

Article

Morpho-Physiological Adjustment of *Swietenia humilis* Zucc. Plants to Varied Nutrient and Light Conditions and Their Performance in Nurseries and Fields Under Soils with Different Preparations

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Abstract: To enhance the plantation performance of *Swietenia humilis* Zucc., a threatened precious woody species from the dry tropics of Latin America, this study examined its morpho-physiological responses to variations in nutrient and light availability. We established a nursery trial with factorial treatments: three levels of fertilization (4, 6, and 8 g L^{−1} of substrate using a controlled-release fertilizer, CRF, 18-6-12) and two shade intensities (60% and 40%), alongside a full sun treatment. The field performance of nursery-raised plants was evaluated under two site conditions (with and without mechanical soil preparation) over 48 months. In the nursery, *S. humilis* exhibited diverse morpho-physiological characteristics influenced by the studied factors, with optimal growth observed at 6 g of the CRF and 40% shade. Mechanical soil preparation significantly improved plant survival, reducing mortality risk by 99.16% and increasing survival probability to nearly 75%. Height growth was also enhanced, being 2.5 times greater in the prepared site compared to that in the unprepared one. *S. humilis* showed acclimatization in the field, producing new foliage with high chlorophyll content. In conclusion, nursery management and soil site preparation influence the field performance of *S. humilis*. These findings have practical implications for improving the management of *S. humilis* in plantations across the dry tropics.

Keywords: conservation; ecophysiology; functional traits; seedling quality

1. Introduction

In various regions of the Latin American dry tropics, establishing forest plantations with native species is promoted to mitigate deforestation's adverse effects [1]. However, high tree mortality during the initial years often leads to project failure. Poor survival is mainly attributed to adverse soil and climatic conditions at plantation sites, including high irradiance levels, weed competition, and compacted soils with low nutrient and water availability [2]. These conditions, coupled with transplanting stress, exacerbate the negative impact on plant survival [3].

Forest nurseries serve as the primary source of plants for plantations, and there is widespread agreement on the pivotal role of nursery-stage plant management in determining field performance [4,5]. So, effective management methodologies should aim to foster

morpho-functional attributes conducive to thriving in specific field conditions. Cultural practices are instrumental in promoting the morphological and physiological traits that influence survival and growth responses [6,7].

The morpho-physiological changes that nursery practices induce are a functional response that derives from modifying or altering factors determining or involved in plant growth [8]. Irradiance and mineral nutrient availability are two of the major abiotic factors that limit plant growth. Faced with variations in the availability of these resources, many plants respond phenotypically, for example, at the leaf level, with changes in leaf area and thickness, and at the whole plant level, with modifications in biomass production and allocation [8,9]. These adjustment mechanisms are a strategy to maintain maximum photosynthesis and growth rates [10,11], which implies for a given genotype the production of different functional phenotypes according to the degree of environmental variability [12,13]. This behavior is strongly regulated by the acclimation capacity of each species, in which the level of plasticity or other conditions of its ecology play a determining role [14,15].

Understanding how plants respond to changes in mineral nutrients and light by recognizing species-specific acclimation responses presents a valuable research opportunity. This knowledge has practical implications for improving nursery and field management techniques of forest species utilized in active ecosystem restoration (plantations) [16,17]. Regarding mineral nutrients, fertilization in forest nurseries plays an essential role in promoting morpho-functional attributes that can be helpful to enhance plant performance under adverse environmental conditions [18]; however, the amount of nutrients provided modifies the magnitude of the plant's response, so it is important to define adequate rates of fertilization for each species [19].

In the same way, proper light management is crucial for producing plants with desirable characteristics, particularly in regions with high irradiance and low relative humidity, such as those in warm or tropical climates. In these regions, growers often use shade nets to protect seedlings from excessive radiation and the resultant heat during all phases of growth [20]. However, shade netting affects plant growth and development, so adjusting the amount of light or shade depending on species' light requirement can regulate plant growth, thereby influencing plant morphology and physiology, as proved experimentally by Basave-Villalobos et al. (2022) [16,17].

Although prior research has examined the effects of nutrients and light availability on forest species, either individually or in combination [9,21], there remains a knowledge gap, particularly for threatened species lacking biological or silvicultural data. Furthermore, much of the existing methodology focuses on controlled or semi-controlled conditions rather than field settings, limiting the ability to fully understand a species' acclimation potential [22,23].

Another essential factor to consider when evaluating the field performance of nursery-grown plants is the site conditions. Survival and growth rates are heavily influenced by soil characteristics, particularly in environments with limiting factors. For instance, in restoration projects, the significant benefits of mechanical soil preparation in enhancing plant survival and growth have been documented [24].

Swietenia humilis Zucc. (Meliaceae), a threatened species native to the dry tropical forests of the Pacific slope (from Mexico to Central America), requires greater understanding to aid in its conservation efforts. Due to habitat fragmentation, its natural populations are dwindling, leading to it being listed as a threatened species in the CITES (the Convention on International Trade in Endangered Species on Wild Fauna and Flora) appendices [25]. Establishing plantations can help mitigate this loss by either conserving existing populations or expanding remnant sizes [26]. Therefore, it is crucial to enhance *S. humilis* management in nurseries and ensure successful plantation establishment in the field. This study aimed to (1) assess how nutrients and light levels affect the morphological and physiological traits of *S. humilis* plants during their nursery stage, and (2) evaluate plantation survival, acclimatization, and growth under different field conditions.

2. Materials and Methods

2.1. Nursery Phase

The study was conducted in a rustic nursery installed on a property in the community of La Bajada, municipality of Coyuca de Catalán, Guerrero, Mexico ($18^{\circ}19'0''$ N and $100^{\circ}40'19.83''$ W), during a period of 14 weeks between April and July 2020. During that time, in the open field, maximum and minimum temperature averages were 34°C and 23°C , respectively, and the relative humidity averaged 54% at 12:00 h (data recorded with a HOBO MX2301A[®]; Onset Computer Corp., Bourne, MA, USA).

2.1.1. Plant Production

Plant material originated from seeds collected in Zacapalco, Buenavista de Cuellar municipality, Guerrero, Mexico. The seed source was chosen based on a prior study evaluating germplasm quality in local sources in Guerrero, Mexico [26], which details the collection site and seed characteristics, including weight, vigor, viability, and germination. Plant production lasted for three months and took place in a container system using rigid 380 mL tube-type polypropylene containers. The substrate comprised a mixture of 60% peat moss, 30% perlite, and 10% vermiculite, supplemented with Multicote 8[®] 18-6-12 + 2MgO + micronutrient controlled-release fertilizer (CRF; Haifa Chemical Ltd., Matam-Haifa, Israel) at doses of 4, 6, and 8 g L⁻¹. Each fertilization level included 150 containers. Seeds were sown directly into the containers at a depth of approximately 2 cm. Germination and emergence occurred under a shade house with 60% shading, with seedlings emerging between 10 and 20 days after sowing.

