

Article

Habitat Type Influencing Survival and Early Growth of *Bertholletia excelsa* Seedlings in the Peruvian Amazon

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Abstract

The Brazil nut tree (*Bertholletia excelsa* Bonpl.) is a non-timber forest product of great ecological and economic importance in the southwestern Amazonian countries. The study aimed to analyze the effects of habitat (natural tree-fall gaps, logged gaps, and field crops) on the survival and early growth of *Bertholletia excelsa* (Brazil nut) seedlings in the Peruvian Amazon. Seedlings were monitored every 2 months for 1 year to record survival and seedling growth. We used linear mixed models to evaluate the effects of habitat type, time, and their interaction on diameter and height growth. The non-parametric Kaplan–Meier method was used to estimate survival probability. This study showed that the survival of *B. excelsa* seedlings was significantly higher in canopy gaps than in crop fields. We also revealed the negative effect of canopy cover on the early height growth. Height growth of surviving *B. excelsa* seedlings was significantly higher in logging gaps than in all other habitats, and in natural tree-fall gaps it was significantly higher than in crop fields, whereas seedlings in logging gaps and crop fields had significantly higher diameter growth than those in natural tree-fall gaps. Our results illuminate the potential of enrichment planting using *B. excelsa* in logged tropical rainforest in the southeast Peruvian Amazon.

Keywords: Brazil nut; canopy gaps; enrichment planting; Madre de Dios; reforestation

1. Introduction

The Amazon Basin harbors the largest extent of tropical forests worldwide [1]. They are considered biodiversity hotspots and provide numerous ecosystem services that benefit people globally [2,3].

The Brazil nut tree (*Bertholletia excelsa* Bonpl.) is a non-timber forest product of great economic importance [4]. It plays a key role in local economies in the southwestern Amazonian countries (Peru, Brazil, and Bolivia) [5,6]. This is because the traditional harvest of nuts from *B. excelsa* trees by local communities typically has a lower impact on the forest than other land uses (e.g., logging) [7,8]. Due to this, the *B. excelsa* tree is considered an icon of sustainable use in the Amazon [9,10]. In addition, this species dominates forest productivity and aboveground carbon storage in southwestern Amazonian forests [11], representing 1.31% of the total above-ground biomass in non-flooded Amazonian forests [12].

The dense and aggregated spatial distribution of *B. excelsa* trees facilitates the harvesting of its fruits in the Amazon regions of Brazil, Bolivia, and Peru [13]. Despite its



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importance, *B. excelsa* is considered vulnerable to extinction by the IUCN [14] and the mature forests where this species grows are threatened by severe degradation due to logging, road construction, agricultural expansion and wildfires [15]. As a consequence of these direct and indirect negative impacts, *B. excelsa* forest stands had low levels of natural regeneration [10,16]. In addition, many studies have shown that high harvest levels can affect the structure of natural *B. excelsa* populations, reducing the rates of naturally recruited seedlings [13,17]. Therefore, the risk of extinction of *B. excelsa* may increase due to overexploitation of seeds and being associated with deforestation and logging can also reduce its biogeographical range [18,19].

Given the low levels of natural regeneration of *B. excelsa* in forests, it is necessary to develop alternatives to improve seedling recruitment and enrich degraded forests [20,21]. In addition, considering the scattered distribution of *B. excelsa* in the Amazon, the difficulty of accessing its habitats [22,23], the biological degradation of its populations, and its photosynthetic plasticity in degraded environments, enrichment plantations for non-timber purposes are justified [24,25]. This framework could be used to restore productivity in degraded and abandoned areas affected by anthropogenic activities in the Amazon, e.g., pastures, logging gaps, abandoned logging roads, and secondary forests. Although several studies in the Brazilian Amazon assess the growth and mortality of *B. excelsa* seedlings in disturbed habitats [23,24], such studies are particularly rare in the Peruvian Amazon.

