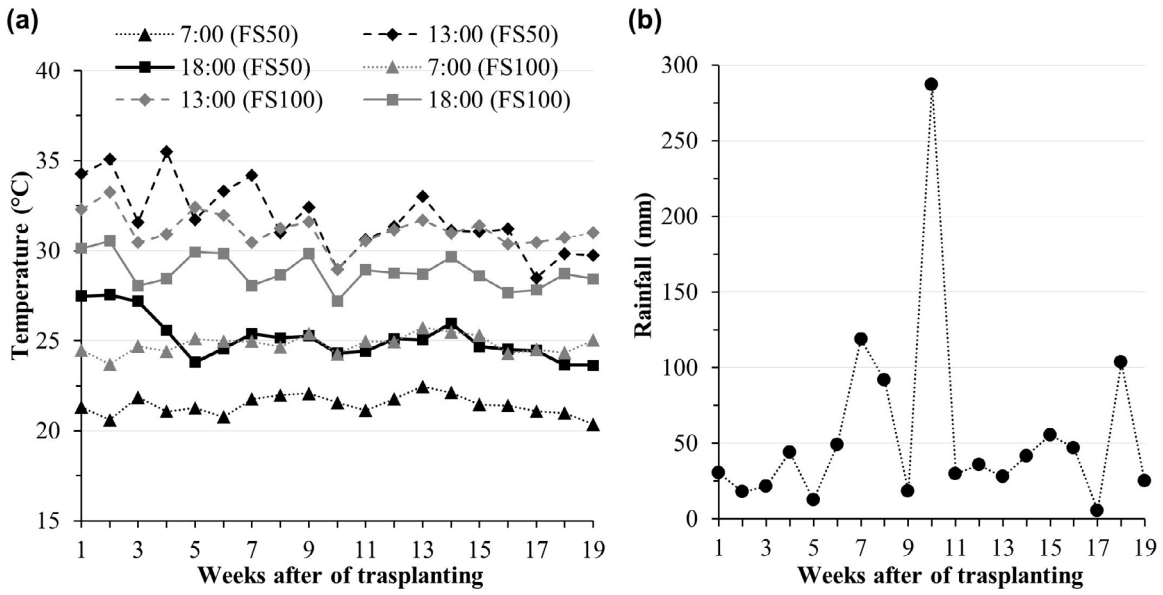

Figure 1. The average weekly temperature at 7:00, 13:00, and 18:00 in full sun at 50 % (FS50) and full sun at 100 % (FS100) environment (a) and accumulated weekly rainfall (b), recorded during the experimental period.

2.5. Data analysis

Normality and homoscedasticity of variance in the data were evaluated according to the Shapiro-Wilk and Bartlet's tests, respectively. A two-way analysis of variance was adopted in Experiment 1 (factors: the presence of CRF x container volume). For the physiological variables of Experiment 2 a split-plot in time experimental design (main plot= light hardening of seedling treatment and subplot= measurements over time) was adopted; meanwhile, a one-way analysis of variance was performed on the morphological variables. In the case of significance ($p < 0.05$), Tukey's posthoc test was adopted to compare the mean between treatments. The analyses were performed in the statistical program S.A.S 9.3.

3. RESULTS AND DISCUSSION

In Experiment 1, a significant interaction was found between the two factors evaluated only for the height ($p = 0.011$), SDM ($p < 0.01$), RDM ($p < 0.001$), and DQI ($p < 0.001$). The main effect of the CRF was significant for the stem diameter ($p = 0.038$), and this factor and the container volume were significant for the SDM/RDM ratio ($p < 0.01$) and the robustness index ($p < 0.05$) (Table 3). The height showed an increase ($p < 0.01$) of 28 % with the presence of CRF in the small bag compared to its absence (40.8 cm versus 52.5 cm), while in the tube trays and the big bag, there was no significant effect (mean = 46.5 cm). Using the smallest container (tube trays, 700 cm^3), the addition of CRF to the substrate significantly increased the seedlings' SDM, RDM, and DQI by +61 %, +37 %, and +41 %, respectively, compared to the values of unfertilized seedlings. In the small bag (1 250 cm^3) there was a significant effect on the SDM (+31 %). The robustness index and SDM/RDM ratio were significantly lower in the tube trays than in the small and big bag, respectively (Figure S1a, supplementary material). The main effect of CRF produced a significant increase of +6%, 9% and +32% in the stem diameter, robustness index, and SDM/RDM ratio, respectively, when the seedlings were fertilized (Table 3).