2.1.2. Experimental Design and Nursery Procedures

After emerging (20 days after sowing), 360 seedlings, homogeneous in height (18 ± 0.5 cm) and diameter (2 ± 0.2 mm), composed of 120 seedlings from each previous fertilization level applied were selected. Then, these were subjected to two shade treatments, consisting of 60 and 40% shade intensities, as well as full sun treatment as a control. Under full sunlight, the average minimum and maximum values of the photosynthetic photon flux density (PPFD) were recorded as 59 and 2460 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, during a photoperiod from 8:00 to 20:00 h (Figure 1).

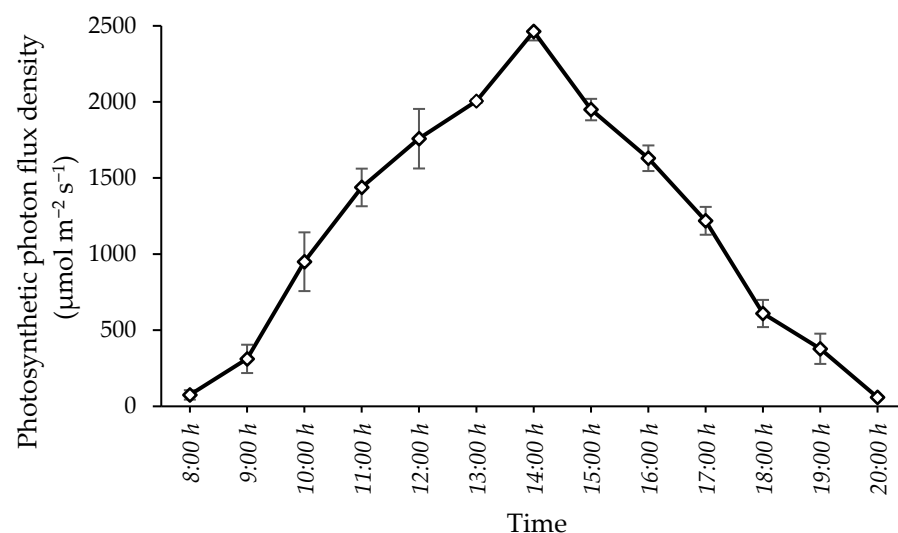


Figure 1. Dynamics of photosynthetic photon flux density during a photoperiod of 8:00–20:00 h in the study area. Measurements were taken with a quantum light meter over 30 days during the study period.

The shading treatments were defined using black polyethylene mesh, with the respective percentage of shade specified by the manufacturer (Plastimallas[®], Mexico City,

Mexico). These types of shade nets are commonly used in forest nurseries, and the shade intensities examined fell within the range of light conditions typically observed under canopy and in clearings or open fields in a tropical dry forest, as reported by Lebrija-Trejos et al. (2011) [27]. The light interception for each shading net was corroborated. For this purpose, simultaneous measurements of PPFD above and below the shade nets were conducted at midday using a quantum light meter (LightScout[®], Spectrum Technologies, Inc. Plainfield, IL, USA) to calculate the percentage of incident PPFD at the seedling height. The values were 40% and 60% PPFD for the 60% and 40% shade treatment, respectively.

These shade treatments were represented by shading houses covered with their respective mesh. Four houses of 1.5 m in length, 1.5 m in width, and 1.5 m in height were constructed for each light condition. Temperature (°C) and relative humidity (%) in each condition ($n = 1$) were recorded daily at 12:00 h with HOBO MX2301A[®] data loggers (Onset Computer Corporation, Bourne, MA, USA) (Table 1).

Fertilization and shade treatments were analyzed using a 3×3 factorial arrangement of treatments in a completely randomized block design with four replications and 10 plants as an experimental unit. The structure of the treatments is described below (Table 1):

Table 1. Description of treatments and average values of the environmental conditions monitored in each shade treatment.

Treatments	Fertilization Level (g L ⁻¹)	Shade Level (%)	Maximum Temperature (T Max.; °C)	VPD * for T Max. (kPa)	Minimum Temperature (T Min.; °C)	VPD for T Min. (kPa)	Relative Humidity (%) †
T1	4	60	37	2.19	21	0.87	65
T2	4	40	35	2.13	21	0.94	62
T3	4	Full sun	34	2.50	23	1.32	53
T4	6	60	37	2.19	21	0.87	65
T5	6	40	35	2.13	21	0.94	62
T6	6	Full sun	34	2.50	23	1.32	53
T7	8	60	37	2.19	21	0.87	65
T8	8	40	35	2.13	21	0.94	62
T9	8	Full sun	34	2.50	23	1.32	53

* VDP: vapor pressure deficit. † Average values during the experimental period.

2.1.3. Plant Sampling and Response Variables

A range of morphological and physiological traits were assessed in three-month-old plants, randomly selected for each replicate and treatment. The plants were removed from the pots, and the growing media were carefully washed off the root plugs using tap water for destructive sampling. The plants were then separated into leaves, stems, and roots. Morphological variables such as shoot height (cm), root collar diameter (mm), and leaf area (cm²) were measured, with the latter determined using Image J 1.53a software [28].

Afterward, each plant part was rinsed with deionized water, oven-dried at 70 °C for 72 h (until reaching constant weight), and weighed to obtain biomass measurements. The biomass (g) of leaves, stems, roots, and total plant were measured using an analytical balance (AND[®] GR-120, A&D Company, Ltd., Tokyo, Japan). Based on these biomass values, the proportions of leaf biomass (%; leaf biomass/total biomass $\times$ 100), stem biomass (stem biomass/total biomass $\times$ 100), and root biomass (root biomass/total biomass $\times$ 100) were calculated. Additionally, the specific leaf area (SLA; cm² g⁻¹) was determined by dividing the leaf area by the leaf biomass. Finally, the Dickson Quality Index (DQI), a key morphological indicator of plant quality, was calculated using the following formula [29]:

$$DQI = \frac{\text{Total biomass (g)}}{\frac{\text{Shoot height (cm)}}{\text{Stem diameter (mm)}} + \frac{\text{Shoot biomass (g)}}{\text{Root biomass (g)}}}$$

Prior to the described destructive sampling, the relative chlorophyll content was assessed using a portable Minolta SPAD 502 Plus meter (Spectrum Technologies, Inc. Plainfield, IL, USA). This assessment was conducted on each plant in quadruplicate, utilizing leaves of the same physiological age, specifically those from the middle part of the foliage. Additionally, the nutrient status was evaluated by measuring the content of nitrogen (N), phosphorus (P), and potassium (K) in leaves (mg leaves^{-1}). Chemical analyses were performed on four composite samples per treatment. The concentration of each element was determined, and biomass data were utilized to calculate the content. Nitrogen was determined using the Micro-Kjeldahl method, phosphorus by photo-colorimetry through reduction with the Vanadate–Molybdate method, and potassium by the direct reading of the digestate in an atomic absorption spectrometer. Nutrient uptake efficiency (NUE; %) was calculated using the following equation [30]:

$$\text{NUE (\%)} = \frac{\text{Plant Nutrient Content (PNC)} - \text{PNC of unfertilized seedlings}}{\text{Nutrient fertilization rate}} \times 100$$

The nutrient content of unfertilized seedlings was analyzed in newly germinated plants. The fertilization rate for nitrogen (N), phosphorus (P), and potassium (K) was calculated per seedling, based on the amount of Multicote 8[®] (18-6-12) fertilizer applied and the nutrient concentrations specified on the product label.