In Madre de Dios, in the Southern Peruvian Amazon, few studies have reported on the growth and survival responses of *B. excelsa* across different habitats. For example, Brouwer et al. [26] evaluated the growth and survival response of *B. excelsa* seedlings in agroforestry systems, natural gaps, pastures, and secondary forests, whereas Garate-Quispe et al. [22] focused on natural clearings and a disturbed old-growth forest. However, there is no study comparing early growth and mortality among natural tree-fall gaps, logged gaps, and field crops, widespread habitats in the Peruvian Amazon.

The present study aimed to analyze the effects of habitat type (natural tree-fall gaps, logged gaps, and field crops) on the survival and early growth of *Bertholletia excelsa* (Brazil nut) seedlings in the Peruvian Amazon. We hypothesized: (1) a higher survival in canopy gaps than in crop fields; (2) the height and diameter growth would respond differently to habitat conditions; and (3) an increasing canopy cover would negatively affect height growth. The results from this study will contribute to our understanding of variations in the growth and survival of *B. excelsa* seedlings during the first year across different habitat types.

2. Materials and Methods

2.1. Study Area

The study was conducted at four sites in the southeastern Peruvian Amazonian region of Madre de Dios, in the districts of Tahuamanu and Las Piedras (latitude 11°55' 54.74" S; longitude 69°5' 38.95" W) (Figure 1). Madre de Dios is a high-biodiversity tropical forest with a hot and humid tropical climate [26], an average annual temperature of 25.4 °C, and a mean annual rainfall of 2120 mm (for 1980–2020). For the study, we considered three habitat types (natural tree-fall gaps, logging gaps, and crop fields) across a gradient of human-induced disturbance, which are typical environments in the study area.

