

Tree diameter growth for three successional stages of Tropical Dry Forest in Minas Gerais, Brazil

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Abstract

The tropical dry forests of Brazil are classified as the most threatened and disturbed ecosystems in the country. We estimate the diameter growth in three successional stages in the Mata Seca State Park, in Minas Gerais, Brazil, through annual measurement of all individuals with more than 5 cm of diameter at breast height in 18 permanent plots (6 plots for each succession stage) in the early, intermediate, and late successional stages, over a period of 5 years (2006-2011). With this information the annual diameter increments for each individual were calculated to determine the diameter increments per stage, plot, and diameter class. The results show the following annual increments for each stage of succession: early (5.02 mm/year), intermediate (2.55 mm/year), and late (1.91 mm/year). We found high similarity in incremental growth between the plots in the

Resumen

Crecimiento diamétrico de árboles en tres estados de sucesión del bosque seco tropical en Minas Gerais, Brasil

Se describen los cambios en la estructura del bosque y la composición florística de tres estados de sucesión del Parque Estatal Mata Seca, en Minas Gerais, Brasil, a través de la medición de todos los árboles mayores de 5 cm de diámetro a la altura del pecho (DBH), en 18 parcelas permanentes en los estados de sucesión temprano, intermedio y tardío de un bosque seco tropical durante un período de 5 años. Utilizando esta información, calculamos el Índice de Importancia del Valor (IVI), el Índice de Complejidad de Holdridge, el Coeficiente de Los bosques secos tropicales de Brasil han se consideran como los ecosistemas más alterados y amenazados del país. Se estimó el crecimiento diamétrico

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intermediate and late stages. The greatest increments in the early stage was in the 15-20 cm diameter class, in the intermediate stage in the 30-35 cm class, and in the late stage in the 45-50 cm class. The dominant species with the highest increments were *Myracrodruon urundeuva* (9.33 mm/year) and *Mimosa hostilis* (10.35 mm/year). Species with lower increments were mostly those of the late stage. The high diameter increment in the early stage and the differences we observed between stages were associated with species composition and biophysical factors that regulate the growth and structure of each forest.

Key words: Permanent plots, successional stages, mean annual increment, tropical dry forest, Tropi-Dry, Brazil

Introduction

Growth of trees and successional development are slower in tropical dry forests (Ewel, 1980; Murphy and Lugo, 1986). Growth in tropical dry forests is limited to short periods of water availability (Quesada, Sánchez-Azofeifa, Alvarez-Añorve, Stoner, Avila-Cabadilla, Calvo-Alvarado, Castillo, Espírito-Santo, Do, Fagundes, Fernandes, Gamon, ... Sánchez Montoya, (2009) and, therefore, the annual diameter increment in dry forests is almost half the increment of rain forests (Murphy and Lugo, 1986). In addition, the availability of leaves for photosynthesis in dry forests depends on soil moisture, water storage in the stem, light, vapour pressure deficit, and photoperiod (Giraldo and Holbrook, 2011).

Although dry forests may be more dynamic than many rain forests in terms of production and loss of biomass (Monge, Quesada & Gonzalez (2002), these forest ecosystems are still considered, in general terms, less dynamic and productive than tropical rain forests (Phillips, Nuñez & Timana (1998); Uslar, Mostacedo & de árboles en tres estados de sucesión en el Parque Estatal Mata Seca, en Minas Gerais, Brasil, mediante la medición anual de todos los individuos con más de 5 cm de diámetro a la altura del pecho en 18 parcelas permanentes (6 parcelas por estado de sucesión), en las estados de sucesión temprano, intermedio y tardío, durante 5 años (2006-2011). Con esta información se calcularon los incrementos de diámetro anual para cada individuo para así estimar los incrementos de diámetro por etapa, parcela y clase diamétrica. Los resultados muestran los siguientes incrementos anuales para cada estado de sucesión: temprano (5.02 mm/año), intermedio (2,55 mm/año) y tardío (1,91 mm/año). Se encontró alta similitud en el crecimiento incremental entre las parcelas en los estados intermedio y tardío. Los incrementos más grandes en el estado temprano fueron en la clase de 15-20 cm de diámetro, en el estado intermedio en la clase de 30-35 cm y en el estado tardío en la clase de 45-50 cm. Las especies dominantes con mayores incrementos fueron Myracrodruon urundeuva (9,33 mm/año) y Mimosa hostilis (10,35 mm/año). Las especies con incrementos más bajos fueron principalmente aquellas del estado tardío. El alto incremento de diámetro del diámetro en el estado temprano y las diferencias observadas entre los estados de sucesión se asociaron con la composición de las especies y los factores biofísicos que regulan el crecimiento y la estructura del bosque.

