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Early Growth Response of Nine Timber Species to Release in a Tropical Mountain Forest of Southern Ecuador

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Abstract: Research Highlights: This study determined that treatment "release from competitors" causes different reactions in selected timber species respective to diametrical growth, in which the initial size of the tree (diametric class) is important. Also, the growth habit and phenological traits (defoliation) of the species must be considered, which may have an influence on growth after release. **Background and Objectives:** The objective of the study was to analyze the diametric growth of nine timber species after their release to answer the following questions: (i) Can the diametric growth of the selected timber species be increased by release? (ii) Does the release cause different responses among the tree species? (iii) Are other factors important, such as the initial diameter at breast height (DBH) or the general climate conditions? **Materials and Methods:** Four-hundred and eighty-eight trees belonging to nine timber species were selected and monitored over a three-year period. Release was applied to 197 trees, whereas 251 trees served as control trees to evaluate the response of diametrical growth. To determine the response of the trees, a linear mixed model (GLMM, R package: LMER4) was used, which was adjusted by a one-way ANOVA test. **Results:** All species showed a similar annual cycle respective to diametric increases, which is due to the per-humid climate in the area. Precipitation is secondary for the diametric growth because sufficient rainfall occurs throughout year. What is more important, however, are variations in temperature. However, the species responded differently to release. This is because the initial DBH and growth habit are more important factors. Therefore, the species could be classified into three specific groups: Positive, negative and no response to release. **Conclusions:** Species which prefer open sites responded positively to release, while shade tolerant species and species with pronounced phenological traits responded negatively. The initial DBH was also an important factor for diametric increases. This is because trees of class I (20 cm to 30 cm DBH) responded positively to the treatment, whereas for bigger or older individuals, the differences decreased or became negative.

Keywords: climate conditions; diametric growths; growth habit; initial DBH; tree competition

1. Introduction

During the last few decades, deforestation and land degradation in tropical forests have been studied extensively, due to their role in the global carbon cycle and climate system [1,2], as well as because of their importance in ecosystem services [3]. Tropical forests cover 7% of the earth's surface but contain 50% of the global forest biomass, and therefore are the most important natural carbon stocks and sinks regarding future global warming [4]. The above ground biomass (AGB) accounts for 70%–90% of the total carbon biomass, mainly stored in the trunks and branches of trees [5]. Furthermore, tropical forests represent 36% of the net primary terrestrial production, which contributes to the regulation of the carbon dioxide (CO_2) concentration in the atmosphere [2,6]. Therefore, the challenge for foresters is to understand the dynamics in tropical forest stands, including the productivity of desired timber species, in order to implement sustainable practices and prevent deforestation and ecosystem destruction [7,8].

Intermediate treatments to improve forest productivity, such as the release or removal of competitors from timber trees, were implemented some decades ago, including implementation in tropical countries [9–11]. The process, in which undesirable species and other competitors near the timber species are eliminated, helps to improve their productivity, because diametric growth is a result of competition for space and resources with other species [12]. This silvicultural treatment allows a diametric increase in trees [13–15] and therefore is frequently applied in managed forests for timber production [11]. Release from competitors is best developed in boreal forests [16] and alpine forests [17], where implementation results in significant diametric increases. Also, in neotropical countries (e.g., Puerto Rico, Nigeria, Guyana, Sarawak and Brazil) this technique has been implemented successfully in managed forests [10,15]. However, in natural tropical forests, the release from competitors around the desired timber species is poorly investigated thus far, because these forest types present an extraordinarily high species density, even though the density of individual species is comparatively low [18]. This generally leads to the decelerated diameter growth of tropical forest trees [19], but growth rates vary significantly between species, depending on their growth habit (early-, mid- or late-successional), age, phenological traits and climatic conditions [20,21].

Timber harvesting in natural tropical forests may have a similar effect to release [22], but the remaining trees often suffer considerable impacts, which can only be minimized by applying directed fall techniques [23]. Nonetheless, an enhanced diametric growth of desirable timber species in natural tropical forests may lead to sustainable forest management if the collectivity of the ecosystems involved are not affected [24]. The same is valid for tropical mountain forests (>1500 m a.s.l.), which have been recognized as being indispensable for all environmental services, such as water production and storage, as well as for water regulation [25], besides their extraordinarily high biodiversity [3]. The high biodiversity of tropical mountain forests is a result of rapidly changing climate conditions caused by the local topography. Generally, air temperature decreases towards higher elevations, but precipitation amounts increase, resulting in fast changing environmental conditions [26–28]. The altitudinal gradients diversify both structurally and floristically the tropical mountain forest [29,30], but also limit the growth of timber species, reducing their diametric growth and therefore their productivity, due to competition with other plant species.

Knowledge on the behavior of timber species within tropical mountain forests respective to release is still lacking, but this silvicultural treatment can promote sustainable natural forest management without ecosystem destruction. In Ecuador, this intermediate treatment was recently implemented, but the effects must be still evaluated. Hence, the objective of this work is to analyze the radial incrementation of nine timber species in a tropical mountain forest in southern Ecuador after their release (removal of competitors). This research aims to answer the following questions: (i) Can the diametric growth of the selected timber species be increased by release? (ii) Does release cause different responses in the tree species? (iii) Are other factors important, such as the initial DBH, seasonality or general climate conditions? To determine the response of the trees, a linear mixed model (GLMM, R package: LMER4) was applied.

