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Does *Ceiba pentandra* (Malvaceae) a light demanding species succumb under deep shading?

Ceiba pentandra (Malvaceae), uma espécie exigente em luz, sucumbe ao sombreamento profundo?

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Abstract

Sumauma (*Ceiba pentandra*) is a fast-growing and light-demanding species that occurs across a wide rainfall range in tropical regions, but it is still unclear how it performs under shading. This work aimed to evaluate leaf traits and biomass allocation of sumauma seedlings in response to different levels of artificial shadings. After a strengthening period of 14 months (at moderate light), the seedlings were submitted to three shading levels for 580 days: moderate shading (T_1: irradiance of 5.59 mol m^{-2} day^{-1}), strong shading (T_2: 1.29 mol m^{-2} day^{-1}), and deep shading (T_3: 0.14 mol m^{-2} day^{-1}). The control (T_0) was seedlings under direct sunlight (15.65 mol m^{-2} day^{-1}). Parameters evaluated were plant growth, biomass allocation to plant organs and leaf traits. Growth and biomass accumulation enhanced with a rise in irradiance, being maximum under direct sunlight and null under deep shading. Sumauma did not succumb under deep shading, as it was able to endure deep shading for 19 months. Under deep shading, the seedlings allocated just a little amount of biomass to leaves and greatly reduced leaf thickness. The whole-plant compensation point was estimated to be 1.0 mol m^{-2} day^{-1}. We concluded that pre-strengthened sumauma seedlings may endure deep shading. These traits combined with the high growth rates of this tree under full sunlight make of sumauma a promising candidate to be tested in reforestation projects.

Keywords: Shade tolerance; Fast growing species; Biomass allocation; Leaf traits; Whole-plant light compensation point.

Resumo

Sumaúma (*Ceiba pentandra*) é uma árvore de crescimento rápido que ocorre em uma ampla faixa pluviométrica em regiões tropicais, mas ainda não está claro como ela se comporta sob sombreamento intenso. Este trabalho teve como objetivo avaliar características foliares e alocação de biomassa de mudas de sumaúma em resposta a diferentes níveis de sombreamento artificial. Após um período de fortalecimento de 14 meses (com luz moderada), as plantas foram submetidas a três níveis de sombreamento por 580 dias: sombreamento moderado (T_1: irradiância de 5,59 mol m^{-2} dia^{-1}), sombreamento forte (T_2: 1,29 mol m^{-2} dia^{-1}) e sombreamento profundo (T_3: 0,14 mol m^{-2} dia^{-1}) e uma testemunha (T_0) sob luz solar direta (15,65 mol m^{-2} dia^{-1}). Os parâmetros avaliados foram crescimento da planta, alocação de biomassa aos órgãos da planta e características foliares. O crescimento e o acúmulo de biomassa aumentaram com o aumento da irradiância, sendo máximos sob luz solar direta e nulos no sombreamento mais profundo. A sumaúma não sucumbiu sob sombreamento profundo e foi capaz de

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suportá-lo por 19 meses. Sob sombreamento profundo as mudas alocaram apenas uma pequena quantidade de biomassa às folhas e reduziram substancialmente a espessura das folhas. O ponto de compensação por luz da planta foi estimado em 1.0 mol m^{-2} day^{-1}. Concluiu-se que mudas pré-fortalecidas de sumaúma podem suportar sombreamento profundo. Esta característica, combinada com sua alta taxa de crescimento sob a luz solar direta, torna essa árvore uma candidata promissora para ser testada em projetos de reflorestamento.

Palavras-chave: Tolerância à sombra; Espécie de crescimento rápido; Alocação de biomassa; Características foliares; Ponto de compensação por luz da planta.

INTRODUCTION

Ceiba pentandra (L.) Gaertn. (Malvaceae) is classified as a fast-growing species and either as mid-successional or long-lived pioneer (Condit et al., 1993; Román-Dañobeytia et al., 2015). It has also been ranked as a large gap-dependent – early successional species (Kitajima, 1994; for the sake of simplicity in this study we classified *C. pentandra* as a mid-successional-large gap dependent species. It produces small seeds (31.8 mg), has low wood density (0.36 g cm^{-3} –at sapling stage, Kitajima, 1994), and when grown under water deficit, elevated CO_2 can mitigate the effect of water stress (Silveira & Marenco, 2023).