The substrate was formulated with 20 % vermicompost which perhaps contributed to improving the amounts of N, P, and exchangeable bases (Table 1), as already demonstrated with other forest species based on organic conditioners (Santos et al., 2020). A formulation of the substrate with 60% of soil also propitiated high quality *Cariniana pyriformis* seedling production, another forest species native to Colombia, at an affordable cost (Prato et al., 2020). Even so, the search for components to substitute the soil at least partially as a principal component is urgent. Normally, the use of soil in the substrates entails the presence of pests or diseases and inadequate physicochemical properties, as well as the negative environmental impact caused by its extraction (Schafer & Lerner, 2022).

Table 3. Values (mean ± standard error) of height (H), stem diameter (SD), shot dry mass (SDM), root dry mass (RDM), Dickson quality index, SDM/RDM ratio, and robustness index (RI) of *Lecythis tuyrana* seedlings, according to the presence of controlled-release fertilizer (CRF) and container volumes at 180 days after sowing.

	CRF (g L^{-1})	volume of container		
		tube trays	small bag	big bag
H (cm)	**0**	40.6 ± 1.1 $^{A\,a}$	40.8 ± 0.5 $^{B\,a}$	45.5 ± 0.3 $^{A\,a}$
	3	46.7 ± 2.3 $^{A\,a}$	52.5 ± 1.3 $^{A\,a}$	47.1 ± 2.5 $^{A\,a}$
	CV (%)	9.9	17.7	2.5
SDM (g seedling^{-1})	**0**	9.23 ± 0.4 $^{B\,a}$	9.28 ± 0.5 $^{B\,a}$	11.62 ± 0.9 $^{A\,a}$
	3	14.91 ± 0.8 $^{A\,a}$	12.20 ± 1.0 $^{A\,a}$	11.96 ± 0.9 $^{A\,b}$
	CV (%)	33.2	19.2	2.0
RDM (g seedling^{-1})	**0**	2.42 ± 0.2 $^{B\,a}$	1.95 ± 0.1 $^{A\,a}$	2.08 ± 0.1 $^{A\,a}$
	3	3.31 ± 0.1 $^{A\,a}$	1.86 ± 0.1 $^{A\,b}$	1.78 ± 0.1 $^{A\,b}$
	CV (%)	22.0	3.3	10.9
DQI	**0**	1.34 ± 0.1 $^{B\,a}$	1.04 ± 0.1 $^{A\,a}$	1.19 ± 0.1 $^{A\,a}$
	3	1.87 ± 0.1 $^{A\,a}$	1.05 ± 0.1 $^{A\,b}$	1.08 ± 0.1 $^{A\,b}$
	CV (%)	23.3	0.7	6.9

	tube trays	small bag	big bag	CV (%)
RI (cm mm^{-1})	5.57 ± 0.2 ^{b}	6.49 ± 0.3 ^{a}	6.27 ± 0.2 ^{ab}	7.9
SDM/RDM ratio	4.20 ± 0.2 ^{b}	5.68 ± 0.4 ^{ab}	6.18 ± 0.3 ^{a}	19.2

	SD (mm)	RI (cm mm^{-1})	SDM/RDM ratio
0	7.25 ^{B}	5.85 ± 0.1 ^{B}	4.77 ± 0.3 ^{B}
3	7.70 ^{A}	6.37 ± 0.2 ^{A}	5.93 ± 0.3 ^{A}
CV (%)	4.3	6.0	15.3

For each container volume, the presence/absence of CRF (or the significant main factor effect) represented by different upper- and lower-case letters in the column and row, respectively, indicate differences between them at 5 % significance, according to Tukey's test.