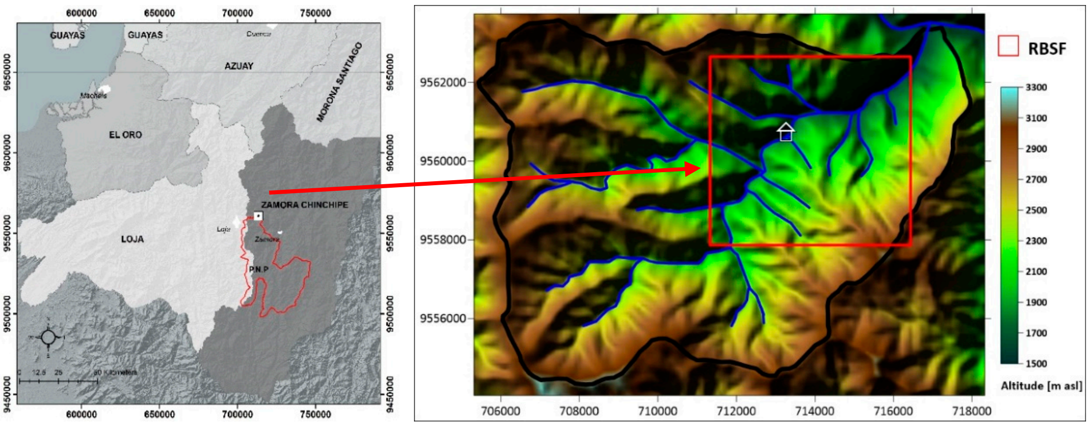
2. Materials and Methods

2.1. Study Area

The study was executed in the primary tropical mountain forest of the "Reserva Biológica San Francisco" (RBSF, 1850 m a.s.l., [31]), located at the eastern escarpment of the south Ecuadorian Andes. The elevation of the catchment [32], which drains into the Amazon Basin, ranges from ∼1700 m a.s.l. at the valley bottom to ∼3200 m a.s.l. at the highest mountain peaks (Figure 1). The natural vegetation in the RBSF is an evergreen tropical mountain forest, which covers the slopes from the valley bottom up to the tree line at ∼2700 m a.s.l. [33]. The forest can be divided into evergreen lower montane forests (up to 2100–2200 m a.s.l.) and upper montane forests, up to the tree line. Above ∼2700 m, a shrub-dominated sub-paramo prevails, where small patches of Elfin forest, the so-called Ceja Andina, dominate the landscape [34]. Both types of montane forest can be subdivided into a lower slope (ravine) forest and an upper slope (ridge) forest [29,30]. The ravine forests are characterized by lower stem density, but simultaneously by greater basal areas (tree diameters) and higher canopies when compared to the ridge forests, where lesser tree species are also present. The difference in forest structure is mainly due to the climatic conditions and prevailing soil types [28,35].

The climate in the catchment is per-humid, with marked altitudinal gradients in air temperature, humidity and rainfall [36]. The annual mean air temperature ranges from 19.4 °C at the valley bottom to 9.4 °C at the highest mountain tops. However, the average diurnal temperature amplitude is lowest inside dense forest stands compared to the other vegetation units present in the study area (pasture and paramo), because the canopy layer shelters the air inside the forest against daily irradiance and nocturnal outgoing radiation [37]. Furthermore, the air inside the tropical mountain forest is generally saturated, because dense canopies hinder the exchange of the air inside the forest with the free atmosphere, while the soils inside the forest stands are commonly saturated [38].

The distribution of rainfall is linked to altitude, due to orographic precipitation formation [36]. The average annual rainfall amounts vary between 2300 mm at the valley bottom and 6700 mm at the mountain tops. These annual rainfall amounts include both rain and fog precipitation, because both clouds and fog deposit water directly onto the vegetation, and therefore both must be considered as a relevant available water input from the atmosphere [26]. The seasonal rainfall distribution shows a clear annual cycle with the main rainy season between May and September (austral winter) and a relative dry season between November and February (austral summer) [36].



(**A**) (**B**)

Figure 1. Location of the study site at the border of the Podocarpus National Park (P.N.P., **A**) and a digital elevation model (UTM 17S) of the San Francisco catchment, including the Reserva Biológica San Francisco (RBSF) area (**B**).

The soils in the RBSF mainly belong to the order of Inceptisols. At the lower parts of the slopes, Dystrudepts are more frequent, whereas at the upper parts Humaquepts and Petraquepts dominate the area [39]. According to Wilcke et al. [40], the soils in mountain forests are characterized by thick organic layers, which store large contents of biomass and nutrients. However, the thickness of the organic layer depends mainly on two factors: The altitude and the slope gradient. At higher elevations, the temperatures are lower and therefore the degradation of the material is decelerated, leading to an accumulation of the organic matter [41]. At steep slopes, the organic layer is generally thinner due to enhanced soil erosion processes, which transport the material to the lower and less inclined parts, where the organic matter is sedimented. These processes also affect the chemical properties of the soils, making the availability of nutrients for plants highly heterogeneous [25].

2.2. Experimental Design

Over the past few decades, several permanent plots have been monitored in a natural tropical mountain forest in southern Ecuador, where the growth of different tree species has been analyzed along with observations of the behavior of the trees, respective to the addition of nutrients [34]. Other studies monitored the DBH increment of the different tree species to estimate the AGB and annual biomass production, as well as the influence of climate factors on the trees at different altitudes [29,35] and alterations of the climate conditions due to deforestation [37,38]. As part of a long-term monitoring forestry project, in January 2003, 52 plots of 2500 m^2 each were installed inside the tropical mountain forest of the RBSF. The plots were located in three different gullies (quebradas) at different altitudes: Quebrada 2 (Q2, 20 plots), quebrada 3 (Q3, 16 plots) and quebrada 5 (Q5, 16 plots). After the plot installation, a forest inventory was carried out and all trees with a DBH greater than 20 cm were marked, as recommended by [42], to analyze the growth of the forest trees. Afterwards, botanical samples were collected and identified taxonomically in the herbarium LOJA.

For the release, only high-quality trees were selected, called "potential crop trees" (PCTs), including nine timber species, because the silvicultural treatment applied here tends to promote sustainable forest management without ecosystem destruction. A PCT is a commercial species with a diameter at breast height (DBH) larger than 20 cm, with a good stem shape and concurrent health [43]. The PCT species selected for this study were: *Tabebuia chrysantha* (Jacq.) G. Nicholson; *Cedrela montana* Turcz.; *Inga acreana* Harms., *Hyeronima asperifolia* Pax & K. Hoffm., *Hyeronima moritziana* Mull Arg., *Podocarpus oleifolius* D. Don ex Lamb., *Nectandra membranacea* (Sw.) Griseb., Dugand. Three of these species are considered to be valuable timbers, namely *Tabebuia chrysantha*, *Podocarpus oleifolius* and *Cedrela montana*, whereas the other six are classified as medium quality timbers. *Tabebuia chrysantha*, *Podocarpus oleifolius and Nectandra membranacea* are hard wood trees of late-succession. *Tabebuia chrysantha* has rings and pores which are easily visible. *Cedrela montana* is a semi-hard wood tree of mid-succession with visible rings and pores. *Inga acreana*, *Hyeronima asperifolia and Hyeronima moritziana* are also semi-hard wood trees of mid-succession, but do not present rings. *Clusia ducoides* and *Ficus subandina* are soft wood trees of early to mid-succession without rings [44].

In the installed plots, a total of 448 PCT individuals were identified, of which 197 individuals were selected for release and 251 were left in their natural environment as a reference (control trees) to compare the effect of the silvicultural treatment to natural conditions. In Q5, eight of the nine PCT species were present, with exception of *Clusia ducuoides*, whereas in Q3, *Ficus citrifolia* and *Inga acreana* were absent and only one individual of *Cedrela montana* was found. The plots in Q2 included all of the selected PCT species, with several individuals (Table 1).

Table 1. Released potential crop trees (PCTs) and reference trees (R) that were monitored in the different gullies (Quebradas: Q2, Q3 and Q5).