Sumauma occurs across a wide range of climatic zones over tropical regions (Gómez-Maqueo & Gamboa-deBuen, 2022). The sumauma tree has several uses. It can be harvested for plywood manufacturing. Sumauma can also be used for the production of fibers and phytopharmaceuticals (Lim, 2012; Gómez-Maqueo & Gamboa-deBuen, 2022). Despite being a species that occurs naturally in floodplain forests, it can thrive in soils with low fertility and limited water availability, indicating high potential for use in reforestation programs (Román-Dañobeytia et al., 2015; Vargas-Simón et al., 2022). Although seeds of sumauna germinate under low light (2% of full sunlight), the seedlings are unable to establish under deep shade conditions (Kyereh et al., 1999). In fact, it has been reported that only 28% of sumauma seedlings can survive for 16 weeks under deep shading (~1% of full sunlight, Augspurger, 1984). However, the minimum light requirement for long-term survival (whole-plant light compensation point) of sumauma seedlings is still unknown. This information is relevant for production of high-quality seedlings, and a key factor for successful reforestation programs.

Depending on how plants respond to changes in light conditions with ontogeny, they can be classified into three groups: (1) shade-tolerant species (slow-growing), (2) light-demanding species (often called pioneer, shade-intolerant, gap-demanding species or fast-growing), and (3) intermediate species (Hubbell et al., 1999; Valladares & Niinemets, 2008). In this context, a light-gap can be defined as a local disturbance created in a closed-canopy forest, e.g. that caused by a dead tree (Hubbell et al., 1999). Shade-tolerant (slow-growing) and light-demanding species (fast-growing) perform distinctly under varying light conditions (Marenco & Vieira, 2005; Camargo & Marenco, 2022). Seedlings of light-demanding species grow in highly-lit environments, whereas those of shade-tolerant species can survive under dimly lit conditions (1–2% full sunlight) for more than one year (Augspurger, 1984; Hubbell et al., 1999). Indeed, Clark & Clark (2001) estimated that seedlings (1-cm-diameter, 50-cm tall) of some non-pioneer rainforest species could require as much as 33-83 years to reach the lower sub-canopy (size of a 10-cm diameter tree). Moreover, species that differ in shade tolerance also diverge in phenotypic plasticity to light, which is inversely related to survival under shading conditions (Valladares & Niinemets, 2008). Thus, the leaf mass per area (LMA) of the light-demanding *Goupia glabra* is responsive to changes in understory light (Marenco & Vieira, 2005). Likewise, sumauma seedlings enhance LMA with a rise in irradiance (Kitajima, 1994). This is important, as changes in LMA may influence photosynthesis per unit mass (Marenco & Vieira, 2005). In general, fast-growing species do not survive under deep shading. However, we still do not know how sumauma seedlings respond to changes in light conditions during growth. Thus, the aim of this study was to evaluate the effects of varying light intensities on sumauma seedlings. Sumauma is a light-demanding species, therefore we expected that sumauma seedlings would not survive for many days under deep shade conditions.

MATERIAL AND METHODS

Plant material and treatments

The experiment was carried out at Campus III (03° 05' 30” S; 59° 59´ 35” W) of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas from April 2019 to November 2020. During this period, the city of Manaus recorded a mean temperature of 27.95°C (ranging from 27.44 °C to 28.50 °C); mean relative humidity was 72.6% and total solar radiation 15.56 MJ m^{-2} day^{-1}; i.e. 32.3 mol m^{-2} day^{-1} of photosynthetically active radiation, PAR –computed from INMET (Instituto Nacional de Meteorologia, 2022).

Sumauma seeds [*Ceiba pentandra* (Malvaceae)] were collected at the Adolpho Ducke Forest Reserve (located just outside the city of Manaus), germinated in vermiculite and after germination the seedlings were transplanted into plastic pots containing 5.0 kg of forest soil (collected from the first centimeters of the upper soil layer), which was amended as described by Silveira et al. (2023). Prior to submitting the seedlings to treatments, they were kept in a greenhouse (at 8.6 mol m^{-2} day^{-1}, Silveira et al., 2023) for 14 months (a pre-treatment or strengthening period). Then, they were transferred to larger pots containing 8 kg of the same forest soil (as described above); by this time, the plants were 6.95 ± 0.7 mm in diameter (at 6 cm from stem base) and 63.5 ± 6.7 cm tall (root collar to apical bud, see footnote in Table 1*)*.

