

Article

# Early response to liberation and climatic seasonality of selected timber species in a Tropical Mountain Forest of Southern Ecuador

Omar Cabrera<sup>1,2\*</sup>, Andreas Fries<sup>3</sup>, Patrick Hildebrandt<sup>1</sup>, Reinhard Mosandl<sup>1</sup>

<sup>1</sup>Institute of Silviculture, Center of Life and Food Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany.

Reinhard Mosandl (mosandl@forst.wzw.tum.de)

Patrick Hildebrandt (hildebrandt@tum.de)

<sup>2</sup>Department of Biological Sciences, Universidad Técnica Particular de Loja, San Cayetano Alto s/n, 1101608 Loja, Ecuador.

\* Correspondence: hocabrera@utpl.edu.ec; Tel.: +00-593-7-370-1444.

<sup>3</sup>Department of Geology and Mine, and Civil Engineering (DGMIC), Universidad Técnica Particular de Loja, San Cayetano Alto s/n, 1101608 Loja, Ecuador

Andreas Fries (aefries@utpl.edu.ec)

## Abstract:

**Research Highlights:** The study determined that selective thinning causes different responses, the initial size of the tree released is an influential factor in the growth of species. The temporality of climate and physiological conditions of each species are influential in the growth. It is evident that the defoliation of certain species is an important factor that limits the growth of the species causing thinning to have a negative response.

**Background and Objectives:** The objective is to analyze the behavior of nine timber species, respective to diametric growth after their liberation. This research aims to answer the following questions: (i) How do the selected tree species react to the liberation? (ii) Can the productivity of the trees (diametric growth) be enhanced by liberation? (iii) Are there other factors that influence the diametric growth of the released trees?

**Materials and Methods:** The study was executed in the "Reserva Biológica San Francisco" where 488 trees were monitored, including nine timber species. Therefore, 197 trees were released (removal of competitors) and 251 trees served as reference. To check whether the initial DBH or other factors, like the selective thinning or climate conditions, determine the diameter growth a linear mixed model GLMM was applied. To adjust the linear mixed model a one-way Anova test was executed.

**Results:** Timber species responded differently to the thinning in comparing to reference trees. Therefore, the species analyzed were separated into three groups (positive, negative, and no response to liberation).

**Conclusions:**

Liberation potentiates the growth of certain timber species that do not defoliate and considered semi-tolerant to shade.

Precipitation and temperature affect all species, but in the defoliate species, it would not be convenient to release them or at least the evidence of these first three years does not show clear differences with control trees.

Increase in trees released are higher in trees of the first two diametric classes in all species, this means that larger trees (i.e older) release does not affect them in a positive way so release should occur in the youngest trees.

**Keywords:** Tropical Mountain Forest, Podocarpus, Cedrela, Tabebuia, Selective Thinning, Diametric Growth.

---

**1. Introduction**

During the last decades, deforestation and land degradation in tropical forests have been studied extensively, due to their role in the global carbon cycle and in the climate system [1, 2], as well as their importance for ecosystem services [3]. Tropical forests cover 7% of the earth surface, but contain 50% of the global forest biomass, and therefore are the most important natural carbon stocks and sinks regarding future global warming, in which the above ground biomass (AGB) accounts for 70% - 90% of the total biomass carbon [4]. Furthermore, the tropical forests represent 36% of the net primary terrestrial production (PNP), which contributes to the regulation of the carbon dioxide (CO<sub>2</sub>) concentration in the atmosphere [5, 2]. Therefore, the challenge for foresters is to understand the dynamics and to estimate the productivity of tropical forest stands, respective to the world's carbon budget and its mitigation for future global warming [6,7].

Interventions to improve forest productivity, such as the release or removal of competitors (liberation) from timber trees were implemented some years ago, including tropical countries. In South East Asia, for example, this practice had been applied since the early 19th century and since the mid-20th century in the Neotropics, in countries like Brazil and Costa Rica [8]. The process in which undesirable species and other competitor around the timber species are eliminated to improve their productivity and to convert these areas into productive forest stands [9].

This silvicultural treatment generally leads to an increase in diametric tree growth [10-12], and it is frequently applied in forest management for timber production [13]. Timber harvesting in forests often has a similar effect as the liberation from competitors [14], but concurrently the remaining trees suffer large impacts, which can only be minimized by applying directed fall techniques [15]. However, an enhanced diametric growth of the trees leads also to an increased absorption of atmospheric CO<sub>2</sub>, because the main part of the biomass carbon is stored in the trunks and branches of the trees [16]. Therefore, an enhanced diametric growth can mitigate the consequences of future global warming [17].

In general, the diametric growth of trees in forests is a result of competition for space and resources with other species, which is especially challenging in the tropical forests, because of their

high biodiversity [18]. In tropical forests species density is extraordinarily high, but the density of individual species comparatively low, which results generally in a decelerated diameter growth of the trees [19]. However, the growth rates vary significantly between the species, depending on age, annual seasonality as well as microclimatic conditions [20, 21].

The same is valid for tropical mountain forests (> 1500 m a.s.l.), which have been recognized as indispensable for all environmental services, such as water production, storage, and their regulation [22], as well as their extraordinary high biodiversity [3]. The high biodiversity of tropical mountain forest is result of fast changing climate conditions caused by the local topography. Generally, air temperature decreases towards higher elevations, but precipitation amounts increase, leading the different environmental conditions [23-25]. The altitudinal gradients diversify structurally and floristically the tropical mountain forest e.g. [26, 27], but also limit the growth of timber species, reducing their diametric growth and therefore their productivity, due to the competition with other plant species.

Over the last decade several permanent plots have been monitored in a natural tropical mountain forests in southern Ecuador, analyzing the growth of particular tree species and the behavior of the trees respective to the addition of nutrients [28] as well as to the release of plus trees [15]. These studies also monitored the monthly DBH increment of the different tree species to estimate the AGB and the annual biomass production. Furthermore, the influence of climate factors on the trees at different altitudes e.g. [29, 26] and the alteration of the climate conditions due to deforestation were investigated [30, 31]. However, regarding the behavior of timber species within the tropical mountain forest respective to liberation is still lacking, but this silvicultural treatment can promote a sustainable natural forest management without ecosystem destruction.

Therefore, the objective of the present work is to analyze the behavior of nine selected timber species in a tropical mountain forest in southern Ecuador, respective to diametric growth after their liberation (removal of competitors). This research project aims to answer the following questions: (i) How do the selected tree species react to the liberation? (ii) Can the productivity of the trees (diametric growth) be enhanced by liberation? (iii) Are there other factors that influence the diametric growth of the released trees?

## 2. Materials and Methods

### 2.1 Study area conditions

The study was executed in the primary mountain forest of the “Reserva Biológica San Francisco” RBSF; 03°58' S, 79°04' W; 1850 m a.s.l. [32], located at the eastern escarpment of the south Ecuadorian Andes inside the Rio San Francisco catchment [33], which drains into the Amazon Basin. Elevation ranges from ~1700 m asl at the valley bottom to ~3200 m a.s.l. at the highest point, the Cerro del Consuelo (Figure 1).

The natural vegetation is an evergreen tropical mountain forest covering the slopes from the valley bottom up to the tree line ~2700 m a.s.l. [34]. The forest can be classified as evergreen lower montane forests (up to 2100–2200 m asl) and upper montane forests up to the tree line. Above ~2700 m, a shrub-dominated sub-páramo prevails, where small patches of Elfin forest, the so-called

Ceja Andina, dominate the landscape [28]. Both types of montane forest can be divided in lower slope (ravine) forest and upper slope (ridge) forest [26, 27]. The ravine forests are characterized by lower stem density, but concurrently by greater basal areas (tree diameters) and higher canopies compared to the ridge forests, where also lesser tree species are present. The difference in forest structure is mainly due to the climatic conditions and the prevailing soil types [25, 29].

The climate in the catchment is perhumid with marked altitudinal gradients in air temperature, air humidity and rainfall [35]. 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 the forest stands (min: ~12.4°C, max: 18.1°C) 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 [30]. Furthermore, the air inside the tropical mountain forest is generally saturated (annual mean RH: ~100%) because the dense canopy hinders the exchange of the air inside the forest with the free atmosphere and the soils inside the forest are commonly saturated [31].

The rainfall distribution is linked with the altitude, due to the orographic precipitation formation [35]. The average annual rainfall amounts vary between 2300 mm at the valley bottom and 6700 mm at the mountain tops, which includes rain and fog water precipitation, because clouds and fog deposit water directly on the vegetation, and therefore must be considered as a relevant available water input from the atmosphere [23]. 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) [35].