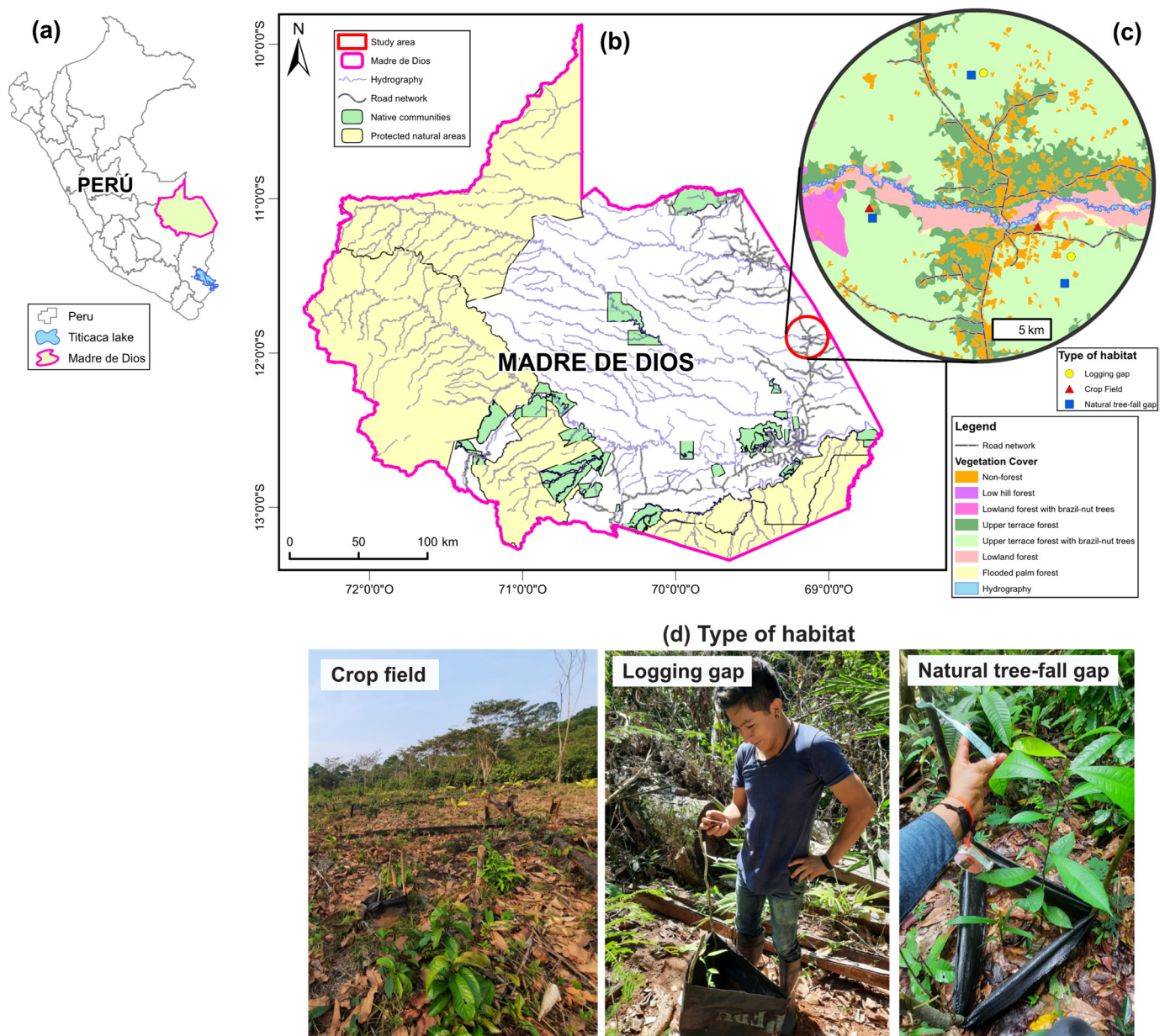


Figure 1. Location of the study area (c) on the map of Peru (a) and Madre de Dios (b), south-west Peruvian Amazon. (d) Photographs of the habitats where the *Bertholletia excelsa* seedlings were planted.

2.2. Study Design

The establishment experiment took place across three habitat types (natural tree-fall gaps, logging gaps, and crop fields) at four study sites. Due to difficulty accessing the sites, limited habitat availability within them, and the need for landowner authorizations, not all habitat types were represented at all sites. Seedlings were grown in a nursery run by Candela-Peru, using a standard substrate for *B. excelsa* (sand, sawdust, and forest soil at 1:1:1 ratio) in polypropylene containers (tubes with a volume of 280 cm³). We used tubes instead of plastic bags because they occupy less space, facilitate transport to the plantations, and can reduce the incidence of pests and diseases [27]. Seeds of *B. excelsa* were obtained from a natural forest near the study area (forest concessions). In the nursery, seedlings were maintained at 80% shade and watered on alternate-day basis.

The experiment was established at the end of the rainy season in April 2021. A total of 259 *B. excelsa* seedlings were planted across three habitats at 4 study sites. Each represented

habitat-by-site combination contained at least 21 seedlings, while not all habitats were available at every site (Table 1). Planting sites and habitats were selected based on land availability and landowner permission. Logging and tree-fall gaps were recently created clearings ranging in size from 260 to 320 m². The field crops were areas abandoned from agriculture available in each site, ranging in size from 0.3 to 0.5 ha. At the time of planting, seedlings were 3 months old and had an average total height of 7.6 ± 2.5 cm. Planting pits with a dimension of 40 cm × 40 cm × 40 cm (10 × 10 m spacing) were prepared in all treatments. In crop fields, at both available sites, only one planting area was used for the experiment. In logging and natural tree-fall gaps, seedlings were planted in multiple gaps per site. Between three and four seedlings were planted in each gap, depending on the availability of these habitats at each site. In addition, to reduce rodent damage, each plant was protected with a 50 cm tall polyethylene sack, placed around it in a triangular shape, and supported by wooden stakes. To simulate natural conditions, no vegetation management was carried out after planting.

Table 1. Location and seedling numbers per habitat type covered by the experiment across four study sites in the southwest Peruvian Amazon. The number of planting areas (gap or field crop) for each site is indicated in parentheses.