After the strengthening period, the seedlings were submitted to four irradiance treatments with 10 replications (plants). There were three shading levels: T_1 (moderate shading), T_2 (strong shading) and T_3 (deep shading), being the control (T_0), seedlings under direct sunlight. To establish a given shading condition, a pipe-frame (2.5 m height) was placed over a greenhouse bench, and then it was covered with a shade-cloth (high-density polyethylene yarn; a schematic drawing of the experiment setup is shown in the Appendix – Figure A1). Furthermore, to improve ventilation, the shade cloth did not cover the first 30 cm above the bench. In the surrounding of the four benches, there were some trees which provided shade in the morning and late in the afternoon. In the treatments, the mean temperatures (measured at 30-min intervals, TR-52, T and D Co. Ltd., Japan) varied from 28 °C (under direct sunlight) to 26–27 °C under shade conditions. Also, in the treatments the daily PAR varied as shown in Table 1 in the Results´ section. Parenthetically, PAR was measured at 15-min-intervals, with a quantum sensor (Li-190SA, Li-Cor, Lincoln, NE, USA) connected to a datalogger (Li-1400, Li-Cor), then the instantaneous PAR values were integrated over time intervals to have the daily PAR (PAR_{day}). The maximum instantaneous PAR (PAR_{max}) was obtained as the mean photosynthetic photon flux daily recorded between 11:45 am and 01:15 pm.

The seedlings were subjected to treatments for 580 days, from April 9th, 2019 to November 9th, 2020 (hereafter referred to as the experimental period). Throughout the experimental period, the seedlings were daily irrigated to keep the soil close to field capacity. During the first 450 days, stem diameter and plant height (from root collar to apical bud) were measured weekly. Stem diameter was measured (at 6 cm from root collar) with digital calipers (0.01 mm resolution). Measurement of plant growth (diameter and height) was interrupted (due to the health emergency related to the Covid-19 pandemic) from August to October (2020). Thus, the last measurement was carried out in the last week of the experimental period (second week of November 2020), when the plant material was harvested and dry matter measured.

Measurement of biomass allocation to plant organs and leaf traits

Once the experimental period was completed (580 days), we measured: biomass allocation to plant organs, relative growth rate (RGR), leaf total non-structural carbohydrate (TNC), the maximum quantum yield of photosystem II (F_v/F_m ratio), leaf mass per area (LMA and its inverse), and the SPAD value (an indicator of the relative chlorophyll content). The leaf trait parameters were measured in leaves produced during the experimental period. The dry matter (DM) of plant organs, leaves (LDM), stem (SDM) and roots (RDM) was measured after drying the plant material at 80°C until constant mass. The total plant dry matter at the end of the experimental period (i.e., at time t_2, TDM_2) was obtained by summing up the DM mass of plant organs, i.e., TDM_2 = LDM + SDM + RDM. We also measured total DM before subjecting the plants to treatments (i.e. at time t_1, TDM_1) by harvesting another set of seedlings. The RGR calculation followed Hunt et al. (2002):

$$\text{RGR (mg g}^{-1}\text{day}^{-1}) = 1000 \times \frac{\ln \text{TDM}_2 - \ln \text{TDM}_1}{(t_2 - t_1)} \tag{1}$$

TDM_1 and TDM_2 values are in grams, so the factor "1000" is used to express the RGR in mg g^{-1} day^{-1}. The *ln* indicates the natural logarithm.

The TNC were obtained after measuring the leaf sugar and starch content (Dubois et al., 1956). The SPAD value (SPAD-502, Minolta Camera Co., Osaka, Japan) was measured on two leaves per plant and ten readings per leaf. We measured leaf fluorescence between 09:00 am and 11:00 am on two leaves per plant, and computed the F_v/F_m ratio as (Björkman & Demmig, 1987):

$$\frac{\text{F}_\text{v}}{\text{F}_\text{m}} = \frac{[\text{F}_\text{m} - \text{F}_0]}{F_\text{m}} \tag{2}$$

where F_v represents the variable fluorescence; F_m, maximum fluorescence (measured after applying a light pulse of 4,500 μmol m^{-2} s^{-1}), and F_0, minimum fluorescence. The F_m and F_0 were measured over a 4-mm diameter disc using a hand-held fluorometer (Fluor Pen FP100, Photon System Instruments, Brno, Czech Republic).