Additionally, net assimilation rates (NARs; $\text{mg cm}^{-2} \text{ day}^{-1}$) were measured to assess the photosynthetic capacity of the plants, as this is a complex physiological parameter influenced by both photosynthesis and respiration processes [31]. NARs were determined using the following formula [31]:

$$\text{NAR} = [(\text{TB}_2 - \text{TB}_1) \times (\ln \text{LA}_2 - \ln \text{LA}_1)] / [(\text{LA}_2 - \text{LA}_1) \times (\text{T}_2 - \text{T}_1)]$$

where TB refers to total plant biomass, LA to leaf area of plants in absolute and logarithmic values (ln), and T to time. In all cases, 1 and 2 refer to an initial and final harvest, respectively, 80 days apart.

Finally, growth was analyzed in the whole plants in terms of relative growth rates (RGRs; $\text{mg g}^{-1} \text{ day}^{-1}$), according to the following equation [32]:

$$\text{RGR} = (\ln \text{TB}_2 - \ln \text{TB}_1) / \Delta t \text{ (days)}$$

where TB_1 and TB_2 refer to the plant total biomass in logarithmic values (ln) in the initial and final harvest, respectively. Δt is the interval of time between harvests (80 days).

The variables were evaluated in a sample size of ten plants per each treatment combination (40 plants per block). In the case of the NAR and RGR variables described above, a sample of 40 plants, harvested before being subjected to the light treatments, was used. These plants had the same measurements in terms of height and diameter as the group of 360 plants and received the same procedure described above for the calculation of leaf area and biomass.

2.2. Field Phase

2.2.1. Outplanting

In August 2020, during the rainy season at the study site, field planting was initiated to address the second objective of the study. The planting took place on a property located in the community of La Bajada (Coyuca de Catalán, Guerrero, Mexico). The site is situated on a gently sloping hillside (3° to 5°) and is primarily used for pasture and firewood extraction. The climate in the area is classified as AW0 according to the Köppen climate classification modified by García [33], characterized by an average annual temperature of 28.6°C and an annual precipitation accumulation of 1033 mm, with the period from June to September experiencing the highest rainfall. May registers the highest temperatures, with average maximums reaching 40°C . The dominant vegetation in the surrounding area comprises trees or shrubs of *Havardia acatlensis* (Benth.) Britton and Rose.

A plantation was established using a split-plot factorial design to evaluate the effects of site conditions and nursery treatments on plant survival, acclimatization capacity, and growth. The land was divided into four main plots: two underwent mechanical soil preparation (prepared site) involving plowing to a depth of 30 cm with a disk harrow, while the other two did not receive any soil preparation (unprepared site). Within each main plot, five planting lines were established. Along each line, one plant from each of the nine nursery treatments (sub-plots) was randomly planted, with a spacing of 2.5 m $\times$ 2.5 m in a square system layout. Planting holes were prepared with dimensions of 20 cm in width and 40 cm in depth.

Soil sampling was carried out on each site for soil chemical and physical analyses. Five topsoil samples (0–20 cm) were collected randomly from each plot using a post hole digger and combined into a composite sample. The soil was analyzed for soil moisture content (SMC; %), texture (clay, silt, and sand fraction; %), bulk density (g/cm^3), pH (H_2O), organic matter (%), and electrical conductivity (dS/m). The prepared site had an SMC of 18.34%, a sandy-clay loam texture with 24% clay, 26% silt, and 50% sand, a bulk density of 0.84 g/cm^3 , a pH of 8.31, 0.74% organic matter, and an electrical conductivity of 0.26 dS/m . The unprepared site recorded an SMC of 15.71%, also with a sandy-clay loam texture, but with 30% clay, 24% silt, and 46% sand, along with a bulk density of 0.90 g/cm^3 , a pH of 8.4, 0.74% organic matter, and an electrical conductivity of 0.22 dS/m .

Prior to planting, the plants underwent a preconditioning period, gradually transitioning them to full light exposure over one week. For plantation management, mechanical weed control was carried out with a machete and hoe in the planting lines as needed. Also, auxiliary irrigation was applied every two months during the dry season (November–May).

2.2.2. Data Collection

Survival, acclimatization capacity, and growth were assessed as indicators of plantation performance. Survival was monitored monthly over a 48-month period, recording the number of deceased plants and their respective dates of death. Acclimatization capacity was measured two months post-planting by quantifying chlorophyll content in new foliage of surviving individuals (three new and fully expanded leaves per plant). This approach accounts for transplanting-stress-induced pigment degradation and loss of original foliage; surviving plants produce new, acclimatized foliage [34]. Chlorophyll content serves as an indicator of acclimation due to its role in leaf absorbance and nitrogen reallocation among photosynthetic compartments [35,36].

Growth was measured monthly as increments in height (cm) and diameter (mm). Height was taken from the base of the stem to the main apex and the diameter at the base using the same reference point for subsequent measurements. With these observations, absolute growth rates in height (cm month^{-1}) and diameter (mm month^{-1}) were calculated.

2.2.3. Statistical Analysis

Nursery and field data were subjected to a two-way ANOVA at a significance level of $\alpha = 0.05$. Prior to this procedure, the assumptions of normality and homoscedasticity were validated. Field growth was compared over a six-month period (between October 2020 and March 2021) when the overall survival ranged from 80% to 70%.

Means were compared with Fisher's DMS test at a 95% confidence level. Statistical analyses were processed with infoStat software version 2008 [37].

The Cox Proportional Hazard (PH) model was used to assess the influence of prior nursery treatments and the condition of the planting site (prepared vs. unprepared) on the probability of plant survival [37]. A dichotomous (0, 1) code-censoring was used to define either failure or censorship. Plants still alive at the end of the study (final census) were coded as 0, while plants which died, i.e., those that resulted in the event of interest (death) were coded as 1. In addition to applying the Cox PH model to identify the influence of the covariates on plant survival, survival curves were estimated by site condition using Kaplan–Meir's method. Differences in survival were tested by the long-rank test [38].

Survival analyses were performed using the survival [39] and survminer [40] packages in R (version 4.4.1) [41].