Site	Coordinates		Number of Seedlings by Habitat			
	Latitude	Longitude	Natural Tree-Fall Gap	Crop Field	Logging Gap	Total
Site 1	11°49'4.57" S	69°8'0.49" W	21 (6)	-	37 (10)	58
Site 2	11°54'31.56" S	69°13'18.74" W	35 (9)	28 (1)	-	63
Site 3	11°55'54.74" S	69°5'38.95" W	-	57 (1)	-	57
Site 4	11°58'24.39" S	69°4'33.83" W	31 (8)	-	50 (13)	81
Total			87	85	87	259

2.3. Data Collection

Seedlings were monitored every 2 months for 1 year to record survival (binary response—1 = living, 0 = dead), stem height (cm), and basal stem diameter (cm). Diameter was measured with a digital vernier caliper (model 78-440LA, Stanley®, Seattle, WA, USA) at the stem base, and plant height was measured with a flexometer (model FH-5M, Truper®, Mexico city, Mexico).

Seedling growth was calculated using two successive evaluations (Equations (1) and (2)). In addition, we considered zero the negative values of seedling growth caused by external factors such as damage from treefall, water stress, and attacks by herbivores and rodents [28].

$$HG = (H_2 - H_1) / (T_2 - T_1) \quad (1)$$

$$DG = (D_2 - D_1) / (T_2 - T_1) \quad (2)$$

where HG = seedling height growth (cm month⁻¹); H₁ = height of the seedling at assessment 1 (cm); and H₂ = height of the seedling at assessment 2 (cm). T₁ = initial reference time (month); T₂ = successive evaluation (two months after H₁). DG = seedling diameter growth (mm month⁻¹); D₁ = diameter of the seedling at assessment 1 (mm); D₂ = and diameter of the seedling at assessment 2 (mm).

A convex spherical densiometer (Model A Forestry Suppliers®, Jackson, MS, USA) was used to quantify canopy cover (%) in each seedling. Canopy cover, using the average of four measurements, was measured for each assessment in this study at 1 m above ground, facing each cardinal point.

2.4. Data Analysis

We used linear mixed models (LMMs) to evaluate the effects of habitat type, time, and their interaction on diameter and height growth, with canopy cover and total height at the time of planting as covariates, and individual plants nested within sites as random effects. Diameter and height growth were natural-log-transformed to meet the assumption of normally distributed residual errors. To remove variables with multicollinearity, the Variance Inflation Factor (VIF) was used. To identify the most parsimonious model and select the set of environmental variables that significantly affected diameter and height growth, we performed model selection using Akaike's information criterion (AICc) with the dredge function in the MuMIn package in R. The total height at the time of planting and habitat type $\times$ time had no significant effect on seedling growth and were removed during model selection. In addition, we used the Kenward–Rogers approximation to estimate the importance and significance (p -values) of model terms. In addition, the emmeans package with Tukey's adjustment was used to examine pairwise comparisons among the levels of the fixed factors.

The non-parametric Kaplan–Meier method was used to estimate survival functions based on time to the occurrence of the event. To compare survival rates among habitat types, the log-rank test was used with Benjamini–Hochberg (BH) adjustment for multiple testing. In addition, Cox proportional hazard regression was used to analyze the effects of canopy cover on seedling lifetimes.

All statistical analyses were performed in the statistical software R version 4.5.2 (The R Foundation, Viena, Austria) and Positron environment 2026.01.0 (Posit Software, Boston, MA, USA), using the packages ggplot2, bestNormalize, lme4, car, lmerTest, MuMIn, emmeans, ggeffects, multcomp, survival, and survminer.

3. Results

3.1. Seedling Survival

In overall, the survival of *B. excelsa* was similar for seedlings establishing in logging and natural tree-fall gaps throughout the experiment. In the first four months after planting, seedling survival across all habitat types similarly performed well (>90%). At the end of the sixth month, the survival probability of *B. excelsa* seedlings in crop fields decreased significantly compared with the other types of habitats. The Kaplan–Meier survival curves showed a significant difference in survival of *B. excelsa* seedlings among habitat types ($\chi^2 = 44.4$; $p < 0.001$) (Figure 2). Survival of *B. excelsa* in logging and natural tree-fall gaps were both significantly higher than those of the crop fields (log-rank test, $p < 0.001$), whereas there was no statistically significant difference between *B. excelsa* seedlings in logging and natural tree-fall gaps (log-rank test, $p = 0.43$). Additionally, there was non-significant relationship between canopy cover and survival probability (Cox regression; $\chi^2 = 2.3$; $p = 0.13$).