To determine the LMA (and the inverse, leaf area per mass LAM), leaf area was measured using a leaf area integrator (Li-3050, Li-Cor), and the leaf mass, as previously described. We also counted the number of leaves, leaflets per leaf, and calculated leaflet size (LLs), as the plant leaf area divided by the number of leaflets (NLL).

Data analysis

The experimental design was completely randomized with four treatments (T_0–T_3), and 10 replications (*n*) per treatment, except for T_3 ($n = 9$, as one plant died during the experimental period). The data were tested for normality (Shapiro-Wilk test) and homoscedasticity ($\alpha = 0.05$), and log-transformed when necessary. The means were compared using the Tukey test ($p = 0.05$). Regression analysis was used to estimate stem growth and biomass accumulation with varying light intensities during the experimental period. We used $p = 0.05$ to infer statistical significance. Statistical analyses were performed with Sigma Plot 11.0 (Systat Software, Inc., San Jose, CA, USA).

RESULTS

The daily PAR received by the seedlings during the experimental period varied from 0.14 to 15.65 mol m^{-2} day^{-1} (Table 1). Seedlings exposed to direct sunlight (T_0) emitted the first branch in the sixteenth week from the beginning of the experiment; while in treatment 1 (T_1) the first branch only appeared in the eighteenth week. In T_2, the first and sole branch appeared in the last week of the experimental period. None of the seedlings under deep shading (T_3) produced a single branch, and one of them died before the end of the experiment.

Table 1. Growth and leaf traits of sumauma seedlings subjected to four light conditions (T_0–T_3) for 580 days.

Treatment	*n*	PAR_{day} (mol m^{-2} day^{-1})	PAR_{max} (μmol m^{-2} s^{-1})	D_G (mm yr^{-1})	H_G (cm yr^{-1})	Leaf number	Leaflet number	LLs (cm^2)	SPAD	F_v/F_m
T_0	10	15.65	786.0	9.32±039a	40.9±1.8b	41.2±4.6a	260.8±31.1a	15.8±0.6c	42.8±2.2c	0.76±0.01a
T_1	10	5.59	329.2	5.38±026b	48.6±1.6a	38.4±4.1a	256.8±24.3a	16.8±0.6bc	45.1±1.3bc	0.76±0.01a
T_2	10	1.29	67.2	2.71±023c	15.1±1.1c	19.4±1.3bc	113.7±10.7bc	25.5±3.0ab	50.2±1.0ab	0.71±0.03a
T_3	9	0.14	8.3	0.23±012d	4.9±1.5d	6.5±1.2c	34.5±8.4c	17.4±4.3bc	46.4±0.6bc	0.71±0.01a
F				245.6	183.5	22.43	24.7	3.33	4.48	2.35
p-value				<0.001	<0.001	< 0.001	< 0.001	< 0.031	0.01	0.09

Abbreviations: D_G: diameter growth; H_G: height growth; PAR: photosynthetically active radiation; PAR_{day}: daily PAR; PAR_{max}: maximum instantaneous PAR; LLs: leaflet size; *n*: number of replications. Within columns different letters indicate significant differences (Tukey test at $p = 0.05$). The SPAD values (relative unit), the F_v/F_m ratio, and the *F* and *p*-values (of Anova) are also shown. Each value represents the mean (± standard error, SE). For further information: plant traits (mean ± standard deviation) at the beginning of the experiment were: diameter = 6.95±0.74 mm, height = 63.5±6.7 cm, leaf number per plant = 14.7±1.8, and leaflet number per plant = 77.7±12.4. At a fully open site, PAR was 32.3 mol m^{-2} day^{-1} (Instituto Nacional de Meteorologia, 2022).

