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Light habitat, structure, diversity and dynamics of the tropical dry forests of the upper Magdalena river

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ABSTRACT

Tropical dry forests are complex and fragile ecosystems with high anthropogenic intervention and restricted reproductive cycles. They harbor unique richness, structural, physiological and phenological diversity. This research was carried out in the upper Magdalena valley, in four forest fragments with different successional stages. In each fragment, four permanent plots of 0.25 ha were established and the light habitat associated with species richness, relative abundance and rarity was evaluated, as well as the forest dynamics that included mortality, recruitment and diameter growth for a period of 5.25 years. In mature riparian forest, species richness was found to be higher than that reported in other studies for similar areas in the Cauca Valley and the Atlantic coast. Values of species richness, heterogeneity and rarity are higher than those found in drier areas of Tolima. Forest structure, diversity and dynamics were correlated with light habitat, showing differences in canopy architecture and its role in the capture and absorption of radiation. The utilization rate of photosynthetic effective radiation in the forest underlayer with high canopy density is low, which is related to the low species richness, while the underlayer under light is more abundant and heterogeneous.

Keywords: Light Extinction Coefficient; Floristic Diversity; Structure; Plant Area Index; Mortality; Photosynthetically Active Radiation, Recruitment

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1. Introduction

The tropical dry forest is characterized by at least one drought season per year, which generates water deficit in the soil with the consequent alterations in the functionality of the vegetation. Thus, defoliation is generated in a large number of species that have adapted to drought under this strategy. However, another group of species remain evergreen, for which the adaptive strategy follows effective and controlled stomatal conductance[1–3]. The diversity of tropical dry forests is simpler than that of tropical rainforests and Andean forests. However, its value lies in the great number of endemic species that can reach between 43% and 73%, which, together with its low growth rates, classify it as a highly fragile ecosystem. Also typical of this ecosystem is the physiological complexity of the species and the spatial distribution patterns of the species and their populations[4–7]. The structure and pattern of diversity in tropical dry forests is contrary to that of rainforests, which increase species richness with their proximity to the equator. The highest species density in tropical dry forests is located more in the northern than equatorial areas[8–10]. The limiting factor in tropical dry forests is the availability of water in the soil, which restricts nutrient leaching processes. This has led to a worldwide change of land use in these ecosystems towards agriculture and livestock production. To this end, agriculture and animal husbandry production strategies based on irrigation systems have been formulated, which has increased food production, and greatly affected the flow of ecosystem services by destroying natural mulch and replacing it with man-made landscapes[11–13].

Colombia's tropical dry forests are located especially in two large regions that correspond to the Caribbean plain and the inter-Andean valleys of the Cauca and Magdalena rivers. In these areas, precipitation is less than 2,000 mm per year. However, the distribution of precipitation determines the particular characteristics of the vegetation. The Caribbean plain has a monomodal climate, while the inter-Andean valleys of the Cauca and Magdalena rivers have a bimodal climate, with the addition of the shadow effect of the mountain ranges[14,15]. Current natural cover in the Upper Magdalena is located in the north and south of the department of Tolima, as well as in the north and south of the department of Huila. The sub-region with the lowest frequency of natural fragments of tropical dry forest and the smallest size corresponds to the south of Tolima-north of Huila, where natural cover does not exceed 2%. Fragments larger than 200 ha in size and with a higher degree of conservation are found in the north of the department of Tolima, with cover 7% greater of the original area[7,16,17]. The results of research on the structure and diversity of tropical dry forests are scarce, and it is even more critical for the values of their dynamics. Only today, people begin to understand the functions of this kind of forest, making it one of the most degraded ecosystems, with a high level of vulnerability and with gaps in knowledge that would allow true conservation, restoration and sustainable use of its ecosystem services[18,19].

Therefore, the present study was conducted in the tropical dry forest areas located in the north of the department of Tolima, which are part of the ecoregion of Alto Magdalena. The objective was to determine the relationship between the light habitat generated by the forest canopy (supply of photosynthetically active radiation in the growth environment) and the structure, floristic diversity and cover dynamics in terms of growth, mortality and reforestation, four secondary forests with different successional stages located on the eastern flank of the foothills of the Central Cordillera are part of the tropical dry forest complex of the geographic valley of the Magdalena river.