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 [36]. According to [37] the soils in the 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 [38]. At steep slopes, the organic layer is generally thinner due to the enhanced soil erosion processes, which transport the material to the lower and less inclined parts of the slopes, where the organic matter is sedimented. These processes also affect the chemical properties of the soils, making the nutrients availability for plants highly heterogeneous [22].

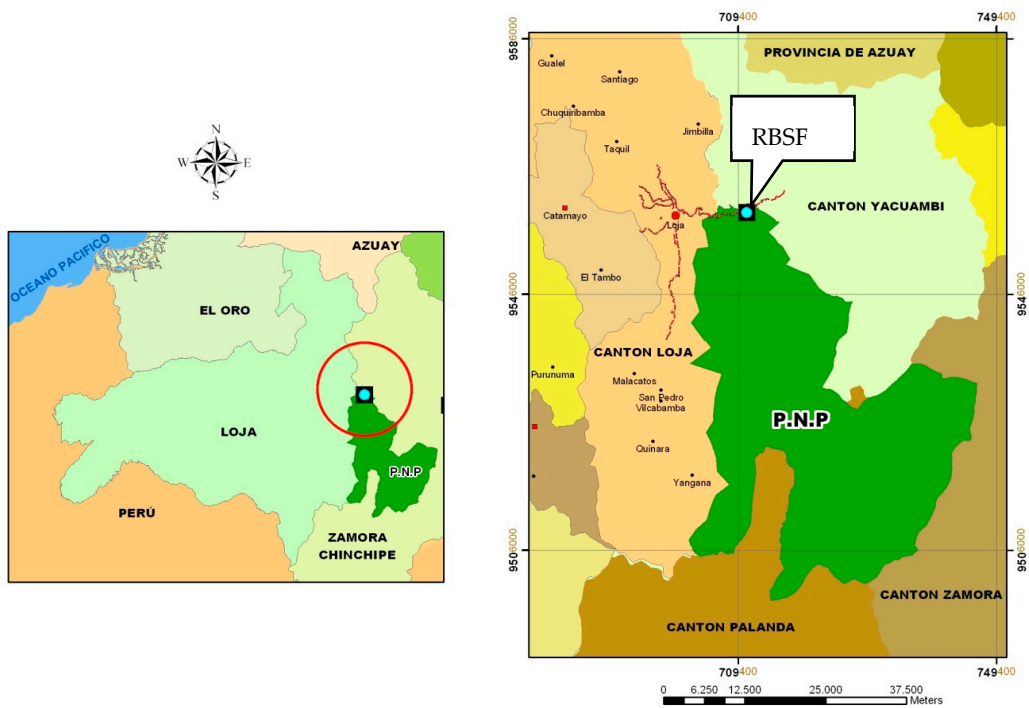


Figure 1. Scheme Location of RBSF.

## 2.2 Plot Installation

As part of a long-term monitoring forestry project, in January 2003, fifty-two plots of 2500 m<sup>2</sup> each were installed inside the tropical mountain forest of the RBSF. The plots were located in three different gullies (quebradas), Quebrada 2 (Q2, 20 plots), Quebrada 3 (Q3, 16 plots) and Quebrada 5 (Q5, 16 plots), at different altitudes. After the plot installation a forest inventory was carried out and all trees with a diameter at breast height (DBH) greater than 20 cm wick were marked, as recommended by [39], to analyze the growth of forest trees. Also, botanical samples were collected and afterwards identified taxonomically in the Herbarium LOJA.

For the selective thinning (liberation) only high-quality trees were selected (Potential Crop Trees, PCT), including nine timber species, because the silvicultural treatment applied here tends to promote a sustainable forest management without ecosystem destruction. The PCT species selected 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., *Clusia ducoides* Engl. and *Ficus subandina* Dugand. Three of these species are considered as valuable timbers (*Tabebuia chrysantha*, *Podocarpus oleifolius* and *Cedrela montana*), whereas the other six are classified as medium quality wood

In the installed plots a total 448 PCT individuals were identified, of which 197 individuals were selected for liberation and 251 left in their natural environment as reference. In Q5 eight of 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 selected PCT species with several individuals (Table 1).

187 Table 1. Released trees and reference trees for each species on each sampling site.

SPECIES	Q5 PCT	Q5 R	Q3 PCT	Q3 R	Q2 R	PCT's	Reference Trees
<i>Cedrela montana</i>	20	14	0	1	7	20	22
<i>Podocarpus oleifolius</i>	1	0	12	7	10	13	17
<i>Tabebuia chrysantha</i>	46	14	0	2	25	46	41
<i>Ficus citrifolia</i>	4	3	0	0	13	4	16
<i>Nectandra membranacea</i>	9	8	5	1	27	14	36
<i>Hyeronima asperifolia</i>	27	10	1	1	15	28	26
<i>Hyeronima moritziana</i>	3	0	16	10	11	19	21
<i>Clusia ducuoides</i>	0	0	37	37	14	37	51
<i>Inga acreana</i>	16	5	0	0	16	16	21
						197	251
TOTAL						448	

188

189 Concurrently, with the forest inventory metallic dendrometers were installed on each selected

190 PCT, as well as on the reference trees, and the initial DBH of each tree measured. By means of the

191 initial DBH, the individual trees were grouped into diametric classes (Class I = 20.1- 30 cm DBH,

192 Class II = 30.1- 40 cm DBH, Class III = 40.1- 50 cm DBH, and Class IV ≥ 50.1 cm DBH), their

193 treatment defined and the monitoring periods (yearly) established, taking also into account the

194 climatic conditions (Table 2).

195 Table 2. Variables used to GLMM model.

ANALYZED VARIABLES	DESCRIPTION	FACTOR
DIAMETER CLASS	Diametric class of liberated and reference trees	Class I: 20.1-30 cm dbh
		Class II: 30.1-40 cm dbh
		Class III: 40.1 -50 cm dbh
		Class IV: >50 cm dbh
TREATMENTS	Removed competitors	Liberated
	Non removed competitors	Reference
PERIOD	Time between initial measurement drived 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



2.2 Selective Thinning

As mentioned before, selective thinning consists in the removal of competitors to improve the space and nutrient availability of the desired species [40, 9]. The treatment is based on the theory that the growth rates of trees are directly related to the quantity of received sun light, therefore all other trees and undesirable species within a given diameter around the desired species are removed to obtain an adequate lighting and to enhance their nutrient availability e.g. [41,42]. (Figure 2).

To determine the competitor of the PCT trees all plots were visited and the tree form, crowns diameter, social position within the forest stand as well as stem quality analyzed and evaluated. All detected competitors were labeled with a plastic tape and removed during a campaign between April and May 2004. The selective thinning included mainly competitor trees, which were cut applying the method of directional falling, to avoid additional damage inside the ecosystem [43].

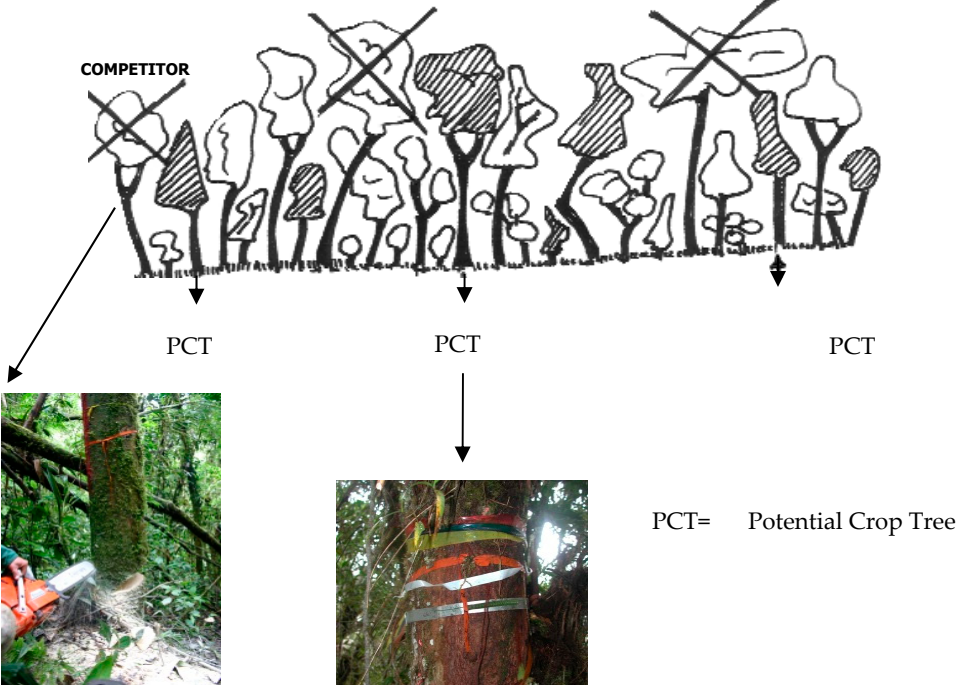


Figure 2. Scheme of the implementation of selective thinning.