The smaller volume of tube trays made the addition of CRF and its composition of micronutrients essential in this container. As stated by Cunha et al. (2021), the production of seedlings in tube trays requires a fertilization supplement regardless of the substrate. In addition, Dias et al. (2018) showed that smaller-volume containers were more sensitive to using CRF to produce *Acrocarpus fraxinifolius*. Combined with cost reduction due to the lower volume of substrate required, tube trays are easier to handle in the nursery and to transport to the establishment site than plastic bags. Although the strong influence of containers on seedling quality has been demonstrated, once established, this positive effect may disappear over time (Mendoça et al., 2020).

Favorable response in seedling growth when the volume of tube trays increased up to 2.3 times with the big bag is due to an increase in space and probably the amount of water and nutrients available in the substrate, compensating for the absence of the CRF (Dias et al., 2018). This would explain the similar values of SDM and RDM between fertilized and unfertilized seedlings. The stem diameter and height, two non-destructive and easily measured quality parameters (Madrid-Aispuro et al., 2020), showed that the three containers did not restrict their growth. In general, the tube trays and the addition of CRF proved to be the best combination because it equalized or increased both the biomass yields by around 50 % and the quality indices, such as the SDM/RDM ratio (4.20) and DQI (1.87), compared to plastic bags.

In Experiment 2, the seedlings were 14 % taller ($p = 0.047$) in the H2 treatment compared to H1. There were no differences in stem diameter between the three treatments (mean = 8.72 mm; $p = 0.369$). This greater height in H2 was not reflected in the seedlings' etiolation when similar robustness index values were observed between the treatments (mean = 5.75 cm mm^{-1}; $p = 0.377$) (Table 4, see also Figure S1b, supplementary material).

The biomass accumulation of the seedlings in SDM and RDM was significantly higher in the H2 treatment, between 18 to 20 % and between 38 to 45 %, respectively, compared to the values obtained when the full sun at 100 % period was longer (H1) or shorter (H3). In addition, when the initial period of the full sun at 50 % environment (H3) was extended, the seedlings, as a measure of acclimation, responded with a greater biomass distribution to the shoot. Therefore, the SDM/RDM ratio was higher (4.22) compared with the H2 treatment (3.44), which responded with a greater distribution to the roots and a higher DQI. The lower light offers also caused a significantly lower DQI of the seedlings when observing the treatment of H3 (2.20) versus H2 (2.88) (Table 4).

This pattern of biomass distribution favors a relative increase in the photosynthetic apparatus at the expense of a more developed root system since the limitation is due to light

(Poorter et al., 2012). It has been noted that seedlings with a lower RDM tend to suffer more from water stress in the field, and the absorption of nutrients from the soil is lower (Poorter et al., 2012). *L. tuyrana* seedlings produced in this environment and then brought to the field in full sun could compromise their survival.

On the contrary, a more extended initial period in the full sun at 100 % environment (H1) and, therefore, solar radiation and exposure to higher temperatures during the day (Figure 1) could cause thermal stress in the seedlings reflected in their lower height and biomass yield compared to the H2 treatment. Damage symptoms were found on the leaves of some seedlings due to excess irradiance (see Figure S1, c and d, supplementary material). However, the intensity of this reduction was similar to what occurred with the H1 treatment. In other words, after seedling emergence, *L. tuyrana* probably behaves as a moderately shade-tolerant species, requiring an initial combination of partial shade and then a high light gradient for development in the early stages. Our results in nursery serve as a starting point for the establishment of field experiments, for instance possibly evaluating monospecific stand of *L. tuyrana* versus agroforestry systems with transitory species that offer a certain level of shade in the early stages of growth.

When the photosynthesis variables were analyzed only the IK and $LSP_{90\%}$ was not affected significantly by light hardening of seedling treatment, measurements over time or the interaction. Other variables were affected by the interaction between the two factors (Table 5 and 6). The LUE and Pnmax in *L. tuyrana* seedlings showed a significant increase (nearly doubling) as a function on time (95 DAS to 180 DAS) in the three light hardening of seedling treatments (Table 5). In the first measurement (95 DAS) for the LUE, the H2 or H3 treatments induced a significant increase of 27% as compared to H1 ($p = 0.003$). Nevertheless, no significant difference was observed between the light hardening of seedling treatments at 130 and 180 DAS. Similarly, no significant differences were observed in the maximum net photosynthesis in response to light curves (Pnmax), indicating that the acclimatization time does not affect the potential carbon capture at the foliar level of these seedlings (Table 5). However, considering a greater biomass allocation to the photosynthetic tissues (SDM) of the H3 treatment, could indicate that *L. tuyrana* seedlings in moderate light environments (50 % irradiance) may be able to use the increased radiation efficiently when transferred at full exposure (100 % irradiance). Discrepancies between the net assimilation rate determined at the leaf level and the accumulation of biomass in plants is a known phenomenon and may be associated, among other factors, with differential nocturnal respiration rates (Medrano et al., 2015).