2. Materials and methods

2.1 Study area

This research was carried out on four natural fragments of tropical dry forest (bs-T) with different successional stages located in the upper part of the geographic valley of the Magdalena River, lands belonging to the Centro Universitario Regional del Norte (Curn) of the University of Tolima in the municipality of Armero-Guayabal in the north of the department of Tolima. The selected forests are part of the slope of the Magdalena River and are located in the foothills of the eastern flank of the Central Cordillera and the Alluvial plain. The flat coordinates of the area are: 4°59'53.48" N and 74°55'38.87".

Regarding climatic characteristics, the study area has an average annual temperature of 27 °C, an average rainfall of 1,750 mm, and a relative humidity of 71%. The altitude above sea level ranges from 475 to 580 m. The climatic assessment shows a bimodal behavior, with a first rainy period between the months of March to May and a second stronger period between September and November[20].

2.2 Sampling

The assessed forest coverage corresponds to forests in four different succession states. The first is an early secondary forest (BST) that is 10 years old, originated from anthropogenic fires and dominated by the Curatella-Xilopia association. The second forest type corresponds to a 20-year-old secondary forest in recovery (BSR), generated by the abandonment of extensive cattle ranching activities and dominated by Cordia alliodora (Ruiz & Pav.) Oken. The third corresponds to a succession in a state of advanced recovery of more than 40 years, which for the purposes of this study will be called mature secondary forest (BSM), with a heterogeneous floristic composition. The fourth forest type corresponds to a mature riparian forest (BRM) dominated by Anacardium and Ceiba whose recovery time exceeds 60 years. In each of the forests, four permanent monitoring units of 0.25 ha (50 × 50 m) were established, with subplots of 10 x 10 m, for a total sampling area per cover type of 1 ha. This sectioning of the sampling unit was due to the size and shape limitations of the remaining fragments.

For all sampling units, all individuals with a normal diameter greater than or equal to 5 cm were recorded, marked, measured and collected. Measurements of normal diameter were made with a diametric tape to the nearest millimeter[21]. The collection of plant materials was carried out in cooperation with the herbarium of Medellin botanical garden and the dendrology Laboratory of the University of Tolima. The first inventory was conducted in June 2009 with subsequent annual monitoring until September 2014, for a time interval of 63 months (5.25 years). New individuals that exceeded 5 cm normal diameter were recorded as incoming or recruited and dead trees were recorded as mortality status[22].

2.3 Structure and diversity

For the assessment of floristic diversity and conventional structural parameters, the Stimate-S 9.1.0 program was used[23]. Measures of species abundance at the intra-community level (species richness, relative heterogeneity and rarity) were selected and measures of similarity and dissimilarity at the inter-community level were used[24–26].

2.4 Forest dynamics

The evaluation of the dynamics for the four forest types included the calculation of mortality, recruitment and diameter growth for the evaluation period of 5.25 years. The mortality rate was determined from the model proposed by Castro *et al.*[27] and recruitment according to the models presented in Melo and Vargas[21]. The mortality pattern contemplated the types of death: broken trunk (TP), fallen root (CR), missing individuals (DE) and cut (COR)[28]. It's the application of traditional deterministic growth model[29].

2.5 Light habitat

To evaluate the light habitat, which indicates the amount of energy used by the forest canopy to carry out the functional processes of assimilation and productivity, direct measurement of the leaf area index (LAI) was used with a LI-2200TC canopy analyzer. The different levels of light absorbed by the canopy of the forests under evaluation were expressed as relative values of photosynthetically active radiation (PAR), which was measured as the unabsorbed radiation on the forest floor surface expressed as the photon flux density of photosynthetic photons ($\mu mol \cdot m^{-2} \cdot s^{-1}$) between 400 and 700 nm of the light spectrum. For this purpose, the LI-191SA-Line Quantum Sensor and LI-190SA-Quantum Sensor and an LI 1400 data collector (LI-COR Inc., Lincoln, NE. USA) are used. Likewise, the light extinction coefficient (K) was derived by applying Beer & Lambert's law[3,30]. This process was performed below the canopy above the soil surface in the center of each 10 × 10 m subplot, and four cardinal readings were recorded. Measurements were taken between 10 am and 2 pm.

3. Results

Table 1 shows the results for the response variables by evaluation levels (structure, floristic diversity, dynamics and light habitat), for the four types of secondary forest in the upper Magdalena (BST: early secondary forest, BSR: recovering secondary forest, BSM: mature secondary forest, BRM: mature riparian forest).