Species	Q5 PCT	Q5 R	Q3 PCT	Q3 R	Q2 R	Total PCT's	Total R
Cedrela montana	20	14	0	1	7	20	22
Podocarpus oleifolius	1	0	12	7	10	13	17
Tabebuia chrysantha	46	14	0	2	25	46	41
Ficus citrifolia	4	3	0	0	13	4	16

Table 1. *Cont.*

Species	Q5 PCT	Q5 R	Q3 PCT	Q3 R	Q2 R	Total PCT's	Total R
Nectandra membranacea	9	8	5	1	27	14	36
Hyeronima asperifolia	27	10	1	1	15	28	26
Hyeronima moritziana	3	0	16	10	11	19	21
Clusia ducuoides	0	0	37	37	14	37	51
Inga acreana	16	5	0	0	16	16	21
					Total	**197**	**251**
						448	

By means of their initial DBH, the individual trees were grouped into four diametric classes (class I = 20.1–30.0 cm DBH, class II = 30.1–40.0 cm DBH, class III = 40.1–50.0 cm DBH, and class IV $\geq$ 50.1 cm DBH). Afterwards, the treatment was defined (release or control) and the monitoring periods (monthly) were established, taking into consideration the general climatic conditions (Table 2).

Table 2. Variables analyzed and the factors included in the applied GLMM model.

Analyzed Variables	Description	Factor
Diameter Class	Diametric class of the released and reference trees	Class I: 20.1–30.0 cm DBH Class II: 30.1–40.0 cm DBH Class III: 40.1–50.0 cm DBH Class IV: >50.0 cm DBH
Treatments	Removed competitors	Released
	Non-removed competitors	Reference
Period	Time between initial measurement drive by climatic seasons	Period I: 12 months Period II: 24 months Period III: 36 months
Precipitation	Accumulated monthly precipitation	mm/month
Temperature	Monthly average temperature	°C/month

2.3. Silvicultural Treatment

As mentioned before (Section 1), release consists of the removal of competitors to improve space and increase the availability of nutrient for the desired species [12,43]. This treatment is based on the theory that the growth rates of trees are directly related to the quantity of sunlight received. Therefore, all other trees and undesirable species or competitors around the desired timber species are removed to obtain adequate lighting and to enhance nutrient availability [45,46] (Figure 2). To determine the competitors of the selected PCT trees, all plots were visited and the tree form, crown diameter and social position within the forest stand, as well as stem quality, were analyzed and evaluated. All detected competitors were labeled with plastic tape and removed during a campaign between April and May of 2004. The release included mainly competitor trees, which were cut using the method of directional falling to avoid additional damage to the ecosystem [10]. Furthermore, no herbicides were applied to the stumps to guarantee the development of species collectivity in their natural environment without alterations or contaminations.

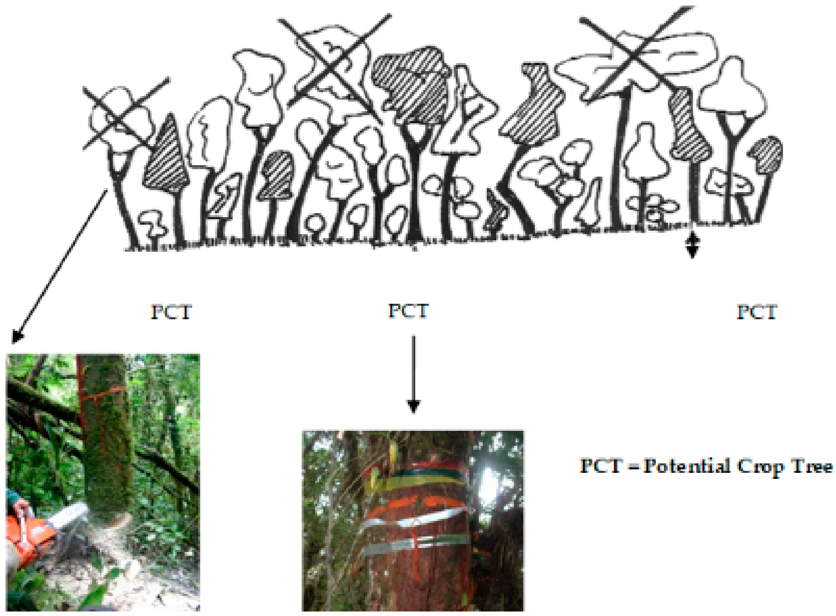


Figure 2. Implementation scheme of the applied silviculture treatment with photos during the campaign (May 2004, place: Q5).

2.4. Data Analysis

To evaluate individuals in the nine selected PCT species, the monthly diameter increase of each tree was measured. The trees were monitored for 36 months and the DBH measurements of each recording, compared to the initial value as well as to the previous data, were used to analyze the effect of liberation on the individual tree species over time. Therefore, metallic dendrometers were used, fixed to the PCTs and control trees, besides specific labels for each tree species and their respective diameter class (Figure 2). Furthermore, to improve the analysis, additional the DBH data of the selected species were included, provided by other studies which estimated AGB and the annual biomass production in the RBSF [34,47].

The diametric increase of the PCTs and reference trees were calculated by means of the equation proposed by [21]. The diametric increase (Di [cm/month]) can be determined as the difference between the initial diameter (Do [cm]) and the subsequent DBH measurement (D1 [cm]), divided by the time between the field campaigns (which is monthly here). The equation was applied to all selected trees after their initial DBH measurement, indicating the monthly DBH increase of each tree. Then, all of the individual monthly results were averaged to obtain the mean increase for each species, considering their specific diametric class. Finally, the average monthly DBH increases were used to calculate mean annual values as well as a value for the entire study period (36 months).

The homoscedasticity of the results was checked by means of the Levene's test [48]. Their normality was checked with the Shapiro–Wilk test [49] using the software R, version 3.2.0 [50]. If significant differences in diameter growth between the PCTs and the reference trees were found, considering the different diametric classes, an exploratory T-test (using the software R) was executed, whereas an independent Tukey test (Tukey HSD function, using the software R) was applied if significant differences between the monitoring periods were determined. Both tests were accepted with p-values ≤ 0.05, meaning that the results were statistically significant.

To check whether the initial DBH (diametric classes) or other factors, like seasonality or climate conditions, determine the diameter growth of the selected timber species, a linear mixed model (GLMM, R package: LMER4) was applied. The linear mixed model combines explanatory categorical factors like diameter class, treatment or climate conditions, and provides a "random" variable for the repeated measurements throughout time (period). To adjust the linear mixed model, a one-way ANOVA test was executed and accepted with p-value ≤ 0.05.