Plant growth in diameter (D_G) increased with a rise in irradiance. Therefore, the highest D_G value was measured under direct sunlight – T_0 (9.32 mm yr^{-1}). While, the highest height growth increment (H_G) was recorded under moderate shading (48.6 cm yr^{-1}, Table 1). Although the seedlings under deep shading (T_3) showed a slightly growth in height over the experimental period, diameter growth was null (Figure 1). Because the seedlings of T_3 had just a few leaves per plant at the end of the experimental period (Table 1), the RGR under deep shading was even slightly negative (–0.03 mg g^{-1} day^{-1}, Table 2). In fact, compared with the leaf number at the beginning of the experiment (mean of 14.7 leaves per plant, footnote in Table 1), the leaf number greatly decreased under deep shading –T_3 (Table 1).

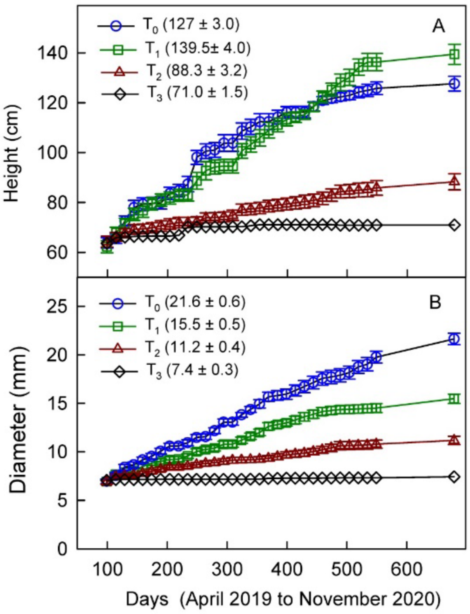

Figure 1. Growth in stem diameter (*D*) and height (*H*) of sumauma seedlings subjected to four light conditions (T_0–T_3) for 580 days (from April 9, 2019– day 99 to November 09, 2020, day 679).The *D* and *H* just before seedling exposure to treatments were 6.95 mm and 63.5 cm, respectively. The vertical bar at each symbol represents the standard error (SE). The numeral in parenthesis shows the mean (±SE) at the end of the experimental period. The SE is not shown when smaller than the symbol size. Further information, as described in Table 1.

Table 2. Traits of sumauma seedlings subjected to four light conditions (T_0–T_3) for 580 days.

Treatment	*n*	LDM (g per plant)	SDM (g per plant)	RDM (g per plant)	TDM₂ (g per plant)	TDM₁ (g per plant)	SRR	RGR (mg g^{-1} day^{-1})
T_0	10	22.3±2.54a	68.4±5.47a	47.1±4.57a	137.8±11.9a	17.85±0.96	1.96±0.08a	3.47±0.23a
T_1	10	19.7±1.41a	38.6±3.22b	23.8±2.43b	82.1±6.7b	18.16±0.88	2.51±0.12bc	2.57±0.14b
T_2	10	9.7±0.87b	15.1±1.47c	10.3±0.81cd	35.0±2.9c	18.06±.79	2.42±0.11c	1.11±0.12c
T_3	9	1.26±0.42c	9.80±0.81d	7.4±0.39cd	18.5±1.3d	18.7±1.22	1.47±0.06d	-0.03±0.03d
F		81.5	91.8	77.5	99.3	0.14	23.8	104.7
p-value		< 0.001	< 0.001	< 0.001	< 0.001	0.93	< 0.001	< 0.001

Abbreviations: t_1: time before seedlings exposure to treatments; t_2: time at the end of the experimental period; RGR: relative growth rate; DM: dry mass; LDM: leaf DM (measured at t_2); SDM: stem DM (at t_2); RDM: root DM (at t_2); TDM₂: total DM (at t_2); TDM₁: total DM (at t_1); SRR: shoot/root ratio. Each value represents the mean (±SE). Within columns different letters indicate significant differences (Tukey test at p = 0.05). Further information, as described in Table 1.

The highest total biomass (137.8 g per plant) was recorded under direct light conditions and the lowest under deep shading (Figure 2, Table 2). In fact, under deep shading the seedlings tended to lose biomass, as the total biomass at the end of the experimental period (18.5 g per plant) was lower than the initial biomass (18.7 g per plant, Table 2). It was estimated that under full sunlight (32.3 mol m^{-2} day^{-1}, Instituto Nacional de Meteorologia, 2022) the seedlings would accumulate 178.8 g per plant, and have a diameter increment of 13.8 mm yr^{-1} (Figure 2).