3.1 Structure

Regarding forest structure, the number of trees (NA) in absolute values and basal area (G) in $m^2 \cdot ha^{-1}$ and maximum stem diameter (dmax.) in cm are shown. In general, the diametric structure of the forests showed inverted J or L trends, which is typical of dynamic canopies. The stage of development of each forest is manifested in the decrease of the diametric range, so that in the early successional coverages the range is short (27.5 cm) in comparison with the coverages of more advanced ages that exceed 60 cm. For the BRM type, there is a bimodal trend that corresponds to the presence of two populations of trees, the first with diametric ranges up to 35 cm and a second population whose diametric range varies between 45 and 110 cm. The accumu-

Table 1. Behavioral structure, diversity, dynamics and light habitat in four types of tropical dry forest in the upper Magdalena

Evaluation level	Variables	Forests			
		BST	BSR	BSM	BRM
Structure	NA	1774	928	388	672
	S	18	27	36	48
	G	21.9	18.7	17.7	34.2
	Dmax.	27.5	55	65	110
	DMg	2.27	3.81	5.87	7.22
	DMn	0.43	0.89	1.83	1.85
	H’	1.38	2.34	2.76	2.98
	E	0.61	0.69	0.83	0.81
	L/D	4.78	5.30	11.24	10.98
Diversity	L/d	2.73	2.97	5.11	8.84
	CH_1	22.25	21.37	36.28	42.79
	Ab_1	3	5	11	14
	Ab_2	2	4	7	5
	U	2	3	5	5
	Uab.	0	1	4	4
	Alpha	4.45	9.21	17.67	18.21
	TMC	2.37	1.37	0.63	0.45
Dynamics	M%	5.78	3.45	2.31	1.87
	R%	3.8	3.2	2.1	1.2
	LAI	8.3	5.1	4.5	3.1
Light habitat	K	0.75	0.63	0.53	0.49
	RFA	16.3	18.2	22.2	25.7

BST: early secondary forest. BSR: recovering secondary forest. BSM: mature secondary forest. BRM: mature riparian forest. NA: number of trees. G: basal area in $m^2 \cdot ha^{-1}$. Dmax: maximum stem diameter in cm. S: number of species. DMg: Margalef species richness. DMn: Menhinick species density. H’: Shannon diversity. E: Shannon’s evenness. L/D: Simpson’s heterogeneity. L/d: Berger Parker dominance. CH_1: species rarity. Ab_1: species with one individual. Ab_2: species with two individuals. U: species represented in a single plot. UAb: unique species in a plot. Alpha: species diversity. LAI: leaf area index. K: light extinction coefficient. PAR: photosynthetically active radiation. TMC: mean growth rate. M%: annual mortality rate. R%: annual recruitment rate.

lation of basal area reaches the highest value in BRM. However, the effect of population size (1,774) on G (21.99) for BST is clear. The trend of basal area accumulation (G) for secondary forests is typical of a chrono-sequence. Therefore, with the progress of forest succession, the population size decreases and the individual reaches a larger size (**Figure 1a**). The BRM manifests a smoother distribution indicating uniformity of populations in the size range. In the accumulation of basal area (**Figure 1b**), the trends are differential and contrary as the succession progresses, so that in the BST the greatest accumulation occurs between the diameter categories of 12.5 and 17.5 cm, while in advanced successions (BSM) the greatest accumulation of basal area is represented in the diameter categories greater than 65 cm, showing opposite patterns.

3.2 Diversity

Regarding floristic diversity, values for Margalef’s species richness index (DMg), Menhinick’s species density (DMn), Shannon’s diversity (H’), Shannon’s evenness (E), Simpson’s reciprocal heterogeneity (1/D) were determined for the four forest types, Berger Parker reciprocal dominance (1/d), species rarity (CH_1), species with only one individual (Ab_1), species with two individuals (Ab_2), species represented in only one plot (U), species only in one plot and only one individual (UAb) and the log series parameter indicating species diversity (Alpha). The BRM and BSM have the highest species richness (S, DMg) and similar densities (DMn). An increase in diversity (H’, E, 1/D, 1/d) with suc-