3. Results

The selected timber species responded differently to release respective to their reference trees (Table 3). Therefore, the species analyzed were separated into three groups (positive response, negative response and no response to release).

3.1. Positive Response to Release

The species that responded positively to release were *Inga acreana* and *Hyeronima asperifolia*, which had a greater diametric increment than their reference trees. *Inga acreana* showed a mean growth of 1.13 cm ± 0.72 (standard deviation) over the whole study period, whereas the control trees showed an increment of only 0.56 cm ± 0.47. The diametric growth of the released trees was not continuous, in which the lowest increment was measured during the first year (1.01 cm ± 0.81), which afterwards increased to 1.16 cm ± 0.61 (second year) and finally to 1.22 cm ± 0.78 (third year). For the reference trees, a more constant growth was observed, but also with the lowest increment during the first year. This may be due to the initiation time of the investigation (June, austral winter), when precipitation generally peaks but the lowest temperatures are typically observed [36,37]. Furthermore, temperatures were lowest in June 2004, directly after the release, compared to the following years, which may have influenced the diametric growth of all species. In general, the highest DBH increments for all species were observed at the beginning of the year (austral summer), when temperatures are highest and enough water is available (Figures 3 and 4).

The released trees of *Hyeronima asperifolia* showed a mean growth of 0.63 cm ± 0.64 over the whole study period, whereas the control trees only had an increase of 0.35 cm ± 0.36 (Table 3). Similar to *Inga acreana*, the diametric growth of *Hyeronima asperifolia* increased during the observation period, which resulted in the highest increment of growth during the third year (0.76 cm ± 0.53). However, the diametric class of the released trees was also important, because smaller trees showed higher DBH increments (Table 4). For *Inga acreana,* increments were exclusively observed in class I (diameter: 20.1 cm to 30.0 cm), whereas *Hyeronima asperifolia* showed increments in all classes, but showed higher values for classes I–III. As shown in Table 5, the enhanced diametric growth of both species was principally caused by the treatment (release), but also the temperature (Figure 3) and precipitation (Figure 4). The diametric class had significant influence for *Hyeronima asperifolia*.

In summary, both species showed higher diametric growth compared to their control trees during the entire study period, which illustrates the expected effects of release, namely improvements in light and nutrient availability, leading to faster DBH growth.

3.2. Negative Response to Release

The species with negative responses to release were *Cedrela montana*, *Tabebuia chrysantha*, *Podocarpus oleifolius* and *Nectandra membranacea*. All of these species showed significantly lower diametric growth respective to their control trees, especially during the second and third year after release (Table 3). The species with the most significant differences were *Cedrela montana* (1.16 cm ± 1.21 vs. 0.87 cm ± 1.24), followed by *Nectandra membranacea* (0.44 cm ± 0.62 vs. 0.26 cm ± 0.32). This is because light and nutrient availability are not the main factors for their DBH increments, what is more important are their growth habits and phenological traits, besides temperature and precipitation (Table 5). However, like the two species which responded positively to release, the highest DBH increments were observed for diametric classes I–III. Only *Tabebuia chrysantha* showed small increments in class IV (diameter over 50 cm) over the whole study period (Table 4).

Table 3. Average annual diameter increase, including standard deviation (SD). Values highlighted (bold) are statistically significant ($p \leq 0.05$).

Species	Treatment				Treatment × Period											
	Control		Released		I				II				III			
					Control		Released		Control		Released		Control		Released	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	Sd	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Inga acreana	0.56	0.47	**1.13**	0.72	0.43	0.36	**1.01**	0.81	0.64	0.36	**1.16**	0.61	0.63	0.66	**1.22**	0.78
Hyeronima asperifolia	0.35	0.36	**0.62**	0.54	0.26	0.34	**0.44**	0.58	0.41	0.39	**0.67**	0.46	0.38	0.34	**0.76**	0.53
Cedrela montana	**1.16**	1.21	0.87	1.24	**1.20**	1.23	0.93	1.38	**1.25**	1.02	0.98	1.55	**1.03**	1.32	0.70	0.63
Tabebuia chrysantha	**0.27**	0.34	0.21	0.41	0.16	0.21	**0.28**	0.62	**0.32**	0.32	0.21	0.28	**0.33**	0.45	0.12	0.15
Podocarpus oleifolius	**0.15**	0.26	0.14	0.46	0.09	0.19	**0.19**	0.68	0.16	0.32	**0.19**	0.35	**0.21**	0.26	0.05	0.13
Nectandra membranacea	**0.44**	0.62	0.26	0.32	**0.25**	0.30	0.26	0.28	**0.34**	0.43	0.25	0.30	**0.76**	0.90	0.27	0.38
Clusia ducuoides	0.10	0.16	0.10	0.21	0.11	0.15	0.10	0.15	0.06	0.10	0.07	0.18	0.12	0.20	0.13	0.29
Hyeronima moritziana	0.12	0.23	0.17	0.22	0.10	0.20	0.12	0.16	0.03	0.06	0.19	0.27	0.25	0.31	0.20	0.20
Ficus citrifolia	1.11	1.04	1.09	1.22	1.12	0.92	1.06	1.21	1.31	1.37	1.15	1.32	0.87	0.69	1.07	1.18

Table 4. Values of diametric increase (cm) per period and the diametric classes of the nine selected timber species.

Species	Periods	Class 1		Class 2		Class 3		Class 4	
		Control	Released	Control	Released	Control	Released	Control	Released
Inga acreana	1	0.43	1.01	0	0	0	0	0	0
Hyeronima asperifolia		0.48	0.45	0.15	0.43	0.15	0.78	0.04	0.1
Cedrela montana		1.01	0.81	1.39	0.47	1.36	1.5	0	0
Tabebuia chrysantha		0.28	0.72	0.14	0.11	0.15	0.07	0.08	0.23
Nectandra membranacea		0.16	0.34	0.27	0.17	0.31	0.17	0	0
Podocarpus oleifolius		0.17	0.12	0.07	0.02	0.03	0.42	0	0
Ficus subandina		1.00	0.88	1.24	1.25	0	0	0	0
Clusia ducuoides		0.13	0.15	0.06	0.08	0.13	0.08	0	0
Hyeronima moritziana		0.12	0.18	0.11	0.06	0	0	0	0
Inga acreana	2	0.64	1.16	0	0	0	0	0	0
Hyeronima asperifolia		0.45	0.73	0.43	0.67	0.35	0.83	0	0.46
Cedrela montana		1.20	0.96	1.31	0.65	1.25	1.33	0	0
Tabebuia chrysantha		0.37	0.44	0.32	0.12	0.19	0.14	0.42	0.13
Nectandra membranacea		0.35	0.41	0.20	0.08	0.46	0.08	0	0
Podocarpus oleifolius		0.08	0.10	0.06	0.04	0.33	0.42	0	0
Ficus subandina		1.35	0.96	1.27	1.33	0	0	0	0
Clusia ducuoides		0.07	0.06	0.11	0.05	0	0.08	0	0
Hyeronima moritziana		0.05	0.25	0.03	0.13	0	0	0	0

Table 4. *Cont*.