The dark respiration rates (Rdark) were estimated by the light response curves, and showed a significative increase in the three treatments as a function of time, reaching 2.4, 9.2, and 4.5 times more than that observed in the respective initial times, 95 at 180 DAS for H1, H2 and H3, respectively (Table 5). The comparison also revealed significant differences between H1 compared to H2 or H3 with 2.4 times ($p = 0.009$; 95 DAS= 0.49 µmol m^{-2} s^{-1} versus 0.21 µmol m^{-2} s^{-1}), and H1 compared to H3 with 3.3 times ($p = 0.006$; 130 DAS= 1.09 µmol m^{-2} s^{-1} versus 0.33 µmol m^{-2} s^{-1}). Therefore, despite a basically similar potential net photosynthetic rate between the two treatments, the reduced values of leaf respiration in the dark of H2 and H3 plants may justify a better net carbon balance due to lower losses caused by the nocturnal respiratory process. For four native species of the Australian subtropical forest, similar acclimation responses to shade were found (Lestari & Nichols, 2016).

Regarding gSw and WUEmax at the leaf level, an increase in stomatal conductance and a decrease in maximum water use efficiency were observed solely as a function of time between for each light hardening of seedling treatments (Table 5). There was no water stress despite this, judging by the weekly rainfall records (Figure 1) outside the nursery, which was also complemented by micro-sprinkler irrigation, the increase in stomatal opening and consequently the reduction in water use efficiency may reflect the increase in leaf temperature associated with the transition from shade environment (50%) to full exposure. Under these circumstances, higher leaf transpiration rates play the important role of reducing leaf temperature during full sun exposure, thus protecting the photosynthetic machinery against heat stress (Clum, 1926).

Regarding the light requirements of the *L. tuyrana* seedlings under the different acclimatization processes, no significant differences were observed in relation to the onset saturation light intensity, IK (mean= 168 µmol m^{-2} s^{-1}) nor in relation to saturation light intensity related to 90% of maximum photosynthesis – $LSP_{90\%}$ (mean= 1 624 µmol m^{-2} s^{-1}) (Table 6). These results indicate that despite the morphoanatomical differences associated with the treatments and relative to the ontogenetic variations of *L. tuyrana* during the 90-day interval (95-180 DAS), there was no significant change in the optimal light intensity (~1 600 µmol m^{-2} s^{-1}) for the seedling establishment phase. However, the light compensation point (LCP), which indicates the onset of light intensity required to the leaf equate photosynthesis and respiratory metabolisms (net $CO_2 = 0$) was significantly higher in H2 (23.6 µmol m^{-2} s^{-1}) and H3 (20.3 µmol m^{-2} s^{-1}) at 180 DAS compared to the respective initial times (5.7 and 2.9 times, respectively). Additionally, the H1 treatment was

higher compared to H2 or H3 at 95 DAS by 2.1 times and H3 at 130 DAS in 1.4 times (Table 6).

Photosynthesis is a biological process that must be understood in a systemic context (Lima Neto et al., 2021; Bassi & Dall'Osto, 2021). An acclimatization process to contrasting light levels, as evaluated in the present study, results in a complex response that reflects the interaction between the phenotypic plasticity inherent in the genetic background of the plant species with the specific environmental stimuli experienced in a temporal context (Vieira et al., 2020). Considering this theoretical basis as a starting point, we can interpret the results obtained in which the acclimatization changes to full sun exposure in *L. tuyrana* had more effects on quantum efficiency adjustments and mitochondrial respiration than on the carbon capture process per se.