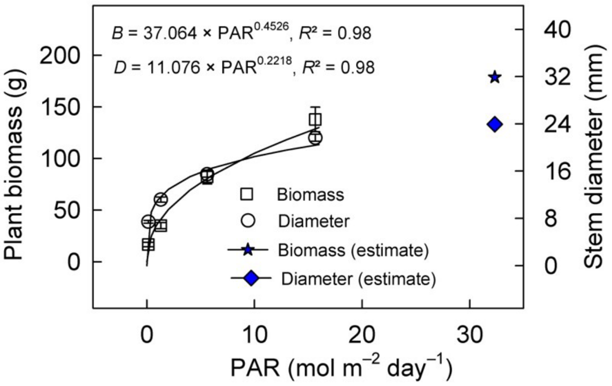

Figure 2. Growth in stem diameter (*D*) and whole plant biomass (*B*) of sumauma seedlings as a function of photosynthetically active radiation (PAR). The estimated diameter (diamond) and biomass (star) at a fully open site (32.3 mol m^{-2} day^{-1}) is also shown. At a fully open site the increment in diameter and the whole plant biomass were estimated to be 13.8 mm yr^{-1} and 178.8 g per plant, respectively. Further information is described in Table 1.

Most of the biomass was allocated to stems and roots (Table 2), while the fraction of biomass allocated to leaves was the least, in particular under deep shading (Table 3). In fact, only 6.8% of total biomass was allocated to leaves under deep shading (T_3), and likewise, biomass allocated to stem and roots was also greatly diminished in this treatment –T_3 (Table 2). Because, the relative amount of biomass allocated to roots was larger in T_0 than in T_1 and T_2, the shoot/root ratio was the greatest under intermediate shadings (2.42–2.51, Table 2). While in T_3, the shoot/root ratio was the lowest because in comparison to root biomass, the biomass allocated to leaves was very low under deep shading (Table 2). Following the trend showed in Figure 1, the greatest relative growth rate was observed under direct sunlight (3.47 mg g^{-1} day^{-1}) and the lowest under deep shading –T_3 (Table 2).

Table 3. Percentage of biomass in plant organs of sumauma seedlings subjected to four light conditions (T_0–T_3) for 580 days.

Treatment	*n*	LDM (%)	SDM (%)	RDM (%)	Total DM (%)
T_0	10	16.2	49.6	34.2	100
T_1	10	24.0	47.0	29.0	100
T_2	10	27.7	43.0	29.3	100
T_3	9	6.8	53.1	40.1	100

Abbreviations: DM: dry mass; LDM: leaf DM (% of total DM at the end of the experimental period, t_2); SDM: stem DM (% of total DM at t_2); RDM: root DM (% of total DM t_2); *n*: number of replications. Further information, as described in Table 2.

The leaf area per mass (LAM) augmented with the increase in shading (182.4 cm^2 g^{-1} under direct sunlight against 358.1 g cm^{-2} under deep shading, Table 4). While, leaf thickness sharply decreased as the intensity of shading increased (Table 4). Thus, the fresh leaf thickness diminished about 30% under deep shading (0.14 mm in T_0 to 0.097 mm in T_3, Table 4). Similarly, total non-structural carbohydrate (TNC) also decreased under deep shading (Table 4). However, in comparison with seedlings grown under direct sunlight, the F_v/F_m ratio was unresponsive to shading. Although the SPAD value did not show a clear trend in response to changes in light conditions, it tended to increase in seedlings of treatment two (Table 1). Thus, considering T_0 (full sunlight) as a baseline, we found that exposing the seedlings to shading for 580 days reduced biomass accumulation and relative growth rate (RGR). Likewise, leaf and leaflet number also decreased as the level of shading increased (Table 1).

Table 4. Leaf traits of sumauma seedling subjected to four light conditions (T_0–T_3) for 580 days.