Species	Periods	Class 1		Class 2		Class 3		Class 4	
		Control	Released	Control	Released	Control	Released	Control	Released
Inga acreana	3	0.63	1.22	0	0	0	0	0	0
Hyeronima asperifolia		0.49	0.82	0.20	0.78	0.44	0.86	0	0.57
Cedrela montana		0.99	0.74	1.06	0.64	1	0.73	0	0
Tabebuia chrysantha		0.47	0.09	0.16	0.15	0.10	0.06	0.59	0.18
Nectandra membranacea		0.37	0.50	0.56	0.05	1.34	0.05	0	0
Podocarpus oleifolius		0.11	0.16	0.20	0	0.30	0	0	0
Ficus subandina		0.86	1.18	0.88	0.95	0	0	0	0
Clusia ducuoides		0.13	0.15	0.09	0.05	0.14	0.18	0	0
Hyeronima moritziana		0.30	0.20	0.17	0.20	0	0	0	0

Class I = 20.1–30 cm, class II = 30.1–40 cm, class III = 40.1–50 cm, class IV $\geq$ 50.1 cm.

Table 5. *P*-values of the variables and the interactions that influence the variability of the diametric increase (GLMM). Significant values ($p \leq 0.05$) are highlighted in bold.

Species	Release		Precipitation		Temperature		Diametric Class		Release × Diametric Class		Release × Precipitation		Release × Temperature		Diametric Class × Precipitation		Diametric Class × Temperature	
	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p	Ch	p
Inga acreana	14.9	**≤0.0001**	0.05	0.81	0.05	0.83	–	–	–	–	0.18	0.66	0.99	0.31	–	–	–	–
Hyeronima asperifolia	33.5	**≤0.0001**	4.1	**0.04**	9.8	**0.001**	16.7	**0.0008**	5.01	0.08	0.0	0.99	0.27	0.6	0.42	0.9	3.5	0.31
Cedrela montana	6.2	**0.01**	15.1	**≤0.0001**	31.9	**≤0.0001**	4.9	0.08	1.5	0.21	1.01	0.31	2.3	0.12	4.5	0.1	5.9	**0.05**
Tabebuia chrysantha	2.3	0.12	13.5	**0.0002**	1.74	0.18	26.3	**≤0.0001**	4.04	0.39	1.9	0.16	0.39	0.52	13.5	**0.003**	0.62	0.88
Podocarpus oleifolius	0.04	0.83	0.09	0.75	0.009	0.92	8.6	**0.01**	1.6	0.5	0.34	0.6	0.2	0.65	0.07	0.96	0.89	0.64
Nectandra membranacea	5.5	**0.01**	14.9	**≤0.0001**	31.8	**≤0.0001**	1.4	0.49	0.12	0.72	2.7	0.9	3.5	0.06	0.2	0.9	2.7	0.2
Clusia ducuoides	0.02	0.86	0.0004	0.98	1.3	0.24	2.4	0.3	0.91	0.63	0.09	0.76	1.1	0.3	2.2	0.33	4.7	0.09
Hyeronima moritziana	1.7	0.19	0.0008	0.98	0.0006	0.98	2.4	0.3	0.07	0.79	0.45	0.5	3.4	**0.05**	0.64	0.72	0.0002	0.99
Ficus citrifolia	0.007	0.93	10.1	**0.001**	8.8	**0.002**	0.46	0.49	0.12	0.72	0.19	0.65	0.17	0.67	1.9	0.16	3.3	0.06

3.3. Null Response to Release

The species that did not show significant responses to release (neither positive nor negative) were *Hyeronima moritziana*, *Clusia ducuoides* and *Ficus citrifolia*, which indicates that other factors have a greater influence on the diametric growth of these species. The diametric growth of *Hyeronima moritziana* (0.12 cm ± 0.23 vs. 0.17 cm ± 0.22) and *Clusia ducuoides* (0.10 cm ± 0.16 vs. 0.10 cm ± 0.21) was generally low (released trees and control trees) over the complete study period, but with generally the highest DBH increments during the third year. In contrast, *Ficus citrifolia* (1.11 cm ± 1.04 vs. 1.09 cm ± 1.22) showed higher DBH increments during the first two years of the study, which can be related to the prevailing climate conditions, because mean monthly temperatures as well as precipitation amounts were higher then, when compared to the third year (Figures 3 and 4). This is confirmed in Table 5, where temperature and precipitation are seen to show significant influence on the diametric growth of *Ficus citrifolia* but are secondary for the other two species (Table 5). Respective to the diametric classes, the three species had the highest increments in class I and class II. Only *Clusia ducuoides* showed small DBH increments in class III (Table 4).