Interestingly, an increase in mitochondrial respiration rates was clearly observed which may mean that carbon losses due to the acclimatization process may even justify a possible mismatch between carbon capture at the leaf level and the growth rate of these plants (Medrano et al., 2015; Leakey et al., 2019). The increase in mitochondrial respiratory activity may in turn be associated with a mechanism for dissipating excess energy in leaves, as mitochondria under stress conditions can act as strong metabolic drains, protecting the photosynthetic machinery to some extent from excess reducing power, as evidenced in several other species (Araújo, Nunes- Nersi, Ferni, 2014; Gago et al., 2020).

Table 4. Values (mean ± standard error) of height (H), stem diameter (SD), robustness index (RI), root dry mass (RDM), shoot dry mass (SDM), RDM/RDM ratio and Dickson quality index (DQI) of *Lecythis tuyrana* seedlings, according to three periods of light hardening (H) at 180 days after sowing.

H	H (cm)	SD (mm)	RI (cm mm^{-1})	SDM	RDM	SDM/ RDM ratio	DQI
				(g seedling^{-1})			
H1	47.0 ± 1.6 ^{b}	8.78 ± 0.3 ^{ns}	5.36 ± 0.3 ^{ns}	17.6 ± 0.9 ^{b}	4.46 ± 0.1 ^{b}	3.95 ± 0.2 ^{ab}	2.37 ± 0.1 ^{ab}
H2	53.6 ± 1.3 ^{a}	8.88 ± 0.2	6.05 ± 0.3	21.1 ± 0.1 ^{a}	6.15 ± 0.3 ^{a}	3.44 ± 0.1 ^{b}	2.88 ± 0.1 ^{a}
H3	49.6 ± 1.9 ^{ab}	8.51 ± 0.1	5.84 ± 0.3	17.8 ± 0.6 ^{b}	4.25 ± 0.2 ^{b}	4.22 ± 0.1 ^{a}	2.20 ± 0.1 ^{b}
CV (%)	6.7	2.2	6.1	10.4	21.1	10.2	14.2

Mean followed by the same letter in the columns do not differ from each other by test Tukey ($p<0.05$). ^{ns} = not significant.

Table 5. Values (mean ± standard error) of light curve fitting model parameters for photosynthetic quantum efficiency (LUE, µmol CO_2 µmol photon^{-1}), maximum net photosynthesis (Pnmax), maximum light-limited net photosynthesis (Pnmax, µmol CO_2 m^{-2} s^{-1}), dark respiratory rate (Rdark, µmol CO_2 m^{-2} s^{-1}) and stomatal conductance (gSw, mmol m^{-2}s^{-1}) and maximum water use efficiency (WUEmax, µmol CO_2 mmol H_2O^{-1}) of *Lecythis tuyrana* seedlings, according to light hardening of seedling treatments (H1, H2 and H3) and measurements over time (days after sowing - DAS).

Variable	DAS	H1	H2	H3
LUE	95	0.039 ± 0.002 $^{C b}$	0.050 ± 0.002 $^{B a}$	*
	130	0.062 ± 0.008 $^{B a}$	0.046 ± 0.007 $^{B a}$	0.048 ± 0.003 $^{B a}$
	180	0.085 ± 0.003 $^{A a}$	0.085 ± 0.007 $^{A ab}$	0.073 ± 0.002 $^{A b}$
	CV (%)	37.1	35.6	29.2
Pnmax	95	7.08 ± 0.51 $^{B a}$	7.27 ± 0.89 $^{B a}$	*
	130	7.57 ± 0.61 $^{B a}$	6.56 ± 0.97 $^{B a}$	6.83 ± 0.63 $^{B a}$
	180	13.14 ± 1.65 $^{A a}$	10.71 ±2.49 $^{A a}$	12.06 ± 1.13 $^{A a}$
	CV (%)	36.3	27.1	39.2
Rdark	95	0.49 ± 0.07 $^{B a}$	0.21 ± 0.05 $^{B b}$	*
	130	1.09 ± 0.17 $^{A a}$	0.40 ± 0.18 B ab	0.33 ± 0.03 $^{B b}$
	180	1.17 ± 0.16 $^{A a}$	1.94 ± 0.41 $^{A a}$	1.48 ± 0.22 $^{A a}$
	CV (%)	40.5	111.6	89.9
gSw	95	0.11 ± 0.011 $^{A a}$	0.11 ± 0.016 $^{B a}$	*
	130	0.16 ± 0.02 $^{A a}$	0.10 ± 0.02 $^{B a}$	0.13 ± 0.02 $^{B a}$
	180	0.17 ± 0.02 $^{A a}$	0.23 ± 0.035 $^{A a}$	0.24 ± 0.03 $^{A a}$
	CV (%)	21.9	49.3	42.0
WUEmax	95	3.94 ± 0.52 $^{A a}$	5.31 ± 0.72 $^{A a}$	*
	130	3.06 ± 0.34 $^{A a}$	4.07 ± 0.53 $^{A a}$	4.61 ± 0.51 $^{A a}$
	180	2.69 ± 0.08 $^{A a}$	2.28 ± 0.18 $^{B a}$	1.90 ± 0.17 $^{B a}$
	CV (%)	19.9	39.2	58.9