3. Results

3.1. Effects of Fertilization and Nursery Light on Morphological and Physiological Characteristics

The interaction between fertilization and shade levels significantly influenced the root collar diameter ($p = 0.0186$), stem biomass ($p = 0.0366$) and its proportion ($p = 0.0275$), chlorophyll content ($p = 0.0031$), as well as nitrogen, phosphorus, and potassium contents ($p < 0.0001$), and the efficiency in the uptake of these minerals ($p < 0.0001$). Fertilization had significant effects only on the proportion of root biomass ($p = 0.0195$). Similarly, significant differences were observed with the main effects of shade treatments, particularly in shoot height ($p = 0.0003$) and specific leaf area ($p = 0.0002$). Other variables assessed did not exhibit statistical differences ($p > 0.05$) (Table 2).

Table 2. Summary of ANOVA ($\alpha = 0.05$) results for the effects of fertilization and shade levels on morphological and physiological variables of *Swietenia humilis* Zucc. plants at nursery stage.

Variables	Factors	<i>p</i> -Value
Shoot height	Fertilization	0.3560
	Shade	0.0003 ***
	Interaction	0.2395
Root collar diameter	Fertilization	0.3448
	Shade	0.3424
	Interaction	0.0188 **
Leaf biomass	Fertilization	0.6050
	Shade	0.7923
	Interaction	0.0550
Stem biomass	Fertilization	0.6612
	Shade	0.3890
	Interaction	0.0366 **
Root biomass	Fertilization	0.6300
	Shade	0.3395
	Interaction	0.5074
Total biomass	Fertilization	0.7709
	Shade	0.4990
	Interaction	0.1030
LBP [‡]	Fertilization	0.8270
	Shade	0.7084
	Interaction	0.1411
SBP	Fertilization	0.1590
	Shade	0.2958
	Interaction	0.0275 **
RBP	Fertilization	0.0195 **
	Shade	0.7664
	Interaction	0.7068
Foliar area	Fertilization	0.6245
	Shade	0.4426
	Interaction	0.0585
Specific leaf area	Fertilization	0.8014
	Shade	0.0002 ***
	Interaction	0.9913

Table 2. Cont.

Variables	Factors	p-Value
Dickson's quality index	Fertilization	0.5940
	Shade	0.2996
	Interaction	0.2258
Nitrogen (N), phosphorus (P), and potassium (K) content	Fertilization	0.0002, 0.0001, 0.0002, resp.
	Shade	0.0362, 0.8745, 0.2251, resp.
	Interaction	<0.0001 ***
N, P, and K uptake efficiency	Fertilization	0.0001
	Shade	0.0107, 0.9891, 0.1811, resp.
	Interaction	<0.0001 ***
Net assimilation rate	Fertilization	0.9955
	Shade	0.5551
	Interaction	0.2762
Relative growth rate	Fertilization	0.7709
	Shade	0.4990
	Interaction	0.1030
Chlorophyll content	Fertilization	0.7336
	Shade	0.0058
	Interaction	0.0031 ***

‡ LBP, SBP, and RBP leaf, stem, and root biomass proportion, respectively. ***, ** Significant at 0.01 and 0.05 levels of probability. Significant p-values are bold-faced.

Plants with the largest diameter (6.27 mm) were those from treatment T8 (8 g of CRF + 40% shade), exhibiting a difference of nearly 1.5 mm compared to plants from T3, produced with 4 g of CRF at full sun (Figure 2a), which had the smallest diameter. A similar pattern was observed in stem biomass, with a 70% difference between the maximum (2.19 g from plants in T8) and minimum values (1.29 g from plants in T3) (Figure 2b). This increase in stem biomass in T8 was reflected in its proportion, with 41.5% of total biomass allocated to this organ (Figure 3). In terms of chlorophyll content, plants from T1 (4 g CRF + 60% shade) exhibited the highest value (40.08 SPAD units), showing a superiority of almost eight units compared to T7 (8 g CRF + 60% shade) plants, which had the lowest value (Figure 2c).

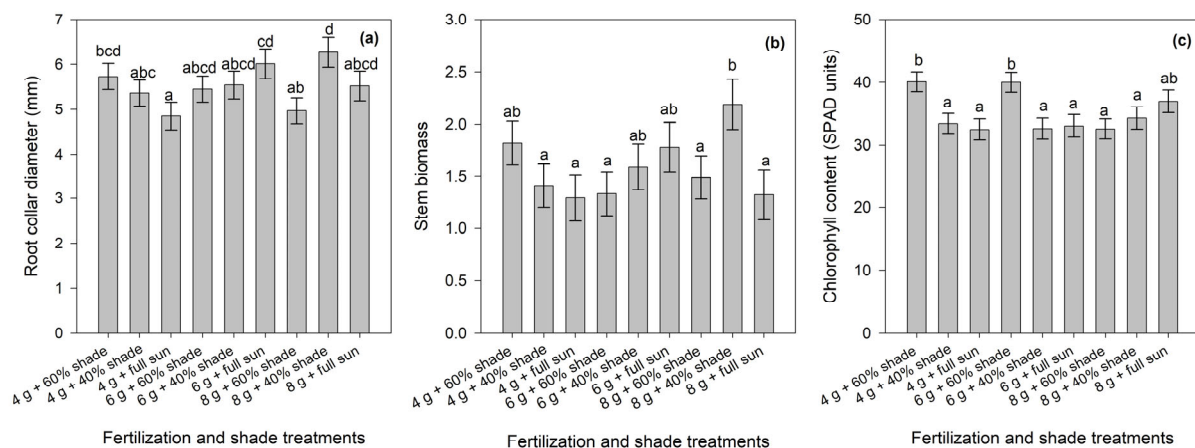


Figure 2. Diameter (a), stem biomass (b), and chlorophyll content (c) (mean $\pm$ S.E.) of *Swietenia humilis* Zucc. plants in response to fertilization and shade in nursery. Bars with a letter in common are not significantly different ($p > 0.05$) according to Fisher's DMS test ($\alpha = 0.05$). Controlled-release fertilizer Multicote 8® 18-6-12 at doses of 4, 6, and 8 g per liter of substrate.