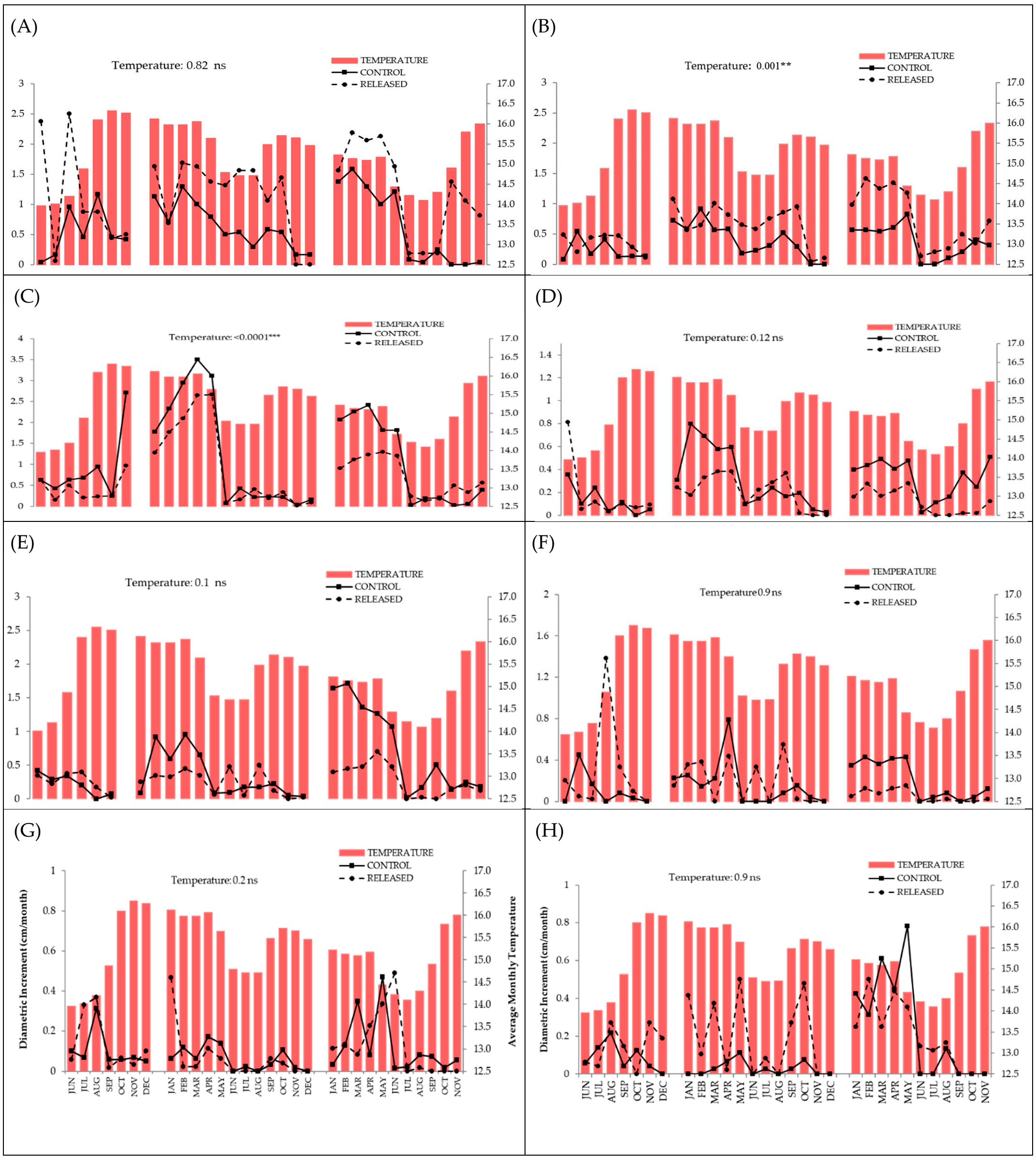


Figure 3. *Cont.*

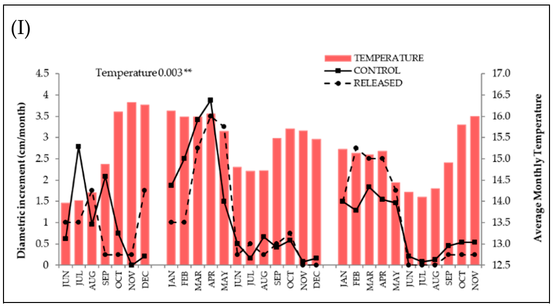


Figure 3. Diameter increase, by period, respective to the mean monthly temperature. (**A**) *Inga acreana*, (**B**) *Hyeronima asperifolia*, (**C**) *Cedrela montana*, (**D**) *Tabebuia chrysantha*, (**E**) *Nectandra membranaceae*, (**F**) *Podocarpus oleifolius*, (**G**) *Clusia ducuoides*, (**H**) *Hyeronima moritziana*, (**I**) *Ficus citrifolia*.