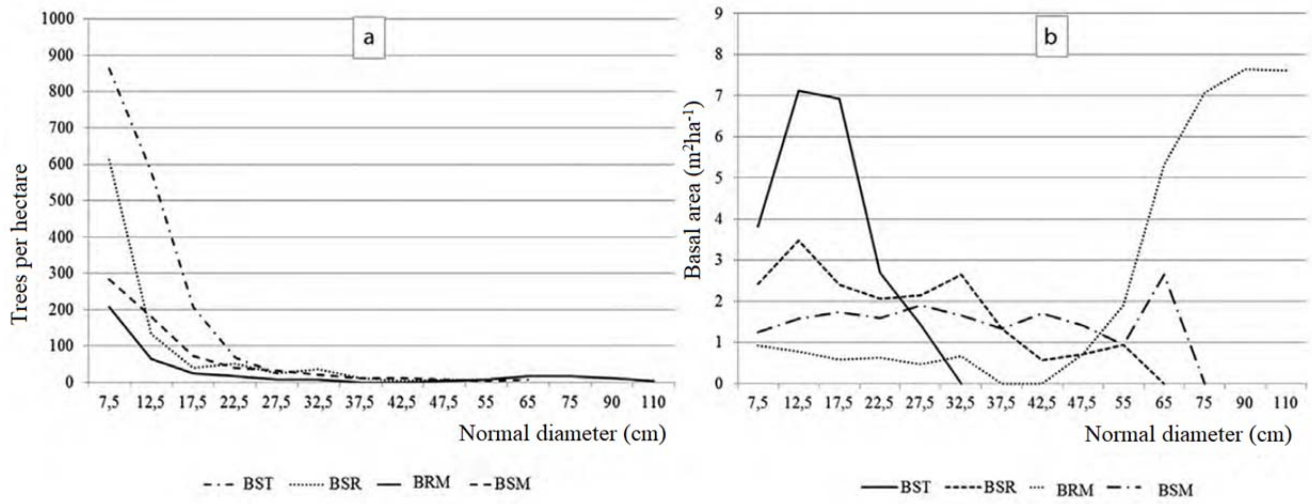

Figure 1. Trends in population distribution (NA) and basal area $m^2 \cdot ha^{-1}$ (G) classified by size, for four secondary forest types in the upper Magdalena. BST: early secondary forest. BSR: recovering secondary forest. BRM: mature riparian forest. BSM: mature secondary forest.

cessional development is evident. In terms of species rarity (CH_1), the BSM and BRM present the highest values. However, despite the homogeneity (E) of the early successional covers (BST and BSR), they contain rare species (Ab_1 and Ab_2), which increases their importance for diversity. According to the results of the alpha index of the logarithmic series, which is considered the most biologically representative measure of diversity, the BSM and BRM have equivalent values (17.67 and 18.21) despite their structural difference. Intercommunity complementarity (**Table 2**) for the evaluated forests, is a measure of biodiversity expressed from Sorensen's similarity index (SR), Jaccard's similarity (JC), percentage of dissimilarity (PD), percentage of remoteness (PR) and euclidean distance (DE). High similarity values (SR, JC) were observed between BST and BSR, BSR and BSM, showing a gradient of species accumulation with successional advancement. There are large differences between the diversity (PD, PR and DE) of BRM and the other secondary forests both in shared species and in the distribution of their abundances.

3.3 Forest dynamics

In the evaluation level corresponding to the dynamic processes of the forest (**Table 1**), the values of the mean growth rate (TMC), annual mortality rate (M%) and annual recruitment rate (R%) were determined. The results show an inverse relationship of TMC with successional advancement, such that the maximum values (2.37 $cm \cdot year^{-1}$) are achieved at BST. Likewise, the same trend is observed for both M% and R%. The highest mortality and recruitment rates (5.78 and 3.8) are found in BST as a result of high competition for resources in contrast to BRM (1.87 and 1.2), which shows a more stable habitat.

3.4 Light habitat

The high leaf area index (LAI, 8.3 m^2 leaf area/m^2 ground area) of the BST canopy allows the optimization of energy, which generates high values in growth rates and increases competition, mortality and recruitment by freeing growth spaces. On the contrary, in the BRM, which has only reached an LAI of 3.1 (m^2 leaf area/m^2 ground area), the functional behavior is inverse, the mature trees generate a canopy with low leaf area, there is less use of radiation and the growth rate, mortality and recruitment have lower values compared to the early successions. The highest LAI in BST (8.3) and BSR (5.1) leads to the lowest intensities in PAR (16 to 18 µmoles photons. $m^2 \cdot s^{-1}$) as a consequence of self-shading, which obeys the planophilic architecture that is defined as the arrangement of leaves and branches inserted in angles fluctuating between 0° and 30° of those two communities, expressed by K = 0.75 and 0.63 respectively. For forests that are in a more advanced successional stage (BRM and BSM), which present LAI of 3.1 and 4.5, additional to the K = 0.49 and 0.53, plagiophilous architecture (arrangements of leaves and branches inserted at angles fluctuating between 30° and 60°), self-shading is lower, leading to higher PAR intensities of 22 to 25 µmoles photons. $m^2 \cdot s^{-1}$ (**Table 1**).