2.3 DBH measurements and Data Analysis

To evaluate the individuals of the nine 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. To analyze the effect of liberation for the individual tree species over time. Furthermore, to improve the analysis antecedent dendrometers measurements (DBH) of the selected species executed by other studies in the RBSF forest were included, which were monitored to estimate the AGB and the annual biomass production [44,28].

The diametric increase of the PCT's and reference trees were calculated by means of the follow equation, taken from [21]:

$$D_i = \frac{D_1 - D_0}{t}$$

Where:  $D_i$ = Diameter increase (cm/month),  $D_o$ = initial DBH (cm),  $D_1$ = DBH (cm) during the different campaigns, and  $t$ = time between measurements.

The equation was applied to all selected trees after their initial DBH measurement, which resulted in the monthly DBH increase of each tree. Then, all individual monthly results were averaged to determine the mean increase for each tree species as well as for their specific diametric class. Finally, the average monthly DBH increases of the individual species were determined to obtain a mean value for each monitoring period as well as for the entire study period.

To analyze the monthly, yearly and total DBH increases, and to determine the influencing factors the Levene's test [45], which assess the homoscedasticity, and the Shapiro-Wilke test [46], which evaluates the normality, were applied, using the software R Version 3.2.0 [47]. If significant differences in diameter growth between the PCT's and the reference trees were found, considering the different diametric classes and the annual season, an additional T-test (software R) was executed, whereas an independent Tukey test (Tukey HSD function, software R) was applied if significant differences between the monitoring periods were identified. Both tests were accepted with  $p \leq 0.05$ , which indicates that the results are statistically significant.

To check whether the initial DBH (diametric classes) or other factors, like the selective thinning or the climate conditions, determine the diameter growth of the nine selected timber species, a linear mixed model (LMER4 package) was applied, which is also included in the statistical software R. The linear mixed model combines explanatory categorical factors like diameter class, treatment or climate conditions, and give a "random" variable for the repeated measurements throughout time (period). To adjust the linear mixed model a one-way Anova test was executed, which was accepted with  $p \leq 0.05$ .

### 3. Results

In general, the selected timber species responded differently to the thinning respect to their reference trees (Table 3). Therefore, the species analyzed were separated into three groups (positive response, negative response, and no response to liberation).

#### 3.1 Positive response to thinning

The species that responded positively to the release were *Inga acreana* and *Hyeronima asperifolia*, which had a greater diametric increment than their reference trees. *Inga acreana* showed a mean growth of  $1.13 \text{ cm} \pm 0.72$  over the whole study period, whereas the control trees only an increment of  $0.56 \text{ cm} \pm 0.47$ . The diametric growth of the released trees was not continuous, in which the lowest increment was measured during the first year ( $1.01 \text{ cm} \pm 0.81$ ), which afterwards increased to  $1.16 \text{ cm} \pm 0.61$  (second year) and finally to  $1.22 \text{ cm} \pm 0.78$  (third year). For the reference trees a more constant growth was observed, but also with the lowest increment during the first year, which is due to the initiation time of the investigation (June), because the main rainy season peaks and concurrently lowest temperatures are observed [30,35]. This may have influence in the diametric growth because highest DBH increments for all species were observed at the beginning of the year when temperatures are highest as well as having sufficient rainfall occurs (Figure 3 and 4).



The released trees of *Hyeronima asperifolia* showed a mean growth of 0.63 cm  $\pm$  0.64 over the whole study period, whereas the control trees only had an increase of 0.35 cm  $\pm$  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  $\pm$  0.53). However, the diametric class of released trees had significantly influenced because smaller trees showed a higher DBH increment. For *Inga acreana* increments were only observed for Class I (diameter: 20.1 cm to 30 cm), whereas *Hyeronima asperifolia* showed increments in all Classes, but which higher values for the Classes I - III (Table 4). As show in Table 5, the liberation of the two species had significant influence in the enhanced diametric growth, but also the temperature (Figure 3), precipitation (Figure 4) as well as diametric class, which especially holds true for *Hyeronima asperifolia*.

In summary, both species showed higher diametric growth compared to their control trees during the whole study period, which illustrates the expected effects of liberation, improving the light and nutrient availability, which leads to a faster DBH growth.

**3.2 Negative response to thinning**

The species with a negative response to liberation were *Cedrela montana*, *Tabebuia chrysantha*, *Podocarpus oleifolius* and *Nectandra membranacea*. All these species showed significant lower diametric growth respective to their control trees, especially during the second and third year after liberation (Table 3). The species with most significant differences were *Cedrela montana* (1.16 cm  $\pm$  1.21 vs. 0.87 cm  $\pm$  1.24), followed by *Nectandra membranacea* (0.44 cm  $\pm$  0.62 vs. 0.26 cm  $\pm$  0.32), because light and nutrient availability is not the main factor for DBH increments; more important were temperature and precipitation, as shown in Table 5. However, like the two species which responded positively to liberation, the highest DBH increments were observed for the diametric classes I-III. Only *Tabebuia chrysantha* showed small increments in class IV (diameter over 50 cm) during the whole study period (Table 4).

295

296 Table 3. Average annual diameter increase. Values highlighted are statistically significant.

SPECIES	Treatment				Treatment x Period											
	Control		Liberated		I				II				III			
					Control		Liberated		Control		Liberated		Control		Liberated	
	$\bar{x}$	Sd	$\bar{x}$	Sd	$\bar{x}$	Sd	$\bar{x}$	Sd	$\bar{x}$	Sd	$\bar{x}$	Sd	$\bar{x}$	Sd	$\bar{x}$	Sd
<i>Inga acreana</i>	0.56	0.47	<b>1.13</b>	0.72	0.43	0.36	<b>1.01</b>	0.81	0.64	0.36	<b>1.16</b>	0.61	0.63	0.66	<b>1.22</b>	0.78
<i>Hyeronima asperifolia</i>	0.35	0.36	<b>0.62</b>	0.54	0.26	0.34	<b>0.44</b>	0.58	0.41	0.39	<b>0.67</b>	0.46	0.38	0.34	<b>0.76</b>	0.53
<i>Cedrela montana</i>	<b>1.16</b>	1.21	0.87	1.24	<b>1.20</b>	1.23	0.93	1.38	<b>1.25</b>	1.02	0.98	1.55	<b>1.03</b>	1.32	0.70	0.63
<i>Tabebuia chrysantha</i>	<b>0.27</b>	0.34	0.21	0.41	0.16	0.21	<b>0.28</b>	0.62	<b>0.32</b>	0.32	0.21	0.28	<b>0.33</b>	0.45	0.12	0.15
<i>Podocarpus oleifolius</i>	<b>0.15</b>	0.26	0.14	0.46	0.09	0.19	<b>0.19</b>	0.68	0.16	0.32	<b>0.19</b>	0.35	<b>0.21</b>	0.26	0.05	0.13
<i>Nectandra membranacea</i>	<b>0.44</b>	0.62	0.26	0.32	<b>0.25</b>	0.30	0.26	0.28	<b>0.34</b>	0.43	0.25	0.30	<b>0.76</b>	0.90	0.27	0.38
<i>Clusia ducuoides</i>	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
<i>Hyeronima moritziana</i>	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
<i>Ficus citrifolia</i>	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