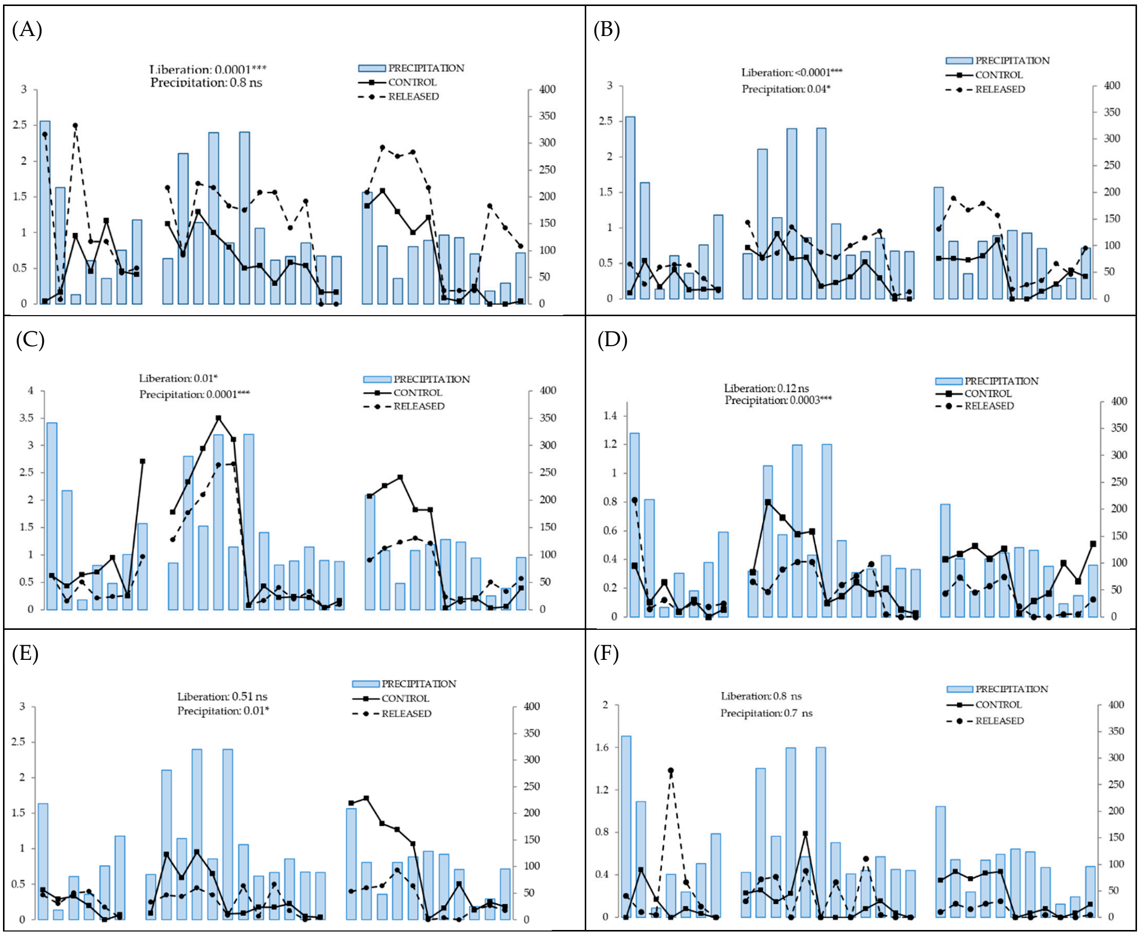


Figure 4. *Cont.*

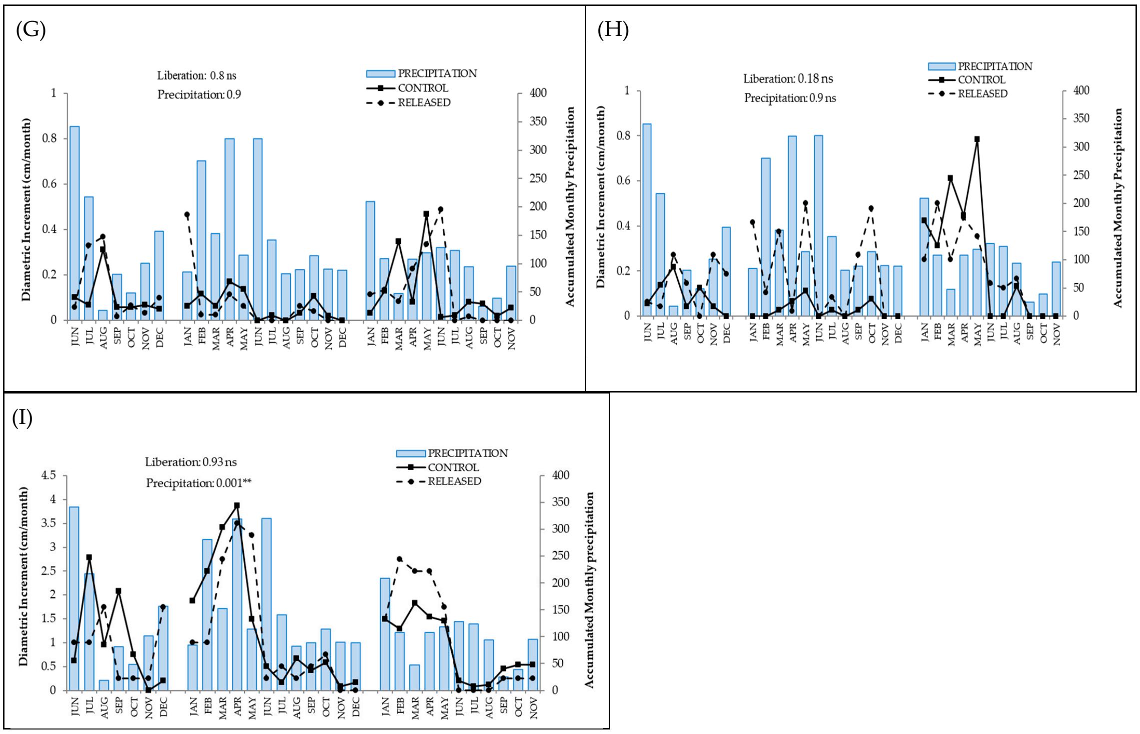


Figure 4. Diametric increase, by period, respective to monthly precipitation. (**A**) *Inga acreana*, (**B**) *Hyeronima asperifolia*, (**C**) *Cedrela montana*, (**D**) *Tabebuia chrysantha*, (**E**) *Nectandra membranaceae*, (**F**) *Podocarpus oleifolius*, (**G**) *Clusia ducuoides*, (**H**) *Hyeronima moritziana*, (**I**) *Ficus citrifolia*.

4. Discussion

The nine selected timber species responded differently to the release because their growth habits, initial DBH (diametric class) and phenological traits, which determined the success of the treatment. Historically, tree growth has been modeled based on different classification criteria, in which the most common criterion are taxonomic affinity, ecological guild and growth dynamics [18,51]. The growth and dynamics of natural tropical forests in Ecuador have been monitored for decades by means of continuous measurements over time [52]. However, the main focus of this work has been determining the influence of climatic factors and ecosystem services, due to the high deforestation rates observed in Ecuador [53,54], but not silvicultural treatments, such as the release from competitors. Monitoring the diametric growth of certain species by adding nutrients to the soil [34] or analyzing the DBH increment, respective to climatic conditions [29,35], are topics that provide knowledge about forest dynamics, but do not contribute to sustainable forest management.

Although the study area corresponds to a natural tropical mountain zone, where marked altitudinal gradients in temperature and precipitation exist [36,37], provoking different physiological responses in the species [55], climate conditions were secondary due to the pre-humid tropical climate in the study area. The relative dry season is formed between austral winter and austral summer (October/November), which is used by many species for phenological processes such as flowering and fruiting [36]. All of the selected PCT species showed a similar annual cycle respective to diametric growth, which was mainly triggered by the slightly higher temperatures during the austral summer period. This also holds true for the species *Cedrela montana* and *Tabebuia chrysantha*, which interrupt their cambial activity, simulating a dormancy period (defoliation), similar to tree species in temperate climatic regions [56], leading to the formation of growth rings.

The released trees of the individual species were separated into three groups based on their diametric class and individual response. The first group consisted of species which responded positively to the release (*Inga acreana* and *Hyeronima asperifolia*), whereas the second group included species which responded negatively (*Cedrela montana*, *Nectandra membranacea*, *Podocarpus oleifolius* and

Tabebuia chrysantha), while the third group of species were those that responded neutrally (*Hyeronima moritziana, Clusia ducuoides* and *Ficus citrifolia*).

The members of the species of genus Inga are generally medium-sized and shade intolerant [57], but some species are only moderately shade tolerant [18]. However, *Inga acreana* grows in relatively open sites, where release improves the environmental conditions and consequently diameter growth [23,58,59]. Nonetheless, as the present study found, this is only valid for smaller individuals (20–30 cm, class I) because larger diameter classes did not show any significant increments.

Hyeronima asperifolia also responded positively to release, which was also stated in [23], which additionally found an interesting early response for this species. However, the early response could not be confirmed by the present study because significant differences between the released and control trees were higher at the end of the observation period (Table 3). Respective to the diametric classes, the highest increments were calculated for classes I–III, whereas class IV only showed small increases for the released trees (Table 4). The differences in growth between the diametric classes were stated in previous studies [7,21], which indicate that diametric growth is strongly dependent on the size of the tree, in which larger trees generally show lower increments. By analyzing the climate conditions (Figures 3 and 4), it is evident that *Hyeronima asperifolia* reduces or suspends growing in June (austral winter) when precipitation amounts are at their highest but temperatures are at their lowest. This behavior was also found in other species in the RBSF area [58], because rainwater is usually stored in the soil and is available for the plants for longer periods or during the whole year. The diametric growth generally occurs during austral summer, when highest temperatures are observed, confirming that temperature variations control the phenological processes and growth rates of the different species in the study area.