Table 3 characterizes the light habitat and links it to forest structure, diversity and dynamics based on a correlation matrix, for the parameters leaf area index (LAI), light extinction coefficient (K), photosynthetically active radiation (PAR), log series diversity index (Alpha), basal area in m^2 ha^{-1} (G), Margalef species richness (DMg), mean growth rate (MT), annual mortality rate (M) and and annual recruitment rate (R). High correlation values were observed between LAI, which expresses the magnitude of canopy cover and the role in radiation capture and absorption, versus floristic diversity, mean growth rates, mortality and recruitment. Negative values in the correlation with diversity indicate that in forests with canopies that have large leaf area (LAI) to capture the low availability of PAR. Species richness is low. More illuminated understories allow the establishment of more species per unit area and

Table 2. Intercommunity diversity values for four secondary forest types in the Alto Magdalena

Comparison	SR	JC	PD	PR	DE
BST-BSR	0.42	0.48	37.26	48.43	22.67
BST-BRM	0.18	0.25	59.37	75.33	36.77
BST-BSM	0.33	0.37	45.93	52.57	23.92
BSR-BRM	0.21	0.29	51.47	63.71	30.73
BSR-BSM	0.53	0.59	29.82	37.39	19.32
BRM-BSM	0.23	0.27	53.31	75.05	31.32

BST: early secondary forest. BSR: secondary forest in recovery. BRM: mature riparian forest. BSM: mature secondary forest. SR: Sorensen similarity. JC: Jaccard similarity. PD: dissimilarity percentage. PR: percentage of remoteness. DE: Euclidean distance.

Table 3. Correlation matrix between light habitat, structure, diversity and dynamics of tropical dry forests

	LAI	**K**	**RFA**	**Alpha**	**G**	**DMg**	**TC**	**M%**	**R%**
LAI		0.9714	-0.9002	-0.8918	-0.4534	-0.8085	0.9696	0.9838	0.9121
		100	100	100	100	100	100	100	100
		0.0286	0.0998	0.1082	0.5466	0.1915	0.0304	0.0162	0.0879
K	0.9714		-0.9568	-0.9702	-0.4562	-0.9041	0.9955	0.9885	0.9664
	100		100	100	100	100	100	100	100
	0.0286		0.0432	0.0298	0.5438	0.0959	0.0045	0.0115	0.0336
RFA	-0.9002	-0.9568		0.9242	0.6651	0.8197	-0.9262	-0.9034	-0.9994
	100	100		100	100	100	100	100	100
	0.0998	0.0432		0.0758	0.3349	0.1803	0.0738	0.0966	0.0006
Alpha	-0.8918	-0.9702	0.9242		0.3307	0.9756	-0.9744	-0.951	-0.9349
	100	100	100		100	100	100	100	100
	0.1082	0.0298	0.0758		0.6693	0.0244	0.0256	0.049	0.0651
G	-0.4534	-0.4562	0.6651	0.3307		0.1242	-0.3706	-0.3536	-0.6413
	100	100	100	100		100	100	100	100
	0.5466	0.5438	0.3349	0.6693		0.8758	0.6294	0.6464	0.3587
DMg	-0.8085	-0.9041	0.8197	0.9756	0.1242		-0.9261	-0.8999	-0.8353
	100	100	100	100	100		100	100	100
	0.1915	0.0959	0.1803	0.0244	0.8758		0.0739	0.1001	0.1647
TC	0.9696	0.9955	-0.9262	-0.9744	-0.3706	-0.9261		0.9959	0.939
	100	100	100	100	100	100		100	100
	0.0304	0.0045	0.0738	0.0256	0.6294	0.0739		0.0041	0.061
M%	0.9838	0.9885	-0.9034	-0.951	-0.3536	-0.8999	0.9959		0.9177
	100	100	100	100	100	100	100		100
	0.0162	0.0115	0.0966	0.049	0.6464	0.1001	0.0041		0.0823
R%	0.9121	0.9664	-0.9994	-0.9349	-0.6413	-0.8353	0.939	0.9177	
	100	100	100	100	100	100	100	100	
	0.0879	0.0336	0.0006	0.0651	0.3587	0.1647	0.061	0.0823	