3.2. Seedling Growth

The best-fit models and their estimated parameters for height and diameter growth of *B. excelsa* seedlings are given in Tables 2 and 3. The LMM for growth height had a better goodness of fit than the LMM for growth diameter. The growth height LMM explained 62% of the overall variance (R^2_c) and 48% of the variance solely for fixed effects, whereas the growth diameter LMM only had an overall R^2_c of 44% ($R^2_m = 21\%$). The random effect of individual plants was significant ($p < 0.001$) for both height and diameter growth models and had a strong effect on R^2 increase, 14% and 23%, respectively. The LMMs revealed significant simple effects of habitat type and month on both height and diameter growth (F-tests, $p < 0.001$). Canopy cover negatively affected seedling height growth (LMM,

$F = 20.43, p < 0.001$). Although there was no significant effect of canopy cover on diameter growth (LMM, $p > 0.05$), this variable was not included in the LMM for diameter growth.

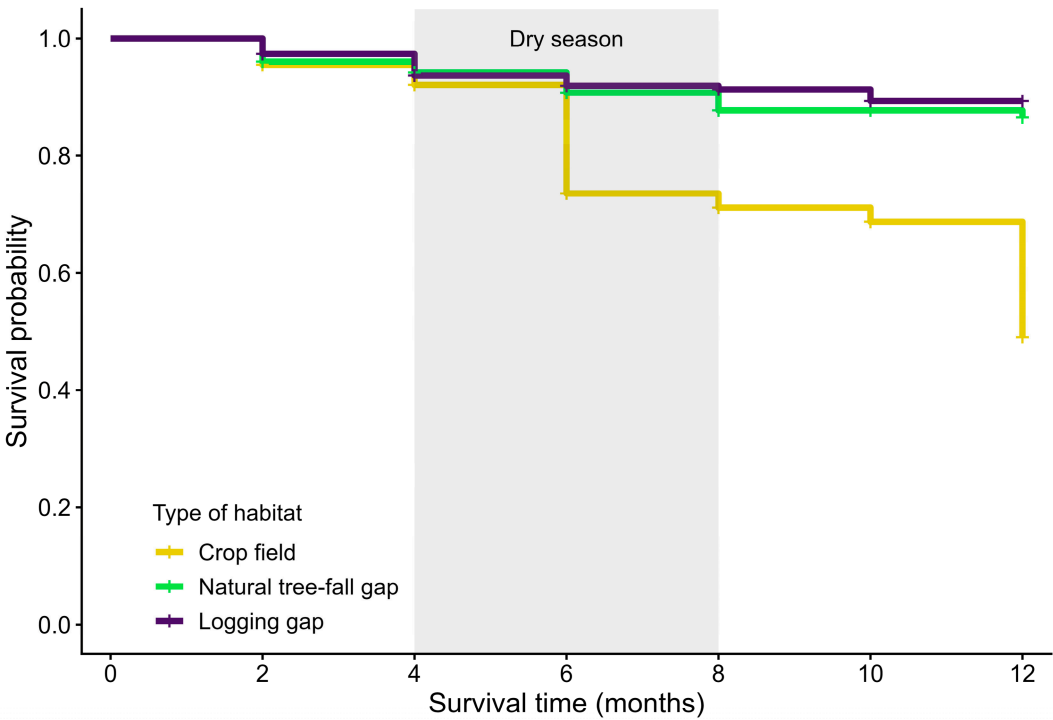


Figure 2. Kaplan–Meier curve illustrating survival probabilities for *Bertholletia excelsa* seedlings by habitat types.

Table 2. Results of linear mixed models testing the effects of canopy cover, habitat type, and time on height and diameter growth of *Bertholletia excelsa* seedlings.