The next group of species showed a negative response to the treatment, which means that release produced an inverse effect, as was expected respective to diameter growth. As [60] indicated, variations in the diameter growth of certain species are related to two factors: First, the amount of light intercepted by the tree and second, the density of the wood. Therefore, an inverse relationship between growth and wood density can be assumed, which is confirmed by this study, because the four species of this group have hard and dense wood. Additionally, *Cedrela montana* and *Tabebuia chrysantha* exhibit defoliation, which also affects their diametric growth [55].

Cedrela montana is a slow-growing deciduous species which forms growth rings in its trunk and has defoliation [61], which is associated with austral winter, when temperature is lowest. Although the seasonal temperature fluctuations are only around 1.5 °C in the study area, other studies have confirmed that temperature is significantly correlated to diametrical growth [42]. The highest diametric increases are observed during the warm season (austral summer), whereas growth is reduced or suspended during the cold season (austral winter). This overall trend matches with the growth rates found in this study. However, the reason for the negative response of *Cedrela montana* may be the time of release (June), because normally the trees begin with the process of leaf change and flower production [42]. Release generated changed light conditions, which may have interrupted the natural phenological cycle of the species. This is confirmed by [23], which also found a negative response to release for *Cedrela montana*, concluding that the negative response is due to the species' marked phenological traits and physiological processes.

Tabebuia chrysantha is also a deciduous species [42] whose defoliation time coincides with *Cedrela montana*, starting in June (austral winter). According to [62], *Tabebuia chrysantha* shows very low diametric increments during austral winter, when the production of new leaves and flowers begins. This is because the tree needs all of its available resources to progress through these physiological stages. Therefore, the time of release for this study may have affected this species, however, the growth rates were similar to the control trees during the first year of observation (Figures 3 and 4). This leads to the assumption that the change in light conditions has also affected the released trees over the following years, because this species prefers shaded sites [57]. Observing Table 4, the control trees showed notably higher diametric increases during years 2 and 3, especially during the austral summer periods.

The negative response of *Podocarpus oleifolius* cannot be explained by the time of release nor the general climate conditions. This is because temperature and precipitation did not produce a significant effect on growth for this species (Table 5). Therefore, the change in light conditions may have affected this species too. However, as the results of the applied statistical model indicated (Table 5), significant differences between released trees and control trees were only found in terms of size (diameter class; $p = 0.01$). As shown in Table 4, *Podocarpus oleifolius* only presented small increments for classes I–III, in which the released trees in class I showed a generally higher diametric growth than the control trees, whereas the control trees had higher increments than the released trees in class II. Class III showed the highest diametric growth rates for both the control and released trees, especially during the first two years of observation. However, during the third year, the released class III trees did not show any increment, explaining the overall trend for the released trees being negative. Therefore, the applied silvicultural treatment was only useful for smaller or younger trees, where their diametric growth was enhanced due to the improved light conditions. For bigger or older trees this factor is secondary. The generally low growth rates of *Podocarpus oleifolius* were also observed in [63], where an average annual growth of 1.7 mm in Costa Rica was calculated. However, the present study only obtained an annual average growth of 0.21 mm, which is confirmed by [34], which investigated *Podocarpus oleifolius* in the RBSF area.

Additionally, for *Nectandra membranacea*, the effect of release was negative. The diametric growth of this species was related to the treatment and the climatic conditions (temperature and precipitation, Table 5), as *Podocarpus oleifolius* and *Nectandra membranacea* showed clear variation in growth between diametric classes (Table 4). Young and small trees (typically class I) reacted positively to release. This is because their diametric increment is higher when compared to the control trees. Nonetheless, in classes II and III, the diametric growths of the released trees were notably lower than the control trees, resulting in a negative response. The negative response of *Nectandra membranacea* was also found in [23], which indicated that light conditions are important for younger trees, but if the tree is established in the ecosystem, other factors such as nutrient availability are more important. Furthermore, too much light may increase plant transpiration and therefore more water is necessary, which may reduce diametric growth.

Ficus citrifolia, *Clusia ducuoides* and *Hyeronima moritziana* showed no response to the treatment, which means that no differences in diametric growth between the released and control trees were found. These species are tolerant to shade and light, and as such, no effect was obtained. However, within the timber species studied, the highest increments were measured for diametric classes I and II (smaller and younger trees), whereas in class III, the increments were strongly reduced, and in class IV they were absent or insignificant (Table 4).

The present investigation, as with most growth studies, was based on traditional forest inventory practices, including diameter measurements and applying a linear model (here, we applied GLMM, R package: LMER4). However, as [64] suggested, to get a better resolution of the growth response of species and individual trees, non-linear models should also be examined. Hence, individual tree variability, as well as the tree's specific location within the ecosystem can be considered in the models. These variables could improve the understanding of the growth response of individual trees after this intermediate treatment [65]. Furthermore, tree-ring series should be analyzed, because they provide more accurate estimations of radial growth than inventory data and allow reconstruction at a fine scale [66]. However, tropical forest trees generally do not form rings, which limits analyses to specific species, however in boreal or alpine forests, where all tree species have growth-rings, this factor should be included. Consequently, developing future studies using this approach can improve the resolution of the growth pattern of trees within forest stands.

5. Conclusions

The silvicultural treatment (release from competitors) that was applied to nine timber species in a natural tropical mountain forest in southern Ecuador resulted in different individual responses.

In general, species which preferred open sites responded positively to release, whereas shade tolerant species responded negatively. Tree species which are light- and shade-tolerant did not show any changes respective to diametric growth. Furthermore, the two species with defoliation (seasonality) responded negatively, which may be due to the time of release (June, during austral winter), which occurred during the time new leaves are built.

All of the selected species showed a similar annual cycle respective to their diametric increase. Generally, growth was observed during the austral summer period, specifically between December and April, when temperatures are highest and sufficient water is available. During austral winter (June to September), most of the species reduced or suspended their growth because of the lower temperatures during this period. Therefore, due to the per-humid climate in the RBSF, precipitation is secondary for diametric growth, because enough rainfall occurs during the year which is then stored in the soil, where water is consequently always available for the plants. What is more important are the small temperature variations between austral summer and austral winter, which are generally used by the plants to begin their phenological processes.

Finally, the initial DBH of the trees (diametric classes) was found to be an important factor for the success of the treatment. Trees of class I (20 cm to 30 cm DBH) generally responded positively to the treatment, whereas for bigger or older individuals, the differences between the released and control trees decreased or became negative. This means that improved light conditions as well as nutrient availability are specifically beneficial for younger trees, which still compete for space and nutrients. Older trees are established within their ecosystem and generally grow slower, which explains why release did not increase their competitive abilities. Therefore, the release of trees in natural tropical mountain forests is only practical for younger trees, which are still competing for light and nutrients.

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