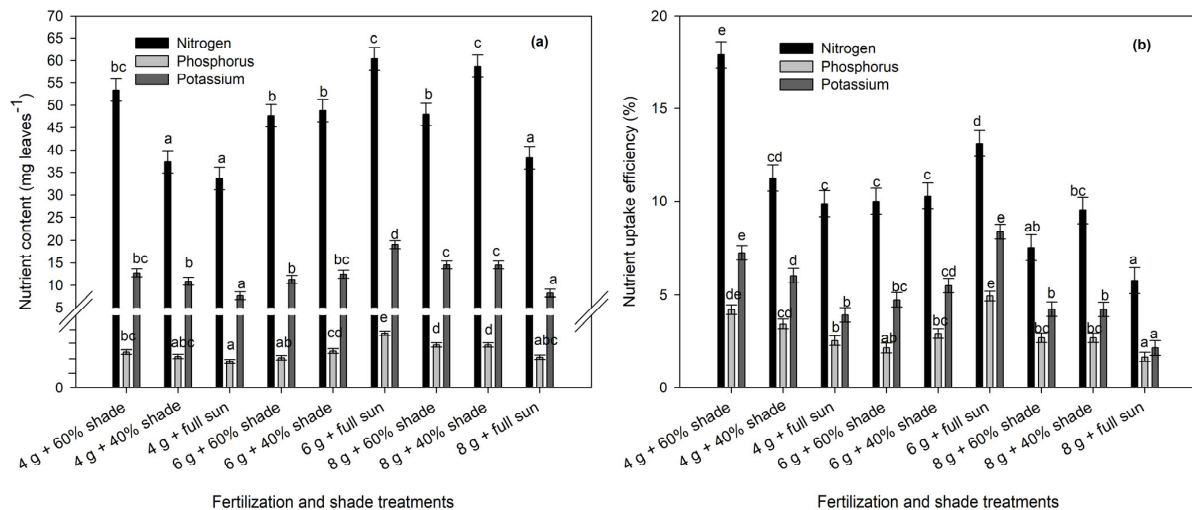


Figure 3. Content (a) and uptake efficiency (b) of nitrogen, phosphorus, and potassium (mean $\pm$ S.E.) of *Swietenia humilis* Zucc. plants in response to fertilization and shade in nursery. For nutrients, bars with a letter in common are not significantly different ($p > 0.05$) according to Fisher's DMS test ($\alpha = 0.05$). Controlled-release fertilizer Multicote 8[®] 18-6-12 at doses of 4, 6, and 8 g per liter of substrate.

In terms of nutrient status, plants from T6 (6 g CRF + full sun) exhibited the highest concentrations of nitrogen (N), phosphorus (P), and potassium (K). These plants showed differences of 80% in N, 108% in P, and 148% in K compared to plants from T3, which had the lowest nutrient contents in this case (Figure 3a). Related to nutrient uptake efficiency, particularly for nitrogen, T1 demonstrated the highest efficiency, tripling the efficiency observed in T9 (Figure 3b). In contrast, phosphorus and potassium uptake was more efficient in T6 plants. These plants showed differences of 198% for phosphorus and 291% for potassium compared to the efficiency of plants from T9 (which, like nitrogen, exhibited the least efficiency in the uptake of these elements) (Figure 3b).

Concerning the effects of fertilization levels, the 4 g CRF dose increased the proportion of biomass allocated to the roots to 21.21%, contrasting statistically with the 18.18% of biomass produced by plants cultivated with 8 g of CRF (Figure 4).

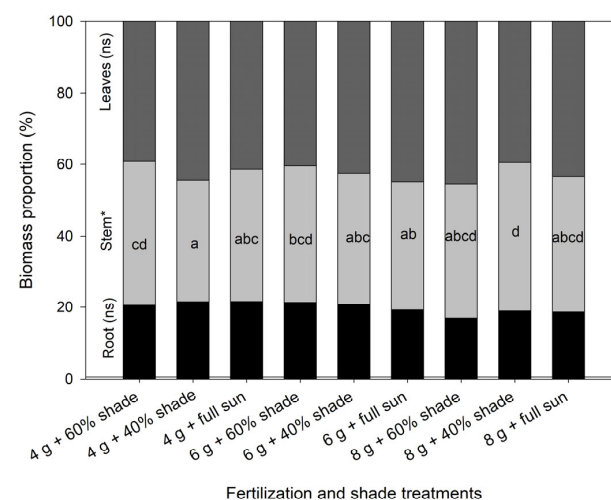


Figure 4. Proportion of biomass in leaves, stem, and root (mean values) of *Swietenia humilis* Zucc. plants in response to fertilization and shade in nursery. ns: non-significant; * statistical differences were observed only in the stem. In this case, segments within bars with a letter in common are not significantly different ($p > 0.05$) according to Fisher's DMS test ($\alpha = 0.05$). Controlled-release fertilizer Multicote 8[®] 18-6-12 at doses of 4, 6, and 8 g per liter of substrate.

Likewise, in the effects of the shade treatments, the plants of the highest shade intensity (60%) showed a difference of 25% in shoot height, compared to those grown at full sun (Figure 5a). Similarly, the specific leaf area was also highest at 60% shade and decreased as shade intensity diminished (Figure 5b).

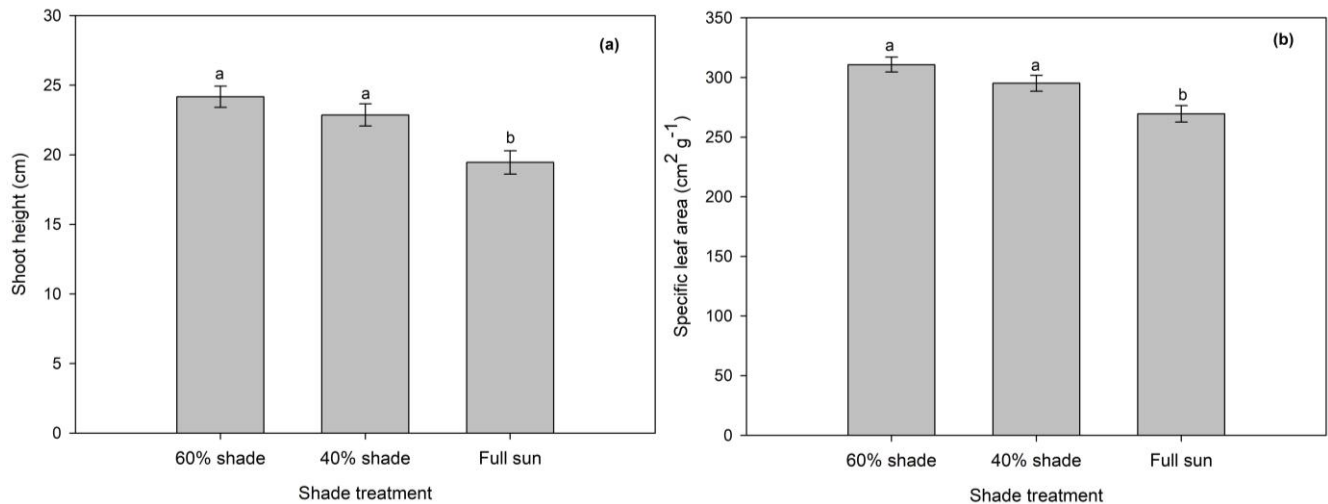


Figure 5. Shoot height (a) and specific leaf area (b) (mean $\pm$ S.E.) of *Swietenia humilis* Zucc. plants in response to shade treatments in nursery. Bars with a letter in common are not significantly different ($p > 0.05$) according to Fisher's DMS test ($\alpha = 0.05$).