297

298

299

300

301

302 Table 4.

Species	Period 1							
	Class 1		Class 2		Class 3		Class 4	
	Control	Liberated	Control	Liberated	Control	Liberated	Control	Liberated
<i>Inga acreana</i>	0.43	1.01	0.00	0.00	0.00	0.00	0.00	0.00
<i>Hyeronima asperifolia</i>	0.48	0.45	0.15	0.43	0.15	0.78	0.04	0.10
<i>Cedrela montana</i>	1.01	0.81	1.39	0.47	1.36	1.50	0.00	0.00
<i>Tabebuia chrysanth</i>	0.28	0.72	0.14	0.11	0.15	0.07	0.08	0.23
<i>Nectandra membranacea</i>	0.16	0.34	0.27	0.17	0.31	0.17	0.00	0.00
<i>Podocarpus oleifolius</i>	0.17	0.12	0.07	0.02	0.03	0.42	0.00	0.00
<i>Ficus subandina</i>	1.00	0.88	1.24	1.25	0.00	0.00	0.00	0.00
<i>Clusia ducuoides</i>	0.13	0.15	0.06	0.08	0.13	0.08	0.00	0.00
<i>Hyeronima moritziana</i>	0.12	0.18	0.11	0.06	0.00	0.00	0.00	0.00
	Period 2							
<i>Inga acreana</i>	0.64	1.16	0.00	0.00	0.00	0.00	0.00	0.00
<i>Hyeronima asperifolia</i>	0.45	0.73	0.43	0.67	0.35	0.83	0.00	0.46
<i>Cedrela montana</i>	1.20	0.96	1.31	0.65	1.25	1.33	0.00	0.00
<i>Tabebuia chrysanth</i>	0.37	0.44	0.32	0.12	0.19	0.14	0.42	0.13
<i>Nectandra membranacea</i>	0.35	0.41	0.20	0.08	0.46	0.08	0.00	0.00
<i>Podocarpus oleifolius</i>	0.08	0.10	0.06	0.04	0.33	0.42	0.00	0.00
<i>Ficus subandina</i>	1.35	0.96	1.27	1.33	0.00	0.00	0.00	0.00
<i>Clusia ducuoides</i>	0.07	0.06	0.11	0.05	0.00	0.08	0.00	0.00
<i>Hyeronima moritziana</i>	0.05	0.25	0.03	0.13	0.00	0.00	0.00	0.00
	Period 3							
<i>Inga acreana</i>	0.63	1.22	0.00	0.00	0.00	0.00	0.00	0.00
<i>Hyeronima asperifolia</i>	0.49	0.82	0.20	0.78	0.44	0.86	0.00	0.57
<i>Cedrela montana</i>	0.99	0.74	1.06	0.64	1.00	0.73	0.00	0.00
<i>Tabebuia chrysanth</i>	0.47	0.09	0.16	0.15	0.10	0.06	0.59	0.18
<i>Nectandra membranacea</i>	0.37	0.50	0.56	0.05	1.34	0.05	0.00	0.00
<i>Podocarpus oleifolius</i>	0.11	0.16	0.20	0.00	0.30	0.00	0.00	0.00
<i>Ficus subandina</i>	0.86	1.18	0.88	0.95	0.00	0.00	0.00	0.00
<i>Clusia ducuoides</i>	0.13	0.15	0.09	0.05	0.14	0.18	0.00	0.00
<i>Hyeronima moritziana</i>	0.30	0.20	0.17	0.20	0.00	0.00	0.00	0.00

303

304 3.3 Null response to thinning

305 Species that did not showed significant response to liberation (neither positive nor negative)  
306 were *Hyeronima moritziana*, *Clusia ducuoides* and *Ficus citrifolia*, which indicates that other aspects  
307 have more influence in the diametric growth of these species. The diametric growth of *Hyeronima*  
308 *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)  
309 were generally low (liberated trees and control trees) over the complete study period, but which  
310 generally highest DBH increments during the third year. In contrast, *Ficus citrifolia* (1.11 cm ± 1.04

vs. 1.09 cm  $\pm$  1.22) showed generally higher DBH increments, especially during the first two years under study. This high DBH increments of *Ficus citrifolia* can be related to the significant influence of temperature and precipitation for its diametric growth, which is 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* also showed small DBH increments in class III (Table 4).

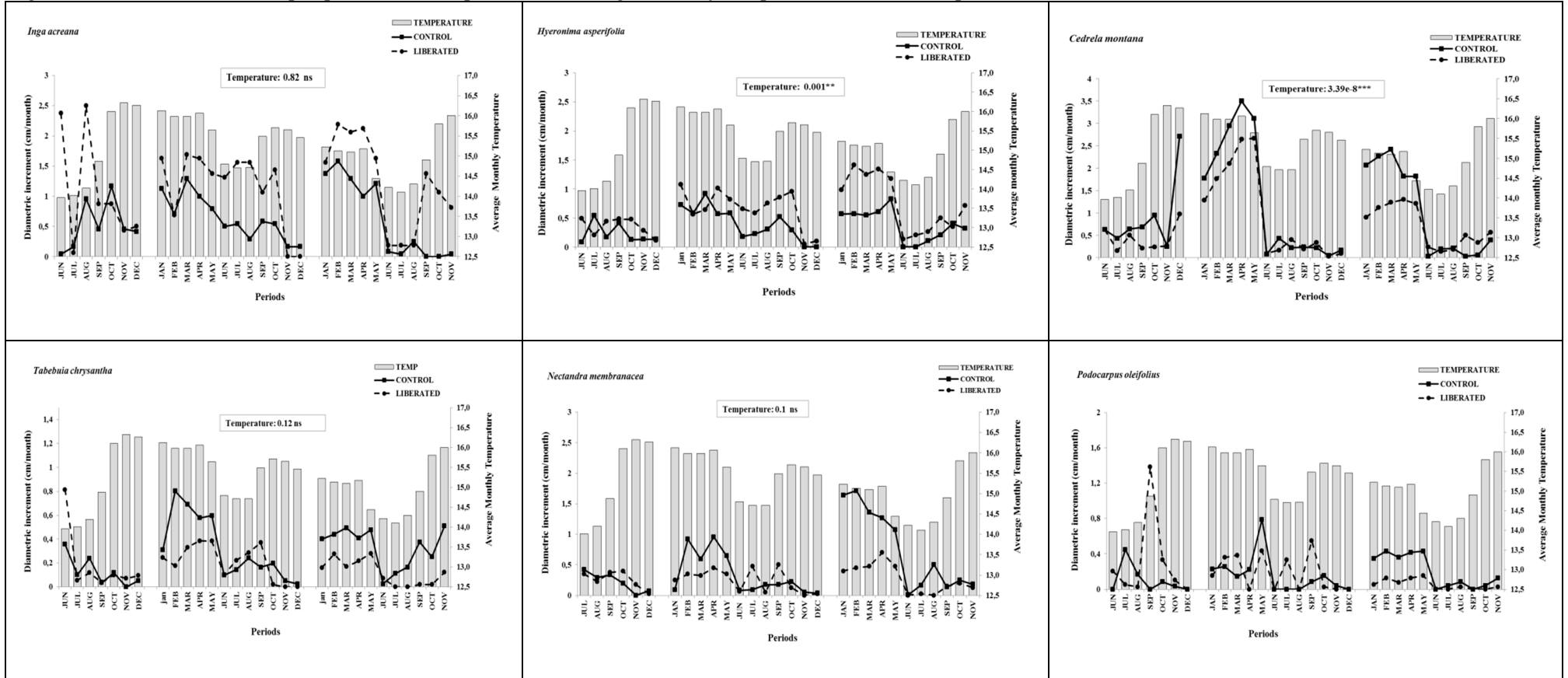
Table 5. P values of the variables and the interactions that influence the variability of the diametric increase.

ESPECIES	Liberation		Precipitation		Temperature		Diametric Class		Liberation x Diametric Class		Liberation x Precipitation		Liberation x Temperature		Diametric Class x Precipitation		Diametric Class x Temperature	
	Ch	<i>p</i>	Ch	<i>p</i>	Ch	<i>p</i>	Ch	<i>p</i>	Ch	<i>p</i>	Ch	<i>p</i>	Ch	<i>p</i>	Ch	<i>p</i>	Ch	<i>p</i>
<i>Inga acreana</i>	14.9	<b>0.0001**</b>	0.05	0.81	0.05	0.83	—	—	—	—	0.18	0.66	0.99	0.31	—	—	—	—
<i>Hyeronima asperifolia</i>	33.5	<b>7.75e-09***</b>	4.1	<b>0.04*</b>	9.8	<b>0.001**</b>	16.7	<b>0.0008**</b>	5.01	0.08	0.0	0.99	0.27	0.6	0.42	0.9	3.5	0.31
<i>Cedrela montana</i>	6.2	<b>0.01*</b>	15.1	<b>0.0001**</b>	31.9	<b>1.57e-8***</b>	4.9	0.08	1.5	0.21	1.01	0.31	2.3	0.12	4.5	0.1	5.9	<b>0.05*</b>
<i>Tabebuia chrysantha</i>	2.3	0.12	13.5	<b>0.0002**</b>	1.74	0.18	26.3	<b>2.7e-5***</b>	4.04	0.39	1.9	0.16	0.39	0.52	13.5	<b>0.003**</b>	0.62	0.88
<i>Podocarpus oleifolius</i>	0.04	0.83	0.09	0.75	0.009	0.92	8.6	<b>0.01*</b>	1.6	0.5	0.34	0.6	0.2	0.65	0.07	0.96	0.89	0.64
<i>Nectandra membranacea</i>	5.5	<b>0.01*</b>	14.9	<b>0.0001***</b>	31.8	<b>1.68e-8***</b>	1.4	0.49	0.12	0.72	2.7	0.9	3.5	0.06	0.2	0.9	2.7	0.2
<i>Clusia ducuoides</i>	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
<i>Hyeronima moritziana</i>	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	<b>0.05*</b>	0.64	0.72	0.0002	0.99
<i>Ficus citrifolia</i>	0.007	0.93	10.1	<b>0.001**</b>	8.8	<b>0.002**</b>	0.46	0.49	0.12	0.72	0.19	0.65	0.17	0.67	1.9	0.16	3.3	0.06