Treatment	LAM ($cm^2 g^{-1}$)	LMA ($g m^{-2}$)	Sugar ($g m^{-2}$)	Starch ($g m^{-2}$)	TNC ($g m^{-2}$)	DLT (mm)	FLT (mm)
T_0	182.4±25d	54.9±0.7a	2.23±0.05b	4.42±0.26a	6.65±0.28a	0.096±0003a	0.140±0003a
T_1	217.0±5.1c	46.3±1.1b	3.18±0.17a	3.91±0.27a	7.09±0.38a	0.080±003b	0.111±0001b
T_2	280.5±5.1b	35.8±0.7c	2.83±0.17a	3.55±0.24ab	6.38±0.31a	0.056±0002c	0.104±0002bc
T_3	358.1±30.5a	29.9±3.3d	1.70±0.06b	2.28±0.31bc	3.97±0.25b	0.036±0003d	0.097±0006c
F	38.94	46.8	16.0	7.33	10.0	90.4	40.1
p-value	<0.001	<0.001	<0.001	<0.001	<0.001	< 0.001	< 0.001

Abbreviations: LAM: leaf area per mass; LMA: leaf mass per area; DLT: dry leaf thickness; FLT: fresh leaf thickness; TNC: total non-structural carbohydrates (sugar and starch). Each value represents the mean (±SE). Within columns different letters indicate significant differences (Tukey test at $p = 0.05$). Further information as described in Table 1.

DISCUSSION

Plant growth depends on the balance between carbon gain via photosynthesis and carbon loss by respiration, and photosynthesis is a function of light intensity (Kozlowski & Pallardy, 1997; Camargo & Marenco, 2012). We found that *C. pentandra* grew faster with increasing irradiance, which is consistent with the results reported by others (Augspurger, 1984; Condit et al., 1993; Kitajima, 1994). We also found that leaf thickness and the leaf mass per area greatly diminished with an increase in shading, indicating high phenotypic plasticity, which is a leaf trait associated with shade-intolerance (Valladares & Niinemets, 2008). Although the response of plants to shading has been studied for decades, the mechanisms involved are complex and still not entirely elucidated (Xu et al., 2021).

In this experiment, we found that plant growth enhanced with a rise in irradiance, and that sumauma withstood deep shading for more than a year. From a physiological perspective, shade tolerance is the plant attribute that reflects the capacity of a plant to endure low light conditions; while, the whole-plant light compensation point defines the lowest amount of light required for plant survival (Valladares & Niinemets, 2008). Even though sumauma seedlings survived for 19 months at an irradiance of just 0.43% of full sunlight, it cannot be concluded that sumauma is shade-tolerant, as at the end of the experimental period the seedlings of T_3 had only a few leaves and a little amount of biomass allocated to leaves, and the leaf non-structural carbohydrates had been depleted by 40% under deep shading. It is evident that despite the survival of seedlings (19 months) under extreme shading, the sustained growth under such low-light conditions was unlikely. This result clearly indicates that below the whole-plant compensation point (irradiance at which net carbon gain of a plant is null), the plant dies once the reserves stored are exhausted (Givnish, 1988; Lusk & Jorgensen, 2013). Kyereh et al. (1999) reported that although sumauma seeds germinated under low light, the seedlings were unable to stablish at 2% irradiance; while in this experiment, the seedlings thrived at 1.29 mol m^{-2} day^{-1} (T_2), which indicates that the whole-plant compensation point is approximately 1.0 mol m^{-2} day^{-1} or 3% full sunlight in the open (i.e. the mean of T_2 and T_3 irradiance rounded to the closest integer).

The SPAD values slightly increased with shading, especially in T_2, in line with the findings of Valladares & Niinemets (2008), who reported an increase in chlorophyll content per unit area under low light. The relatively high SPAD value found in T_3 indicates that the little amount of light available under deep shading avoided premature chlorophyll degradation. In this context, as it has been found that leaf senescence can be induced by darkness (without photosynthesis darkness leads to carbon starvation), which promotes chlorophyll degradation (Wang et al., 2022).

The F_v/F_m is a measure of the maximum photochemical efficiency of photosystem II, being a value of 0.83 considered optimal for most plant species (Björkman & Demmig, 1987). In this regard, we found that small changes in SPAD values did not modify the F_v/F_m ratio, which remains unaltered over treatments ($p = 0.09$, Table 1). This probably occurred because in the range of chlorophyll contents normally found in vascular plants, changes in leaf chlorophyll concentration have little effect on the F_v/F_m (Björkman & Demmig, 1987). Evidently when the chlorophyll content is drastically reduced (e.g. by dark-induced senescence), the F_v/F_m ratio decreases (Wang et al., 2022), which did not occur in this experiment, as mentioned above.