3.2. Site Condition Effects

The condition of the planting site significantly affected plant survival, whereas nursery treatments did not have an influence (Table 3). According to the Cox PH model, a hazard ratio of 0.008434 was obtained, indicating that the risk of mortality was reduced by nearly 99.16% when plants were established in mechanically prepared soil (Table 3). As a result, the number of plants surviving until the final monitoring was significantly higher ($p < 0.0001$) on the prepared site compared to that on the unprepared site, where survival did not exceed 50% during the first 12 months of the study (Figure 6).

Table 3. Results of the Cox PH model used for analyzing field survival of *Swietenia humilis* Zucc. plants as a function of nursery treatments and site condition.

Variable Name	Coef.	Std. Err.	z	$p > z $	Haz. Ratio
Site condition: prepared	−4.775535	0.714109	−6.687	<0.0001	0.008434
Nursery treatment (NT) T2	−0.182119	0.690812	−0.264	0.7921	0.833502
NT-T3	−0.614066	0.73291	−0.838	0.4021	0.541146
NT-T4	−0.634756	0.701698	−0.905	0.3657	0.530065
NT-T5	−0.564382	0.713937	−0.791	0.4292	0.568711
NT-T6	−0.550174	0.709879	−0.775	0.4383	0.576849
NT-T7	1.169328	0.679742	1.72	0.0854	3.219829
NT-T8	−0.040628	0.727728	−0.056	0.9555	0.960186
NT-T9	−0.024916	0.699501	−0.036	0.9716	0.975392

Nursery treatment T1 was considered as control because it involved a lower level of fertilizer and light.

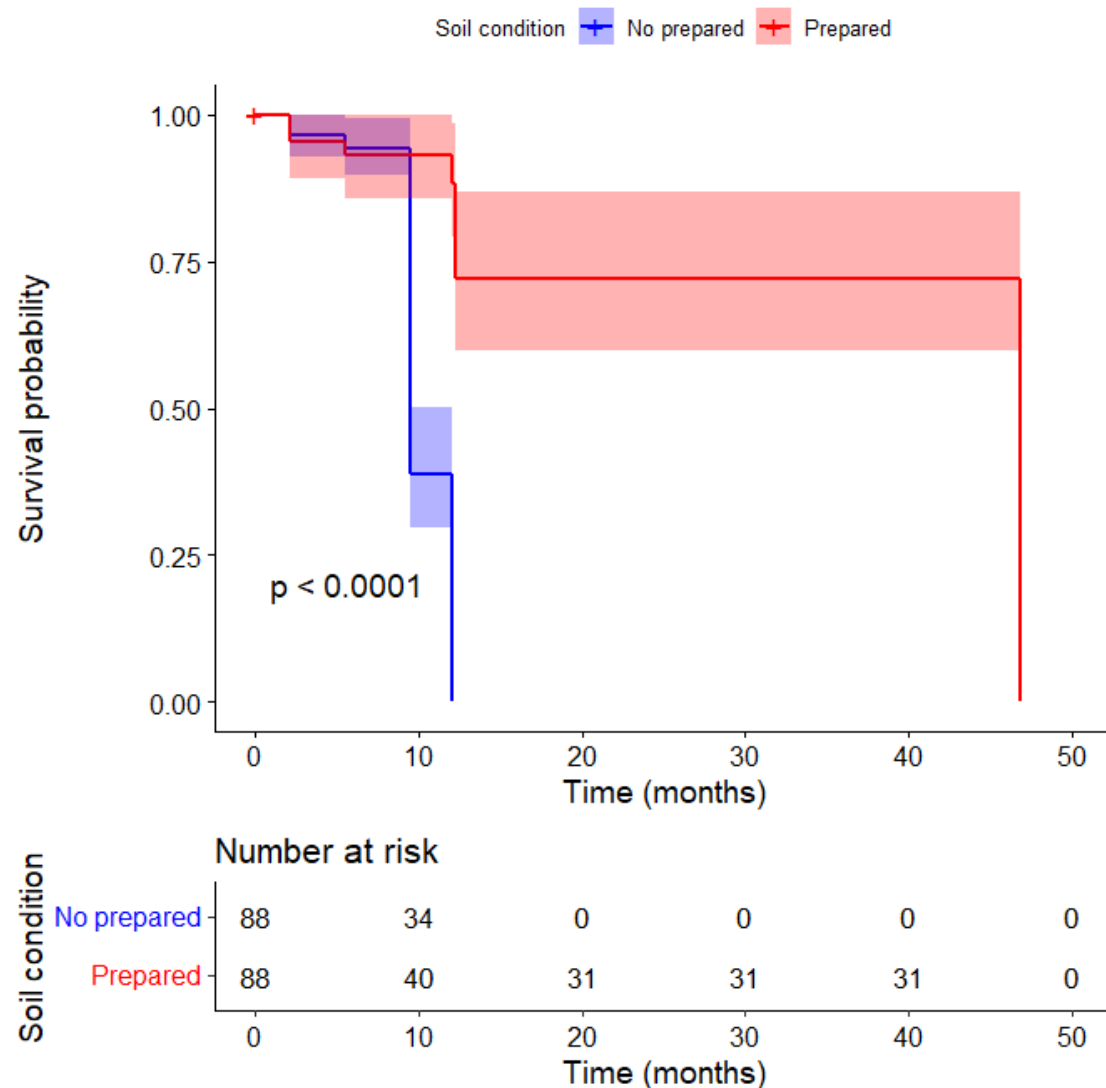


Figure 6. Kaplan–Meier survival curves adjusted to assess the probability of survival of *Swietenia humilis* Zucc. plants based on soil site conditions (mechanically prepared soil vs. unprepared soil).

Likewise, site condition significantly affected plant chlorophyll content ($p = 0.0002$). Two months after establishment, the plants with the highest chlorophyll contents (26.38 ± 0.51 S. E.; SPAD units) were those in the prepared site with a difference of 15% in relation to those in the unprepared site (23 ± 0.51 S. E.; SPAD units).

Height growth showed significant differences among nursery treatments ($p = 0.0263$) and between planting site conditions ($p = 0.0002$) (Figure 7). For the first case, T3 plants were superior in absolute growth rates with a growth rate twice as high as that recorded by T4 plants (6 g + 70% shade), which had the lowest growth rate (Figure 7a). Similarly, 2.5-times higher growth rates were observed in the prepared site (Figure 7b). Additionally, diameter growth exhibited a synergistic interaction between nursery treatments and site conditions ($p = 0.0047$). The most favorable response was observed with T3 plants in the prepared site, showing a nearly nine-times higher growth compared to the lowest growth observed with T1 in the unprepared site (Figure 7c).