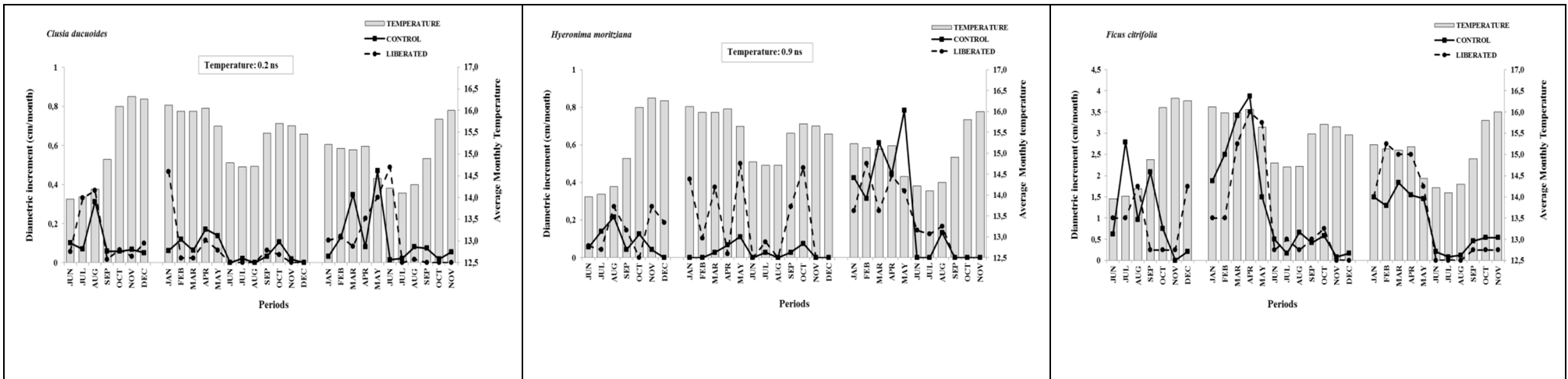
326

327

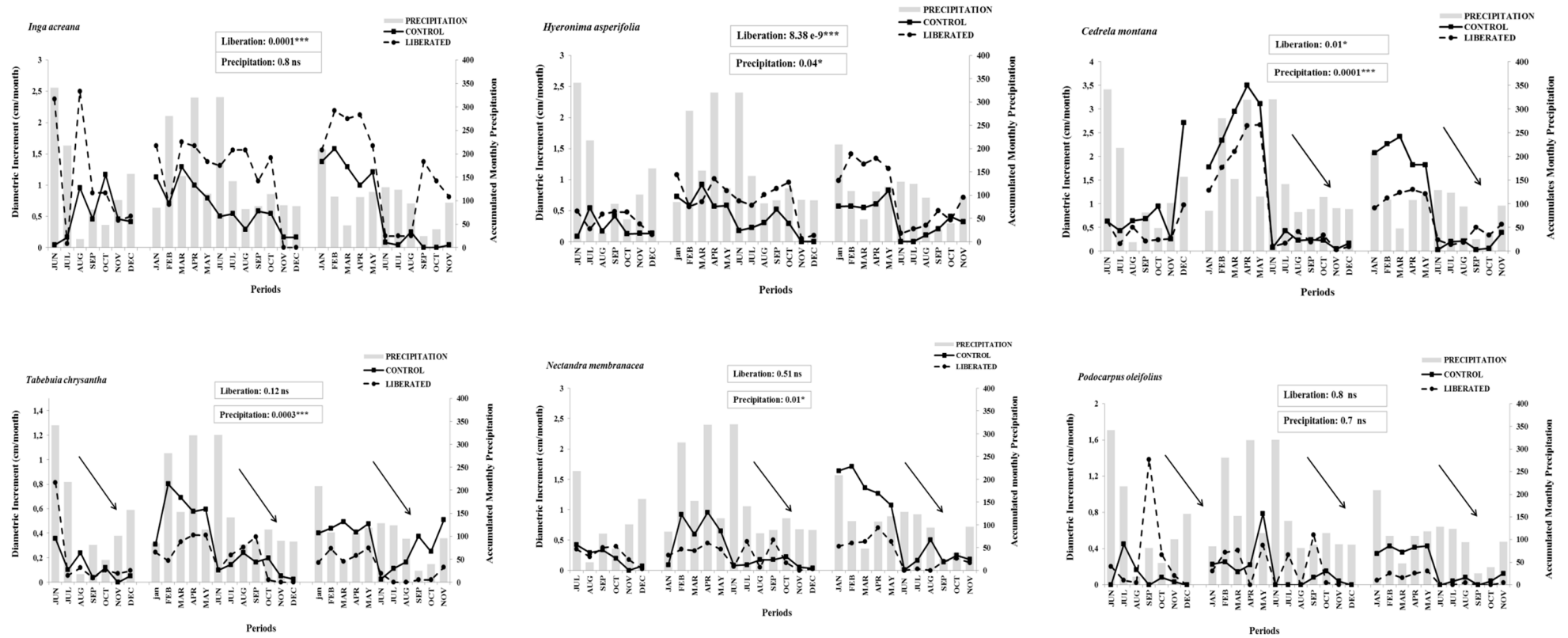
Figure 3. Diameter increment, per period with respect to the average monthly temperature of the nine species studied.

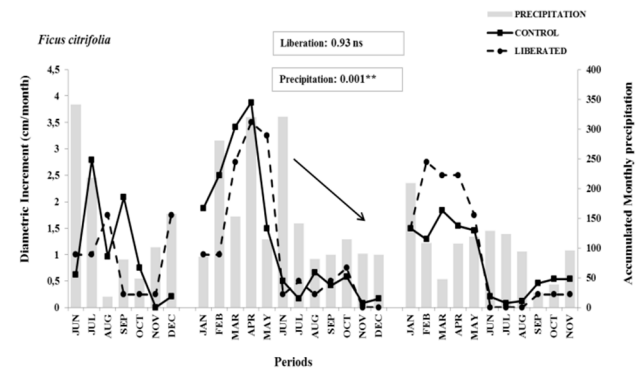
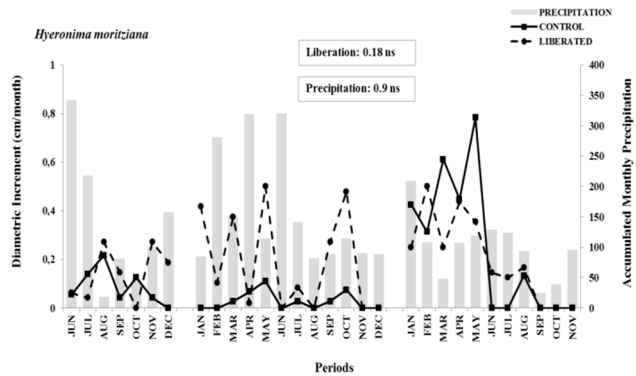
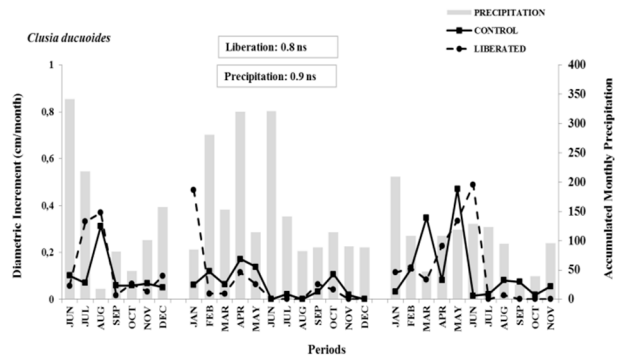






329 Figure 4. Diametric increase of the nine species studied, by period with respect to the release and monthly cumulative precipitation.