We observed that in comparison with T_1 and T_2, the shoot/root ratio decreased under direct sunlight (T_0), because a relatively large amount of biomass was allocated to roots in T_0. Under the light conditions of T_1 and T_2, the relative amount of biomass allocated roots decreased, while the fraction of leaf biomass increased, which increased the shoot/root ratio. This indicates that under the light conditions of T_1 and T_2, carbon allocation to leaves is of high priority. In fact, in tropical rainforests the biomass allocation to leaves is the major component of the aboveground net primary productivity (Clark et al., 2013; Hofhansl et al., 2015). Therefore, a little amount of biomass allocated to leaves is a sign of severe stress, which may ultimately cease growth, as observed in T_3.

We expected that sumauma seedlings would not survive under deep shading (0.43% of full sunlight at a fully open environment). However, our results showed the survival of sumauma seedlings under deep shade (only one of the 10 individuals evaluated under this condition died). This is an important indicator, as it shows that pre-strengthened sumauma seedlings are capable of surviving under deep shading conditions for a long period (> 1 yr), while growing rapidly under favorable light conditions. The capability of sumauma seedlings to withstand for a long period of time (19 months) without succumbing to adverse light conditions is quite remarkable. Sumauma has the ability to withstand flooding and to thrive in low-fertility soil (Noldt et al., 2008). It can also grow under limited water availability (Gómez-Maqueo and Gamboa-deBuen, 2022). Altogether all these characteristics make of the sumauma tree a good candidate to be used in reforestation programs, as suggested by Román-Dañobeytia et al. (2015) and Vargas-Simón et al. (2022).

CONCLUSION

Plant growth was greatly improved with a rise in irradiance, and hence maximum biomass accumulation occurred under direct sunlight. It was estimated that the whole-plant compensation point is about 1.0 mol m^{-2} day^{-1} (~3% full sunlight in the open). Because sumauma is a fast-growing tree, we had expected the seedlings would not survive many days under deep shading. Notwithstanding, the great majority of them did not succumb under deep shading. This occurred even when under deep shading the seedlings allocated just a little amount of biomass to leaves and ceased to grow. We conclude that the 14 months the plants were kept in the greenhouse (at moderate shading) prior to deep shading exposure allowed them to store energy (e.g. non-structural carbohydrates), which were most likely used to sustain respiration during the exposure to deep shading. Altogether these results demonstrate that sumauma is not only a fast-growing and light demanding species, but it also exhibits high plasticity in response to changing light conditions, as the seedlings subjected to deep shading, drastically change leaf and plant traits. These results improved understanding of this multipurpose tree, a potential candidate to be used in reforestation programs.

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APPENDIX – Schematic drawing of the experiment setup

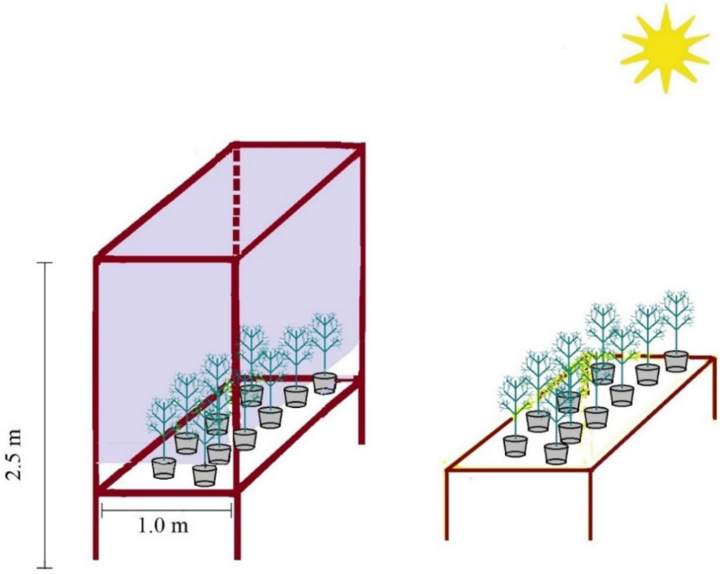

Figure A1. Schematic drawing of the experiment setup showing the seedlings under shading conditions and under direct sunlight (the drawing is not in scale).