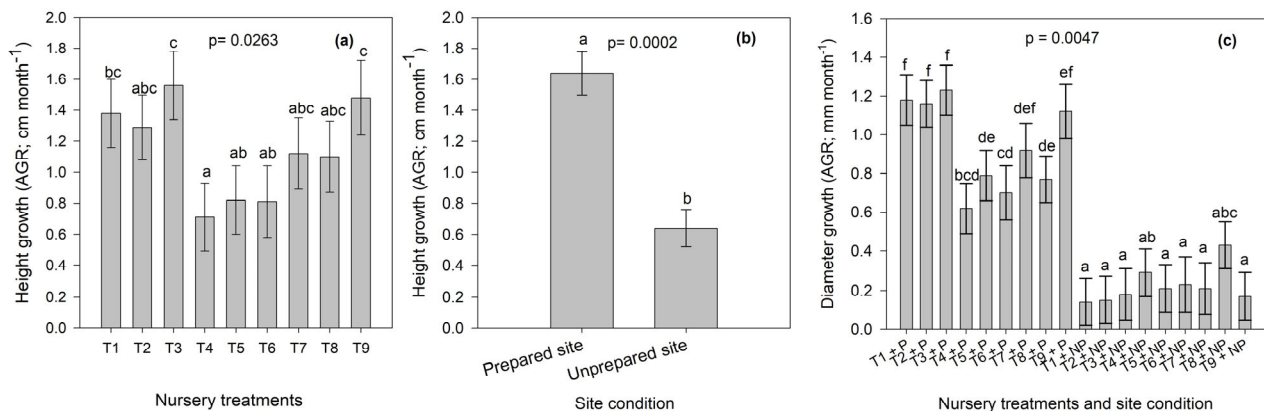


Figure 7. Growth rates in height and diameter (mean $\pm$ S.E.) of *Swietenia humilis* Zucc. plants by effect of nursery treatments (a), site conditions (b), or their interaction (c). T1: 4 g N + 60% shade; T2: 4 g + 40% shade; T3: 4 g + full sun; T4: 6 g + 60% shade; T5: 6 g + 40% shade; T6: 6 g + full sun; T7: 8 g + 60% shade; T8: 8 g + 40% shade; T9: 8 g + full sun. N refers to doses of the controlled-release fertilizer Multicote 8[®] 18-6-12. P: prepared site, NP: unprepared site. Bars with different letters are significantly different ($p > 0.05$) according to Fisher's DMS test ($\alpha = 0.05$).

4. Discussion

4.1. Variation in Morphological and Physiological Traits of *Swietenia humilis* in Response to Nutrients and Shade

S. humilis plants exhibited varying morphological and physiological traits based on the levels of nutrients and light in the nursery. Many attributes were influenced by either the combined or individual effects of these factors, indicating diverse acclimation responses. The impact of fertilization and light on diameter, stem biomass and its proportion, and chlorophyll content is primarily attributed to their crucial roles in plant growth, affecting photosynthetic activity and mineral nutrition processes [13]. This aligns with Gong et al. (2016) [9], who suggested that plasticity in response to one environmental factor may be influenced by another.

In natural environments, fluctuations in irradiation influence nutrient availability in the soil [42]. The root's nutrient supply relies partly on the concentration of nutrients in the soil solution [43], with fertilization defining this condition, especially in inert growing media like the one used in this study. Additionally, nutrient transport into plants from the root surface is largely regulated by transpiration, which generates the driving force for ion displacement [44,45]. Hence, light conditions are linked to nutritional processes. This relationship between fertilization and light explains the increased diameter and biomass production and allocation in plants receiving 8 g of fertilizer and 40% shade. This dose likely supplied nutrients in sufficient quantity to elevate their external concentration, while the 40% shade provided an adequate light intensity for photosynthetic activity without subjecting the photosynthetic apparatus to excessive water loss through transpiration, as seen in high sunlight exposure [22]. This is supported by higher vapor pressure deficit values observed in treatments exposed to full sun or open-sky conditions, which can lead to elevated transpiration rates [6].

Regarding the chlorophyll content, the lowest CRF dose (4 g) and highest shade environment (60% shade) resulted in the highest pigment levels. This response contradicts the expectation that a higher nitrogen supply would increase chlorophyll due to its role as the primary constituent of biomolecules [45]. However, it is possible that the 4 g CRF dose was sufficient to promote chlorophyll production in light-restricted plants, as this fertilizer product (with 18% N concentration) provided nearly 275 mg N plant⁻¹, a level within the range required by other fast-growing tropical species [46,47]. Conversely, the response to shade levels is logical since under shaded conditions, plants adjust to optimize light capture and absorption, indicating an increased investment in light-capturing antenna complexes [48].

The highest contents of nitrogen (N), phosphorus (P), and potassium (K) were observed with 6 g CRF at full sun. On the one hand, this confirms that this dosage provided nutrients at sufficient levels to promote mineral accumulation, as observed in *Pithecellobium dulce* (Roxb.) Benth plants [47]. On the other hand, regarding light, this response supports the idea about the influence of light environment on plant nutrient dynamics, where response in nutrient assimilation can be species-nutrient-specific, as demonstrated in a study involving *Crescentia alata* Kunth and *Enterolobium cyclocarpum* (Jacq.) Griseb plants [16].

Nevertheless, increased nutrient supply diminishes the efficiency of their utilization by plants [43,49,50]. This is supported by the observed responses in the efficiency of nitrogen (N), phosphorus (P), and potassium (K) uptake, where plants utilized fertilizer more effectively at lower doses, particularly for nitrogen. Nitrogen's high mobility and transport mechanisms facilitate its efficient uptake [45,51]. As for phosphorus and potassium, the 6 g CRF dose was found to be optimal due to the fertilizer's formula and nutrient ratio, ensuring a higher supply of these elements. This is particularly relevant for phosphorus, which has a low diffusion coefficient and requires sufficient concentrations in the soil solution for effective utilization [45].

Furthermore, the nutrient efficiency of *S. humilis* can be attributed to the individual effect of fertilization levels on the proportion of root biomass. Among the three-fertilizer dosage, the 4 g dose promoted a higher allocation of biomass to roots. This suggests that the lower nutrient supply compared to higher doses stimulated increased root formation. Such a response is considered a mechanism employed by plants to enhance their root volume and surface area available for ion uptake [43,52]. By increasing root system density, plants can optimize nutrient uptake by minimizing the distance over which nutrients need to be transported through the soil [50].

Regarding the effects of shade treatments on shoot height and specific leaf area, no differences were observed between the two levels of shade. There are taxa that, although they are primarily light-demanding, can develop a phenotype acclimated to shaded conditions, enabling them to function effectively in environments with reduced light availability [16,53]. However, the observed increase in these variables as light availability decreased reflected typical acclimation responses observed in many plants in heterogeneous light environments [22,54]. These characteristics are highly plastic, and under light limitation, plants tend to elongate their stems as an important strategy to maximize light capture in competitive environments, as noted by Masarovičová et al. (2016) [8]. This response is also considered a shade escape mechanism [22].