#### 4. Discussion

Historically the trees growth has been modeled based on different classification criteria, the most common have been the taxonomic affinity, ecological guild they belong to the species, similar growth dynamics, even different statistical approaches [18] and different models to interpret the growth and performance of different types of forest plantations whether in biodiverse tropical forests [48]. Natural tropical forests of Ecuador have been monitored for several decades [49] re measurements are continuous over time, considering only the influence of climatic factors affecting the entire forest.

Although the study area corresponds to tropical mountain zone, there is a marked temporality in terms of temperature and precipitation, which evidently causes different physiological responses in *Cedrela montana* and *Tabebuia chrysantha*, that interrupt the cambial activity simulating a dormancy period like a temperate climate zones [50] a phenomenon that directly affects the diametric growth of these species, the formation of rings of growth corroborates this situation of temporality [51].

Monitoring of forest growth and particular species based on experimentation as adding nutrients to the soil [28] or release of trees plus [15]. 2008), are topics that provide knowledge about the effect of activities forestry and effectiveness when implementing experimentally.

In our study, we separate the 9 species monitored in three groups, the first group consists of species that have responded positively to the release (*Inga acreana* and *Hyeronima asperifolia*), species responded negatively (*Cedrela montana*, *Nectandra membranacea*, *Podocarpus oleifolius*, *Tabebuia chrysantha*) and species responded neutrally (*Hyeronima moritziana*, *Clusia ducuoides*, *Ficus citrifolia*).

*Inga acreana* and *Hyeronima asperifolia* respond positively to thinning. For *Inga acreana* difference between treatments is obvious. The species of genus *Inga* are considered as medium-sized and shade intolerant according to [52], while according [18], some species of the genus are considered shade intolerant or moderately shade tolerant, *Inga acreana* grows and thrives best in relatively open and light areas, being so, the effect of thinning improves conditions diameter growth, corroborating the benefits of thinning for this species [15, 53, 54]. Not finding individuals in larger diameter classes, only individuals between 20 -30 cm DAP discussed in this first phase (36 months), and there is no data on the growth behavior in larger diameter trees.

Liberated trees growth averaged more than the control trees, plus show a marked seasonality in rainfall and temperature being the period from January to June which presents highest average precipitation. In *Inga acreana* the effect of the two climatic variables are minimized in respect to the effect of thinning on individuals of the species and show no significance in the model.

In *Hyeronima asperifolia* the response of trees to liberation is positive. [12] refer to the liberation based on thinning as a valid method for increasing the growth and yield of selected trees. Likewise, [15], assert that *Hyeronima asperifolia* has an interesting early response, although the difference between the thinned trees and control trees, is not significant in this period. Reference trees grew more are in Class III 20-30 cm dbh, while the trees that grew released were larger Class V (40-50 cm dbh), according to [40] what happens with the trees of timber species after implementing various treatments (including refining and selective harvesting) is that trees released are those with the

greatest increase (0.39 and 0.71 cm / yr) and (0.47 cm / year and 0.86 cm / yr). Liberated trees creates better conditions of light, resulting in a diametric increase, [21] in the Brazilian Amazon found that there are significant differences in diameter growth of larger trees an event also ratified by [6] which determine the pattern of growth in diameter is strongly dependent on the size of the tree.

The growth of *Hyeronima asperifolia* in both treatments shows a significant decrease in June of each period, with a recurring pattern not only in this species, but found in other species in the same area, studied by [53]. Despite being a per humid area, there are seasons when the humidity decreases, this being one of the processes who run, in many species, phenological processes such as flowering and fruiting. In the analysis of growth, we include temperature, it turned out, the temperature has a more immediate influence precipitation, as rainwater is usually stored for relatively long periods in soil and is consumed by the plants according to their need while the temperature is fluctuating and directly influences the plants, in this specific case, the increase in diameter of the liberated trees coincides with increasing temperature.

In the next group of species released trees grow less than the trees control, i.e. the release of the trees produced an inhibitory effect on diameter growth. [55] developed a hypothesis, which state that the variation in the diameter growth of trees of certain species is related to two factors, the first is the amount of light intercepted by the tree and the second is the density of the wood. The expected result being an inverse relationship between growth and wood density of the species studied, the result of his research he found that the correlation was higher between wood density and growth than the correlation between growth and the amount of light intercepted. The three species with market value are in this group, the four species have hard and dense wood; *Tabebuia chrysantha* and *Cedrela montana* have defoliation.

*Cedrela montana*, is a deciduous species which forms growth rings in its trunk [39] and whose defoliation is associated with the end of the wettest time and the start of the coldest season lasts approximately 3 months (although the fluctuation is just 1.5 ° C in the season), the authors found that the temperature is significantly correlated with cambial growth increases during the warmest season January through April and decreases in the coldest months, a trend that matches the pattern of growth that we find and showing that the release affects negatively and correlates with low air temperature, especially in the study area, having the possibility that other climatic regional factors produce changes in the pattern of growth. Regarding the growth of this species, [56] refer to the slow growth of the species, both in Colombia and Ecuador.

The growth trend regardless of whether they were released or not, decline significantly. There is a marked trend throughout the year and the release of individuals apparently affects the growth process more than usual, since at this time the trees of this species begin a process of changing leaves and flower production [39].

In the first year of monitoring [15] show that *Cedrela montana* responds negatively to the release. The same pattern is observed over the first three years and as was said above, if the growth of the species is associated with the seasonality of precipitation and temperature, thinning will not positively affect the species that has marked seasonality in their physiological processes.

*Tabebuia chrysantha* is also a deciduous species [39], time where defoliation begins coincides with the beginning of the driest season starting June. Released trees and control trees slow growth in June, time in which according to [57] begins production of new leaves and flowers, using all resources to perform these two physiological stages, leaving for later a growth phase coinciding with the wettest season. The release does not fulfill an important role in the growth of the trees and the recurring pattern of growth *Tabebuia chrysantha* is linked to the presence of precipitation.

In *Podocarpus oleifolius* the precipitation and release does not produce a significant effect on growth, the opposite occurs, i.e.: control trees grow more than released trees. The growth peaks seen in Figure 4, which belong to the trees released, did not differ significantly in the overall average, the statistical model shows significant differences in terms of size (diameter class) of trees released ( $p = 0.01 *$ ), but the interaction between treatment and diametric class is not significant, meaning that the release has a different answer depending on the initial diameter of the tree, but does not produce significant positive effect. The growth of some species of the genus has been studied, [58] determined that in Costa Rica the average annual growth in *Podocarpus oleifolius* var. *macrotachyus* reached 1.7 mm, while in our study the annual average maximum was 0.21 mm, a fact corroborated by [28] in which it refers to the slow growth of *Podocarpus oleifolius* in the same area of study of this work.

In *Nectandra membranacea*, released trees grow less than the control trees, in the first period, immediately after releasing the trees, there is a certain rise in trees released, a phenomenon which is also cited by [15] in the following monitored periods showing more growth in the control trees than the released trees. Precipitation is a factor that significantly influences the dynamics of growth of the trees of this species, unlike the temperature has no significance in the model. In the initial period from January to June is where the trees grow in both treatments, in the second semester growth is lower.

In *Ficus citrifolia*, temperature and precipitation are significant factors in the growth of trees. In the first two periods the control trees have the highest average growth, while in the last monitoring period coinciding with seasonality of temperature and precipitation trees released show a blunting growth that is not significant with respect to total for the period.

In *Clusia ducuioides* precipitation and temperature have no significant effect on diameter growth of trees. In the first evaluation made by [15] note a minimum difference in growth of control trees contrasting with the trees released.

In *Hyeronima moritziana*, as in previous species, the release does not significantly influence the diametric increase. Neither precipitation nor temperatures are significant when analyzing the difference in diameter growth of trees. There are no significant differences in the diameter growth of the control trees in relation to the released trees, nor growth peaks that coincide with the seasonality of precipitation or temperature, a behavior that is shown in some of the species studied.

## 5. Conclusions

We conclude that release potentiates the growth of timber species that do not defoliate and considered semi-tolerant on shade, of between 20-30 cm DAP.



Precipitation and temperature affect all species of the forest, but in the defoliate species, it would not be convenient to release them or at least the evidence of these first three years does not show clear differences with control trees.

The increase in trees released are higher in the individuals of the first two diametric classes in all species, this means that larger trees (ie older) release does not affect them in a positive way so release should occur in the youngest trees.

**Author Contributions:** Conceptualization, R.M.; methodology, R.M; O.C.; formal analysis, O.C. and A.F.; writing—original draft preparation, O.C.; A.F.; writing—review and editing, O.C., A.F. R.M. P.H.