Variable	Response Variable												
	Height Growth						Diameter Growth						
Fixed Effect	df	ddf	F-Value	VIF	p-Value	Variance Explained	Fixed Effect	df	ddf	F-Value	VIF	p-Value	Variance Explained
Canopy cover	1	176.6	20.46	2.19	<0.001	$R^2_c = 0.62$ $R^2_m = 0.48$	Type of habitat	2	10.1	14.86	1.01	<0.001	$R^2_c = 0.44$ $R^2_m = 0.21$
Type of habitat	2	25.3	18.15	2.20	<0.001		Month	5	788.0	49.92	1.01	<0.001	
Month	5	767.1	208.37	1.01	<0.001								
Random effect			Variance	Residual	p-value		Random effect			Variance	Residual	p-value	
Plant Site			0.09 0.005	0.23	<0.001 0.989		Plant Site			0.006 0.0001	0.016	<0.001 0.585	

R^2_c = conditional R^2 (variance including both fixed and random effects). R^2_m = marginal R^2 (fixed effects only). ddf = residual degrees of freedom, or degrees of freedom in the denominator.

Pairwise comparisons revealed that height growth was significantly higher during the first two months than during the remaining 10-month follow-up period, and this difference persisted throughout the study. However, after the second month, height growth rates were similar (Figure 3A). In contrast, diameter growth was significantly lower during the first two months and increased significantly over time (Figure 3B). Seedling height growth was significantly higher in logging gaps than in all other habitats, and height growth in natural tree-fall gaps was significantly higher than in crop fields. On the other hand, seedlings in logging gaps and crop fields had significantly higher diameter growth than those in natural

tree-fall gaps. However, the differences between logging gaps and crop fields were not statistically significant.

Table 3. Estimated parameters of linear mixed models testing the effects of the canopy cover, type of habitat, and time on height (a) and diameter (b) growth of *Bertholletia excelsa* seedlings.

Fixed Effects	Response Variable							
	(a) Height Growth				(b) Diameter Growth			
	Est	SE	Confidence Interval		Est	SE	Confidence Interval	
			2.50%	97.5%			2.50%	97.5%
Intercept	2.194	0.070	2.058	2.331	0.131	0.017	0.099	0.164
Type of habitat: natural tree-fall gap	0.244	0.094	0.059	0.429	−0.095	0.020	−0.134	−0.057
Type of habitat: logging gap	0.477	0.087	0.307	0.647	−0.023	0.021	−0.064	0.017
Month: 4	−1.361	0.047	−1.454	−1.269	0.096	0.013	0.071	0.120
Month: 6	−0.976	0.052	−1.078	−0.874	0.134	0.014	0.107	0.161
Month: 8	−1.264	0.053	−1.368	−1.160	0.150	0.014	0.122	0.178
Month: 10	−1.108	0.054	−1.213	−1.004	0.192	0.014	0.164	0.221
Month: 12	−1.039	0.055	−1.146	−0.931	0.177	0.015	0.148	0.206
Canopy cover	−0.007	0.002	−0.010	−0.004				

Est = estimate. SE = standard error.