For light hardening of seedling treatment and measurements over time, different upper and lower-case letters in the column and row, respectively, indicate differences between them at 5% significance according to Tukey's test.

Table 6. Values (mean ± standard error) of light curve fitting model parameters for saturation light onset (IK, μmol m^{-2} s^{-1}), light required for 90% of maximum photosynthesis ($LSP_{90\%}$, μmol m^{-2} s^{-1}) and light compensation point (LCP, μmol m^{-2} s^{-1}) of *Lecythis tuyrana* seedlings, according to light hardening of seedling treatments (H1, H2 and H3) and measurements over time (days after sowing - DAS).

Variable	DAS	H1	H2	H3
IK	95	194 ± 15 ^{Aa}	154 ± 22 ^{Aa}	*
	130	157 ± 23 ^{Aa}	162 ± 24 ^{Aa}	151 ± 12 ^{Aa}
	180	174 ± 22 ^{Aa}	158 ± 27 ^{Aa}	188 ± 20 ^{Aa}
	CV (%)	10.6	2.5	15.4
$LSP_{90\%}$	95	1 821 ± 100 ^{Aa}	1 431 ± 198 ^{Aa}	*
	130	1 580 ± 183 ^{Aa}	1 470 ± 147 ^{Aa}	1 431 ± 115 ^{Aa}
	180	1 718 ± 185 ^{Aa}	1 756 ± 165 ^{Aa}	1 782 ± 126 ^{Aa}
	CV (%)	7.1	11.7	15.9
LCP	95	13.0 ± 2 ^{Aa}	4.2 ± 1 ^{Bb}	*
	130	17.0 ± 2 ^{Aa}	7.5 ± 2 ^{ABb}	7.0 ± 1 ^{Bb}
	180	14.0 ± 2 ^{Aa}	23.6 ± 5 ^{Aa}	20 ± 3 ^{Aa}
	CV (%)	14.2	88.2	68.1

For light hardening of seedling treatment and measurements over time, different upper and lower-case letters in the column and row, respectively, indicate differences between them at 5 % significance according to Tukey's test

4. CONCLUSIONS

After six months of growth in the nursery, tube trays and 3 g L^{-1} substrate with a CRF are recommended because it significantly increases the height, biomass accumulation, and Dickson quality index in *L. tuyrana* seedlings. Even in this container and without the CRF, the seedlings had a better balance between the aerial and root part, although a lower growth than in the big plastic bags. Despite light requirements remaining similar among the different acclimation treatments and throughout time (95 to 180 DAS), a light intensity of approximately 1 600 μmol m^{-2} s^{-1} is considered optimal for *L. tuyrana* seedlings growth.

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SUPPLEMENTARY MATERIAL

The following online material is available for this article:
Figure S1. Visual aspect of *Lecyhis tuyrana* seedling according to slow-release fertilizer x volume container – experiment 1 (a) and light acclimatation – experiment 2 (b) 170 and 180 days after sowing, respectively, and visual symptoms of damage to seedling leaves due to excess irradiance after going from 50 % shadow to full sun environment (c and d).

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