**Funding:** The first author wishes to thank the German Foundation for Research (DFG) for the funding to implement the experiment. Technical University of Munich (TUM) and the Universidad Tecnica Particular de Loja (UTPL) for the facilities for the writing of the manuscript.

**Acknowledgments:** to Dr. A. Fries for the handling of the climatic data, to Dr. Sven Gunter for his help in the implementation of the experiment in the field and thanks to all the co-authors for their valuable comments to improve the manuscript.

References

- Olander, L. P.; Gibbs, H. K.; Steininger, M.; Swenson, J. J. & Murray, B. C. Reference scenarios for deforestation and forest degradation in support of REDD: a review of data and methods. *Environ Res Lett*, **2008**, 3, 025011. DOI 10.1088/1748-9326/3/2/025011.
- Pan, Y.; Birdsey, R. A.; Fang, J.; Houghton, R.; Kauppi, P. E.; Kurz, W. A.; Phillips. O.; Shvidenko.A.; Lewis, S.L.; Canadell, J. G.; Jackson, R.; Pacala, S.W.; McGuire, D.; Piao, S.; Rautiainen, A.; Sitch, S.; Hayes, D. & Ciais, P. A large and persistent carbon sink in the world’s forests. *Science*, **2011**, 333, 988-993. DOI: 10.1126/science.1201609.
- Beck, E.; Bendix, J.; Kottke, I.; Makeschin, F. & Mosandl, R. *Gradients in a tropical mountain ecosystem of Ecuador*. Springer Science & Business Media: Berlin, Germany, 2008. ISBN 978-3-540-73526-7.
- Saatchi, S. S.; Harris, N. L.; Brown, S.; Lefsky, M.; Mitchard, E. T.; Salas, W.; ... & Petrova, S. Benchmark map of forest carbon stocks in tropical regions across three continents. *P Natl Acad Sci*, **2011**, 108, 9899-9904. DOI: 10.1073/pnas.1019576108.
- Malhi, Y. & Phillips, O. L. Tropical forests and global atmospheric change: a synthesis. *Philos T Roy Soc B*, **2004**, 359, 549-555. DOI 10.1098/rstb.2003.1449.
- Clark, D. A. & Clark, D. B. Assessing the growth of tropical rain forest trees: issues for forest modeling and management. *Ecol appl*, **1999**, 9, 981-997. DOI 10.1890/1051-0761(1999)009[0981:ATGOTR]2.0.CO;2.
- Canadell, J. G. & E. D. Schulze. Global potential of biospheric carbon management for climate mitigation. *Nat. Commun.* **2014**, 5, 52-82. DOI 10.1038/ncomms6282.
- Wadsworth, F. H. Forest production for tropical America. USDA Forest Service: Washington, USA.2000.
- Andresen, E.; Pedroza-Espino, L.; Allen, E. B. & Pérez-Salicrup, D. R. (2005). Effects of selective vegetation thinning on seed removal in secondary forest succession. *Biotropica*, **2005**, 37, 145-148. DOI 10.1111/j.1744-7429.2005.04058.x
- Lampretch, H. Silvicultura en los Trópicos: dinámica de los bosques tropicales húmedos. Eschborn: Deutsche Gesellschaft für Technische Zusammenarbeit. Instituto de Silvicultura de la Universidad de Gottingen. Gottingen: Germany, 1990.
- Kammesheidt, L.; Dagang, A. A.; Schwarzwäller, W. & Weidelt, H. J. Growth patterns of dipterocarps in treated and untreated plots. *Forest Ecol Manag*, **2003**, 174, 437-445. DOI: 10.1016/S0378-1127(02)00077-4.
- Wadsworth, F. H. & Zweede, J. C. Liberation: acceptable production of tropical forest timber. *Forest Ecol Manag*, **2006**, 233, 45-51. DOI 10.1016/j.foreco.2006.05.072.
- Fredericksen, T.S. & Putz, F.E. Silvicultural intensification for tropical forest conservation. *Biodivers. Conserv.* **2003**, 12, 1445–1453. DOI: 10.1023/A:102367362.

14. Silva, J. N. M.; de Carvalho, J. D.; do Ca Lopes, J.; De Almeida, B. F.; Costa, D. H. M.; de Oliveira, L. D. & Skovsgaard, J. P. Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. *Forest Ecol Manag*, **1995**, *71*, 267-274. DOI: 10.1016/0378-1127(94)06106-S.
15. Günter, S.; Cabrera, O.; Weber, M.; Stimm, B.; Zimmermann, M.; Fiedler, K.; Knuth, J.; Boy, J.; Wilcke, W.; Lost, S.; Makeschin, F.; Werner, F.; Gradstein, R. & Mosandl, R. Natural forest management in neotropical mountain rain forests—an ecological experiment. In *Gradients in a tropical mountain ecosystem of Ecuador*, Beck, E.; Bendix, J.; Kottke, I.; Makeschin, F. & Mosandl, R. Eds.; Springer: Berlin, Germany, 2008; pp. 347-359. ISBN 978-3-540-73526-7.
16. Sprugel DG. 2002. When branch autonomy fails: Milton's Law of resource availability and allocation. *Tree Physiol*, **2002**, *22*: 1119 – 1124. DOI: 10.1093/treephys/22.15-16.1119.
17. Leoni, J.M.; da Fonseca, S.F.; Schöngart, J. Growth and population structure of the tree species *Malouetia tamaquarina* (Aubl.) (Apocynaceae) in the central Amazonian floodplain forests and their implication for management. *Forest Ecol Manag*. **2011**, *261*: 62–67. DOI: 10.1016/j.foreco.2010.09.025.
18. Adame, P.; Brandeis, T. J. & Uriarte, M. Diameter growth performance of tree functional groups in Puerto Rican secondary tropical forests. *Forest Syst*, **2014**, *23*, 52-63.
19. Vlam, M.; Baker, P. J.; Bunyavejchewin, S.; Mohren, G. M. J.; Zuidema, P.A. Understanding recruitment failure in tropical tree species: insights from a tree-ring study. *Forest Ecol Manag*, **2014**, *312*, 108–116. DOI 10.1016/j.foreco.2013.10.016.
20. Péliissier, R. & Pascal, J. P. Two-year tree growth patterns investigated from monthly girth records using dendrometer bands in a wet evergreen forest in India. *J Trop Ecol*, **2000**, *16*, 429-446.
21. Da Silva, R. P.; dos Santos, J.; Tribuzy, E. S.; Chambers, J. Q.; Nakamura, S. & Higuchi, N. Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. *Forest Ecol Manag*, **2002**, *166*, 295-301. DOI: 10.1016/S0378-1127(01)00678-8.
22. Bendix, J.; Beck, E.; Bräuning, A.; Makeschin, F.; Mosandl, R.; Scheu, S. & Wilcke, W. Eds. *Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of south Ecuador*; Springer Science & Business Media: Berlin, Germany, 2013. ISBN 978-3-642-38136-2.
23. Bendix, J.; Trachte, K.; Cermak, J.; Rollenbeck, R. & Nauß, T. Formation of convective clouds at the foothills of the tropical eastern Andes (South Ecuador). *J Appl Meteorol Clim*, **2009**, *48*, 1682-1695. DOI 10.1175/2009JAMC2078.1.
24. Girardin, C. A. J.; Malhi, Y.; Aragao, L. E. O. C.; Mamani, M.; Huaraca Huasco, W.; Durand, L. & Salinas, N. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biol*, **2010**, *16*, 3176-3192. DOI 10.1111/j.1365-2486.2010.02235.x
25. Moser, G.; Leuschner, C.; Hertel, D.; Graefe, S.; Soethe, N. & Iost, S. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biol*, **2011**, *17*(6), 2211-2226. DOI 10.1111/j.1365-2486.2010.02367.x.
26. Werner, F. A. & Homeier, J. Is tropical montane forest heterogeneity promoted by a resource-driven feedback cycle? Evidence from nutrient relations, herbivory and litter decomposition along a topographical gradient. *Funct Ecol*, **2015**, *29*, 430-440. DOI 10.1111/1365-2435.12351.
27. Paulick, S.; Dislich, C.; Homeier, J.; Fischer, R. & Huth, A. (2017). The carbon fluxes in different successional stages: modelling the dynamics of tropical montane forests in South Ecuador. *Forest Ecosystems*, 2017, *4*, 5. DOI 10.1186/s40663-017-0092-0.
28. Homeier, J.; Leuschner, C.; Bräuning, A.; Cumbicus, N. L.; Hertel, D.; Martinson, G. O.; Spann S. & Veldkamp, E. Effects of nutrient addition on the productivity of montane forests and implications for the carbon cycle. In Bendix, J.; Beck, E.; Bräuning, A.; Makeschin, F.; Mosandl, R.; Scheu, S. & Wilcke, W. Eds. *Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of south Ecuador*; Springer Science & Business Media: Berlin, Germany, 2013. ISBN 978-3-642-38136-2.
29. Dislich, C. & Huth, A. Modelling the impact of shallow landslides on forest structure in tropical montane forests. *Ecol Model*, **2012**, *239*, 40-53.
30. Fries, A.; Rollenbeck, R.; Göttlicher, D.; Nauss, T.; Homeier, J.; Peters, T. & Bendix, J. Thermal structure of a megadiverse Andean mountain ecosystem in southern Ecuador and its regionalization. *Erdkunde*, **2009**, *321*-335. DOI 10.3112/erdkunde.2009.04.03.