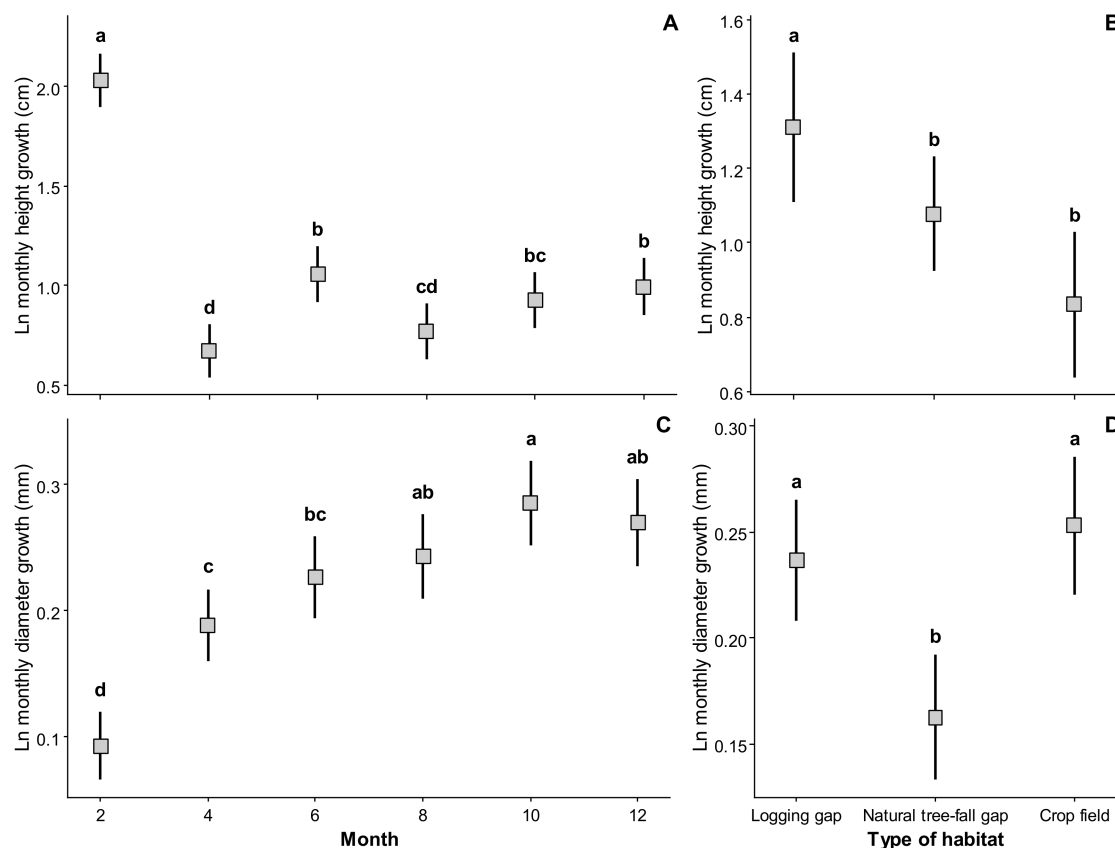


Figure 3. Marginal effects of habitat type (B,D) and month (A,C) on height and diameter growth of *Bertholletia excelsa* seedlings. The gray squares represent the estimated marginal means, and the lines represent the predicted effects with 95% confidence intervals. Different lowercase letters indicate significant differences among groups (months or habitat types) at $p < 0.05$.

4. Discussion

The growth in height and diameter of seedlings are critical indicators of nutrient use efficiency [29] and play an important role in the early survival of plants [30]. In this study, the facilitation effects on growth and survival of *B. excelsa* seedlings varied by

habitat type, with logging and natural tree-fall gaps promoting higher survival. However, growth responses differed between diameter and height. Our results partially support the hypothesis that the intermediate-light canopy gaps can facilitate the early growth and survival of *B. excelsa* seedlings. In addition, the negative effect of canopy cover on height growth reinforces the central hypothesis of this study and aligns our results with previous studies conducted in the Amazon region.

4.1. Seedling Survival

Canopy gaps usually had a positive effect on the early survival of tree seedlings [31]. In our study, the overall survival probability of *B. excelsa* seedlings is lower in crop fields compared with canopy gaps. This finding is consistent with previous research in *B. excelsa* [22,26], indicating that during the earliest stages of seedling life, the survival probability may be higher in sites with intermediate light conditions (forest gaps) than in the understory and in sites with full sunlight exposure (field crops or plantations) [32,33].

The low survival rates of *B. excelsa* in crop fields may be due to its sensitivity to environmental variations [14] and probably the high levels of solar radiation in this type of habitat. The Peruvian Meteorological and Hydrological Service reported higher daily sunshine hours (6.7 to 8.1) and a greater solar radiation during the dry season (on average, 5.5 kWh/m² and up to 15 kWh/m²) compared to other seasons. In addition, Madre de Dios experiences increased temperatures and a significant decline in rainfall during the dry season [34,35]. Thus, high solar radiation may negatively impact the water content of exposed soils, which could lead to increased drought stress in seedlings [26,36]. This aligns with our findings because we found an increase in mortality during the dry season (from June to August, Figure 2). Another reason for the low survival found in this study, especially in crop fields, could be the use of small seedlings (on average, height: 7.6 ± 2.5 cm), because seedlings of *B. excelsa* less than 25 cm tall can be vulnerable to rodent attacks on the hypocotyl at the base of the stem [26,37]. Therefore, using larger seedlings (height > 40 cm) can potentially enhance the survival probability of *B. excelsa* [26,38] because taller seedlings keep their height growth advantage over time [39]. In addition, a recent study has revealed that larger seedlings (height > 40 cm and root collar diameter > 5 mm) can achieve better growth during the first year of establishment [40].