At the leaf level, thickness is also adjusted to enhance light capture and absorption. In shaded environments, leaves tend to be thinner due to a lower biomass-to-area ratio, whereas in high light exposure, this ratio increases, promoting thicker leaves [10]. In leaves exposed to high irradiance, increased thickness is often associated with a thicker mesophyll, originating from an increase in the thickness of palisade parenchyma and spongy parenchyma, as demonstrated in leaves of *Cordia trichotoma* (Vell.) Arráb. ex Steud. and *Machaerium brasiliense* Vogel [55]. This anatomical feature aids in dissipating excess radiation by extending the path length of light through scattering [13].

4.2. Field Performance

Field performance serves as the ultimate evaluation of nursery management practices, as the morphological and physiological attributes acquired by plants significantly impact their ability to acclimate to soil and climatic conditions at the planting site [56]. Indeed, the survival, acclimatization, and growth responses of *S. humilis* underscore the critical role of nursery cultural practices, as well as the decisive influence of site conditions [57].

Firstly, the higher survival rate in the prepared site was attributed to the improved physical soil conditions resulting from mechanical preparation, consistent with findings by Löf et al. (2012) [24]. Soil preparation aided in decompacting and reducing bulk density, albeit marginally. Decompaction enhances soil aeration and water infiltration, increasing soil moisture and modifying drainage, conditions conducive to root growth [58]. The

survival rate exceeding 70% in the prepared site suggests this beneficial effect, as water availability is the primary limiting factor for plant survival and growth in dry tropics [27,59].

In addition to the survival response, the impact of soil preparation on chlorophyll content, quantified as a field acclimation indicator, is noteworthy. Most surviving plants exhibited renewed foliage, indicating leaf-level acclimation expressed through the production of new, already acclimated foliage with altered physiology, as noted by Wyka et al. (2007) [12]. This was supported by the observed renewal of foliage and increased chlorophyll presence in this study. Chlorophyll, a crucial photosynthetic pigment, plays a pivotal role in determining leaf absorbance and represents nitrogen reallocation between various photosynthesis-involved compartments [35,36]. Under high light conditions, a greater allocation of nitrogen to electron transport capacity and soluble proteins is required, favoring photoprotection mechanisms, as reported with *Guazuma ulmifolia* Lam. [60]. Nevertheless, the acclimation mechanism observed in *S. humilis* in the field differs from that of its congener *Cedrela fissilis* Vell. plants, which acclimate by modulating morphological and physiological changes in pre-existing leaves that were previously formed under specific light conditions [53].

Regarding field growth, the effect of soil preparation on height can be attributed, in part, to factors discussed in relation to survival. It is plausible that with soil preparation, roots were able to grow deeper, facilitating adequate plant establishment [24]. However, the superior growth response of T3 plants (4 g CRF + full sun) is difficult to explain. In nursery evaluations, this treatment did not excel in any variable allowing for the inference of its performance based on a specific characteristic, such as stem diameter, which influences plant response in the field [61].

However, it is noteworthy that plants in the T3 treatment received a dose of 4 g of CRF, which promoted a greater allocation of root biomass. This morphological characteristic is crucial in sites with soil moisture restrictions [62]. Additionally, T9 plants (8 g CRF + full sun) also exhibited exceptional growth without statistical difference from T3. Both treatments were exposed to open-sky conditions, suggesting that plants in this condition were likely pre-acclimatized compared to those produced in shade, contributing to their superior field performance.

The pre-acclimation hypothesis is supported by a study on *Enterolobium contortisiliquum* (Vell.) Morong, where plants grown in full light developed morpho-anatomical and physiological characteristics conducive to better performance in open-field conditions [63]. This finding was corroborated by the performance of a *P. dulce* plantation in the dry tropics [17]. Dynamic acclimation mechanisms may explain such behavior [23], as *S. humilis* plants cultivated in shade likely experienced greater photoinhibition damage upon field establishment. This is a common repercussion experienced by plants in their photosynthetic apparatus due to abrupt changes in light environments, which is exacerbated in the field by other environmental factors such as humidity and temperature [34].

In practice, plants typically undergo a preconditioning stage at the end of the nursery production period to reduce transplanting stress before being released into the field [64]. Following this principle, plants grown in shade were gradually exposed to sunlight for a week in an attempt to pre-acclimatize them. Some species, like *Tabebuia chrysotricha* (Mart. Ex DC.) Standl., may fully reestablish their photosynthetic activity within this period [65]. However, for species like *S. humilis*, this timeframe might not have been sufficient for compensation. For instance, *C. fissilis* requires up to 30 days to regulate the damage caused by photoinhibition and achieve stable acclimatization to the new light environment [53]. Future studies are needed to analyze the acclimation dynamics of *S. humilis*, particularly through the evaluation of instantaneous physiological parameters related to photosynthetic acclimation, which were not assessed in this study.

Regarding fertilization, in the case of T9 plants, the higher dose they received suggested that residual fertilizer likely remained in their root ball. This residual fertilizer served as an external supply of nutrients in the field, highlighting one of the advantages of using controlled- or slow-release fertilizers in forest plant production [66,67]. This inference

was supported by the fact that T9 plants exhibited the lowest nutrient uptake efficiency in the nursery.

Finally, the growth in diameter corresponded with the increase in height, with the effect of nursery treatments combining with soil preparation at the site. This synergistic interaction holds significant practical implications for enhancing the nursery production of this threatened species and establishing plantations in dry tropic regions. It underscores the relevance of nursery practices, yet their effectiveness depends on the conditions of the planting site, making soil preparation decisive in this context. This evidence lays a foundation for enhancing the success of plantation projects in dry tropic regions by demonstrating the suitability of *S. humilis* for open-field plantations and underscoring the importance of both nursery management and site preparation.

5. Conclusions

In the nursery stage, *S. humilis* plants exhibited variations in morphological and physiological characteristics due to fertilization and shade levels. Several functional and quality attributes were affected by the interaction of these factors or their individual effects, highlighting diverse acclimatization responses. In field performance, survival was determined by site conditions, with soil mechanical preparation being crucial to enhance it. Additionally, the acclimation capacity of *S. humilis* increased with site preparation, evident through the formation of new leaves with high chlorophyll content. Both nursery management and planting site conditions independently influenced height growth, while the synergistic effects of these factors determined diameter growth. Although further studies are needed to quantitatively define specific plant quality indicators and to assess the influence of site conditions across a broader range of soil types, these findings, analyzed from a functional perspective, hold significant practical implications for enhancing nursery management practices and successfully establishing *S. humilis* plantations in future dry tropical restoration projects.

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