31. Fries, A.; Rollenbeck, R.; Nauß, T.; Peters, T. & Bendix, J. Near surface air humidity in a megadiverse Andean mountain ecosystem of southern Ecuador and its regionalization. *Agr Forest Meteorol*, **2012**, *152*, 17-30. DOI 10.1016/j.agrformet.2011.08.004.
32. Ohl, C., & Bussmann, R. Recolonization of natural landslides in tropical mountain forests of Southern Ecuador. *Feddes Repertorium*, **2004**, *115*, 248-264. DOI 10.1002/fedr.200311041
33. Brehm, G.; Homeier, J. & Fiedler, K. Beta diversity of geometrid moths Lepidoptera: (Geometridae) in an Andean montane rainforest. *Divers Distrib*, **2003**, *9*(5), 351-366. DOI 10.1046/j.1472-4642.2003.00023.x
34. Curatola Fernández, G. F.; Obermeier, W. A.; Gerique, A.; López Sandoval, M. F.; Lehnert, L. W.; Thies, B. & Bendix, J. Land cover change in the Andes of Southern Ecuador—Patterns and drivers. *Remote Sens*, **2015**, *7*(3), 2509-2542. DOI 10.3390/rs70302509.
35. Fries, A.; Rollenbeck, R.; Bayer, F.; Gonzalez, V.; Oñate-Valivieso, F.; Peters, T. & Bendix, J. Catchment precipitation processes in the San Francisco valley in southern Ecuador: combined approach using high-resolution radar images and in situ observations. *Meteorol Atmos Phys*, **2014**, *126*, 13-29. DOI 10.1007/s0070.
36. Schrumpf, M.; Guggenberger, G.; Valarezo, C. & Zech, W. Tropical montane rain forest soils. Development and nutrient status along an altitudinal gradient in the south Ecuadorian Andes. *Erde*, **2001**, *132*, 43-59.
37. Wilcke, W.; Oelmann, Y.; Schmitt, A.; Valarezo, C.; Zech, W. & Homeier, J. Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. *J Plant Nutr Soil Sc*, **2008**, *171*, 220-230. DOI 10.1002/jpln.200625210.
38. Martinson, G. O.; Corre, M. D. & Veldkamp, E. Responses of nitrous oxide fluxes and soil nitrogen cycling to nutrient additions in montane forests along an elevation gradient in southern Ecuador. *Biogeochemistry*, **2013**, *112*, 625-636. DOI 10.1007/s10533-012-9753-9.
39. Bräuning, A.; Volland-Voigt, F.; Burchardt, I.; Ganzhi, O.; Nauss, T. & Peters, T. 2009. Climatic control of radial growth of *Cedrela montana* in a humid mountain rainforest in southern Ecuador. *Erdkunde*, **2009**, *63*, 337-345. DOI 10.3112/Erdkunde.2009.04.04.
40. De Graaf, N. R.; Poels, R. L. H. & Van Rompaey, R. S. A. R. Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. *Forest Ecol Manag*, **1999**, *124*, 123-135. DOI 10.1016/S0378-1127(99)00057-2.
41. Dawkins, H. C. The refining of mixed forest: a new objective for tropical silviculture. *Empire Forestry Review*, **1955**, 188-191.
42. Louman, B.; Valerio, J. & Jiménez, W. Bases ecológicas. Silvicultura de bosques latifoliados húmedos con énfasis en América Central. Serie Técnica. Manual Técnico, **2001**, *46*, 19-78.
43. Peña-Claros, M.; Fredericksen, T. S.; Alarcón, A.; Blate, G. M.; Choque, U.; Leaño, C. ... & Putz, F. E. Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *Forest Ecol Manag*, **2008**, *256*, 1458-1467. DOI 10.1016/j.foreco.2007.11.013.
44. Leuschner, C.; Moser, G.; Hertel, D.; Erasmi, S.; Leitner, D.; Culmsee, H. ... & Schwendenmann, L. Conversion of tropical moist forest into cacao agroforest: consequences for carbon pools and annual C sequestration. *Agroforest Syst*, **2013**, *87*, 1173-1187. DOI 10.1007/s10457-013-9628-7.
45. Levene, H. Robust Tests for Equality of Variances, In Contributions to Probability and Statistics, ed. I. Olkin, Palo Alto, Calif.: Stanford University Press, USA, 1960, 278-292.
46. Shapiro, S.S. and M.B. Wilk. An Analysis of Variance Test for Normality (Complete Samples), *Biometrika*, **1965**, *52*: 591.
47. R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria. 2015. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
48. Vanclay, J. K. Modelling forest growth and yield: applications to mixed tropical forests. *School of Environmental Science and Management Papers*, 1994, 537. ISBN 0 85198 913 6.
49. Neill, D. Dinámica de bosques amazónicos: Diez años de registro en parcelas permanentes de la Estación Biológica Jatun Sacha. In Asanza, M.; Neill, D.; Sandoval, S. & Welling, J. Eds. *Resúmenes del tercer Congreso Ecuatoriano de Botánica*. Quito, Ecuador, 2000. Pp 79.
50. Bräuning, A.; Homeier, J.; Cueva, E.; Beck, E. & Günter, S. Growth dynamics of trees in tropical mountain ecosystems. In *Gradients in a tropical mountain ecosystem of Ecuador*, Beck, E.; Bendix, J.; Kottke, I.; Makeschin, F. & Mosandl, R. Eds.; Springer: Berlin, Germany, 2008; pp. 347-359. ISBN 978-3-540-73526-7.

604

605

606

607

608

609

610

611

612

613

614

615

616

617

618

619

620

621

622

623

624

625

51. Bräuning, A. & Burchardt, I. Detection of growth dynamics in tree species of a tropical mountain rain forest in southern Ecuador. *TRACE-Tree Rings in Archaeology, Climatology and Ecology*, **2006**, 4, 127-131.

52. Palacios, W. & Jaramillo, N. Ecological forest species groups in Northeastern Ecuador and their importance for the management of indigenous forest. *Lyonia*, **2005**, 6, 55-75.

53. Baker, T. R.; Swaine, M. D. & Burslem, D. F. Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. *Perspect Plant Ecol*, **2003**, 6(1-2), 21-36. DOI 10.1078/1433-8319-00040.

54. Kariuki, M.; Rolfe, M.; Smith, R. G. B.; Vanclay, J. K. & Kooyman, R. M. Diameter growth performance varies with species functional-group and habitat characteristics in subtropical rainforests. *Forest Ecol Manag*, **2006**, 225, 1-14. DOI 10.1016/j.foreco.2005.07.016.

55. King, D. A.; Davies, S. J.; Supardi, M. N. & Tan, S. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Funct Ecol*, **2005**, 19, 445-453. DOI 10.1111/j.1365-2435.2005.00982.x.

56. Bare, M. C. & Ashton, M. S. Growth of native tree species planted in montane reforestation projects in the Colombian and Ecuadorian Andes differs among site and species. *New Forests*, **2016**,47, 333-355. DOI 10.1007/s11056-015-9519-z.

57. Bendix, J.; Rollenbeck, R. & Reudenbach, C. Diurnal patterns of rainfall in a tropical Andean valley of southern Ecuador as seen by a vertically pointing K-band Doppler radar. *Int J Climatol*, **2006**, 26, 829-846. DOI 10.1002/joc.1267.

58. Bauch, J.; Quiros, L.; Noldt, G., & Schmidt, P. Study on the wood anatomy, annual wood increment and intra-annual growth dynamics of Podocarpus oleifolius var. macrostachyus from Costa Rica. *J Appl Bot Food Qual*, **2012**, 80, 19-24.