On the other hand, in agreement with previous studies in Madre de Dios [22,41], the survival of *B. excelsa* seedlings was higher in canopy gaps. The findings of the study confirm the relevance of canopy cover for seedling growth.

4.2. Seedling Growth

Several studies have demonstrated that the growth rate of *B. excelsa* seedlings is higher within the first year in partially deforested areas (such as canopy gaps) than in areas with intact vegetation or in extensively deforested areas [22,26]. In the current study, we found that *B. excelsa* grew best in canopy gaps, particularly logging gaps, although different growth patterns were observed depending on diameter and height. Thus, *B. excelsa* had the highest diameter growth in field crops, while its height growth was the lowest. In natural tree-fall gaps, *B. excelsa* seedlings had the smallest diameter growth of all the habitats, but they grew taller than in crop fields and shorter than in logging gaps. These differences can mainly be attributed to variations in canopy cover [22,24,42] because *B. excelsa* is considered a gap-dependent, strongly light-demanding species [24,33] and highly sensitive to changes in microsite quality [26,43]. Under higher light conditions, *B. excelsa* seedlings can shift allocation and their leaf physiological traits (e.g., higher stomatal conductance and photosynthetic rates) that support rapid diameter and height growth [44,45]. Probably due to this, seedlings grew much more rapidly in logging gaps than in natural tree-fall gaps,

because logging gaps are usually larger than natural tree-fall gaps [46] and may therefore generate high-light conditions. Meanwhile, *B. excelsa* seedlings in crop fields had greater growth in diameter compared to those in the canopy gaps. Because seedlings in canopy gaps face greater competition for light, they may accelerate investment in vertical growth to gain access to light [22,47].

Opening the canopy can generate significant changes in the forest's microclimatic variables [46]. Thus, greater light availability in gaps may increase seedling growth rates by increasing photosynthetic rates [48]. Our results suggest that canopy cover (a proxy of light availability) is one of the most critical limiting factors for the initial growth of *B. excelsa* [17], because height growth was significantly associated with the percentage of canopy cover.

4.3. Practical Applications and Limitations of the Study

The findings have implications for future reforestation, plantations and enrichment initiatives using *B. excelsa* in the Amazon. Considering the high survival and growth rates of *B. excelsa* in canopy gaps, this type of habitat should be considered in forest-enrichment efforts on sites with low levels of natural regeneration. Thus, the management of these habitat types can be valuable for the sustainable nut harvesting in *B. excelsa* stands in the Amazonia [10]. However, these implications should be interpreted within the limitations of the present study. Limitations of the study include short-term data (one-year monitoring), small initial seedling size, lack of a fully crossed site-by-habitat design and limited environmental covariates such as soil physicochemical properties. In addition, logging gaps and crop fields were not available at the same sites. Thus, the comparison between these habitats relies largely on differences among sites rather than within-site replication and cannot be completely separated from site-level environmental differences, which should be considered when generalizing the results and implementing recommendations derived from this study.

5. Conclusions

This study showed that the survival of *B. excelsa* seedlings was significantly higher in canopy gaps than in crop fields. The facilitation effects of habitats on *B. excelsa* seedlings varied by growth metric (diameter or height). Surviving *B. excelsa* seedlings had greater height growth in logging gaps than in the other habitat types assessed, whereas diameter growth was highest in crop fields and logging gaps. We also revealed the negative effect of canopy cover on the early height growth, but not in the diameter growth. Therefore, our results highlight the potential of enrichment planting using *B. excelsa* in logged tropical rainforest in the southeast Peruvian Amazon.

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