LAI: Leaf area index. K: light extinction coefficient. PAR: photosynthetically active radiation. Alpha: log series diversity index. G: basal area in $m^2 \cdot ha^{-1}$. DMg: Margalef species richness. TC: mean growth rate. M%: annual mortality rate. R%: annual recruitment rate.

there is more heterogeneity of growth niches. Likewise, a negative correlation was detected between the LAI and the survival of the tree community. Basal area has a low correlation with light habitat, mainly due to the influence of the large trees of the BRM that share the same habitat as smaller trees of the secondary forests. Mortality correlates positively with LAI and K, otherwise with RFA. Recruitment has a similar trend.

4. Discussion

The evaluated forests in general show a chrono-sequence that allows the increase of the values of diversity and structural complexity offered by the succession of the natural cover of the tropical dry forest of the Upper Magdalena as expressed by Mendoza[31] in preliminary studies in fragments of tropical dry forest of the Caribbean coast and Magdalena valley. The values of structural parameters and species richness, heterogeneity and species rarity (**Table 1**) for BST, BSR and BSM are relatively higher than those found by Fernandez *et al.*[20] for the south of the department of Tolima, an area with a drier climate (1,350 mm of mean annual precipitation). This is in agreement with Gentry[9,32], who states that species richness is associated with the availability of moisture in the environment. Regarding the BRM, the species richness is the highest reported for this type of cover in tropical dry forest areas, since studies by Linares & Fandiño[15], Cabrera & Galindo[33] and Etter[16] recorded a lower density of species in similar study areas in the Cauca Valley and the Atlantic coast.

In terms of intercommunity diversity (**Table 2**), the successional complex of secondary forests shows gradual changes in floristic composition, which is associated with successional development after the interruption of anthropic activity. This increase in species in correlation with the recovery of ecosystem services and forest functionality has been studied by Kalascka *et al.*[10] in Mesoamerican dry forests.

There are great differences found in growth (TC), mortality (M) and recruitment (R) rates for the four tropical dry forest types shown in **Table 1** compared to similar studies conducted in tropical dry forests in Nicaragua[34], which may be associated with both orography and moisture availability, which for the eastern flank of the central mountain range are related to the mountain range shade effect that increases the relative humidity value, generating a better growth environment.

The growth of the individual tree and of the forest as a whole depends to a large extent on its functionality, that is, on how it obtains the resources offered by the environment and how it uses them. The main factors are the light and water in the soil[35], which is expressed in the distribution and quality of the canopy. The canopy directly influences the accumulation of biomass, whose differential distribution in its structural components varies according to the competition relationships generated by neighboring trees located in its living space[36]. Regarding the values of the variables describing light habitat and their correlation with forest dynamics (**Table 3**), for the four evaluated canopies (BST, BSR, BSM, BRM), the direct effects of IAF, K, and RFA on growth, mortality, and reforestation are clear. Thus, the highest mortality and recruitment rates are generated under canopies with high LAI and maximum K values. That is, there is dependence on self-shading due to the maximum leaf area of the crown and the structure described by the crown affect the capture of radiation and the consequent productivity of the forest community, which directly affects both the structure of plant communities and their floristic diversity[37], similar relationships between functionality and cover types have been found by Sterck *et al.*[38], Craine and Dybzinski[39], which supports the present results for the tropical dry forests of the Upper Magdalena.

5. Conclusions

There is a direct relationship between the availability of light resources and the dynamics of the tropical dry forest. The highest growth rates of BST are associated with habitats with high availability of PAR, which is absorbed by a canopy with high LAI, resulting in high growth that generates an increase in mortality rates. The freed spaces are occupied by new individuals waiting for the opportunity to grow. For more advanced successions such as BSM, the canopy that characterizes the forest structure has a lower LAI, which allows greater availability of resources in the understory allowing a greater diversity of habitats that are occupied by various types of species, hence the greater heterogeneity and structural complexity. The consequence is lower growth and greater stability between mortality and recruitment, which owe their dynamics to factors endogenous to the biotic community.

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