Palabras clave: Parcelas permanentes, estados de sucesión, incremento medio anual, bosque seco tropical, Tropi-Dry, Brasil

Saldias (2004). For this reason, tropical dry forests are more susceptible to human disturbance, because their growth and regeneration rates are lower, reproduction is seasonal, and most plants are dependent on animal pollination (Bawa, 1974; Frankie, Baker & Opler, 1974; Murphy and Lugo, 1986; Hamrick and Murawski, 1990; Bullock, Mooney & Medina, 1995; Jaimes and Ramirez, 1999; Cascante, Quesada, Lobo, Fuchs, 2002; Fuchs, Lobo & Quesada, 2003; Quesada et al., 2009). However, although dry forests grow more slowly than rain forests, dry forests can regain their structure after disturbance faster than wet forests, which have a more complex structure (Ewel, 1980; Murphy and Lugo, 1986). Water is the most limiting resource in dry forests, because of the length of the dry season (Whigham, Zugasty, Towle, Cabrera-Cano, O'Neill & Ley, 1990; Clark and Clark, 1992; Enquist and Leffler, 2001). Therefore, these ecosystems are more susceptible to threats due to climate change, given that this global threat will probably alter the amount and distribution of rainfall in these regions (Jaramillo, Martínez-Yrízar & Sanford, 2011), which could alter the growth and development of these forests.





Revista Forestal Mesoamericana Kurú | Vol.14 Núm.35 (2017) pág.24-32 ISSN: 2215-2504 | DOI: 10.18845/rfmk.v14i35.3150 | <u>revistas.tec.ac.cr/kuru</u> The great interest in the productivity of dry forests in secondary successional stages is important, because these stages cover a greater area than old-growth forests in all regions with tropical dry forests (Sánchez-Azofeifa, Kalácska, Quesada, Calvo-Alvarado, Nassar, Rodriguez, 2005). Relevant information on growth and development allows us to analyze the paths taken and the time required for recovery of this forest type, and the degree to which they can recover (Jaramillo et al., 2011). However, little research has been conducted on these topics in tropical dry forests in Brazil (Vieira and Scariot, 2006).

Major socio-economic pressure experienced by tropical dry forest has made them one of the most deforested and least protected ecosystems in America (Janzen, 1988; Sánchez-Azofeifa et al., 2005; Neves, Braga, Espírito-Santo, Delabie, Fernandes & Sánchez-Azofeifa, 2010; Sánchez-Azofeifa & Portillo-Quintero, 2011; Calvo-Alvarado, Sánchez-Azofeifa & Portillo-Quintero, 2013). Due to high rates of deforestation and its restricted and fragmented distribution, tropical dry forest can be considered the most threatened ecosystem in Brazil (Espírito-Santo, Cássio, Anaya, Barbosa, Fernandes, Sánchez-Azofeifa, Scariot, Eustáquio de Noronha & Andrade, 2009). Only 5,015 km² of dry forest in Brazil are under protective categories, representing only 6.2 % of the dry forest of that country (Portillo-Quintero and Sánchez-Azofeifa, 2010). Mata Seca State Park (MSSP) in the north of Minas Gerais is one of these protected areas.

The loss of these forests is a serious threat to biodiversity and ecosystem services, including the protection of water resources of the Sao Francisco basin, which is the second largest in Brazil and the main source of water for the state of Minas Gerais. In response to this situation, the "Tropy-Dry" project, funded by the Inter-American Institute for Global Change Research (IAI) and the U.S. National Science Foundation (NSF), has carried out a series of important studies in this park, with the purpose of generating information to promote conservation and proper management of dry forests in that region.

This study aims to identify and analyze growth rates in three successional stages of tropical dry forest in MSSP, Minas Gerais, Brazil. Our results will contribute to the understanding of the growth dynamics during natural succession and encourage others to model growth rates for applications to silvicultural management, approaches to conservation of biodiversity, and rates of carbon sequestration.

Materials and Methods

Study site

The study was conducted in MSSP (Fig 1), a unit of integrated conservation and protection created by expropriating farm land in 2000, and managed by the Forestry State Institute (IEF- Instituto Estadual de Florestas). MSSP, has an area of 15,466 hectares at an elevation of 452 m.a.s.l and is situated in the São Francisco river valley, in the Minas Gerais state in Brazil. The exact location is between coordinates 14°48'36" - 14°56'59" S and 43°55'12" - 44°04'12" W.

The climate of the region is considered tropical semiarid (Köppen classification) or tropical dry forest (Holdridge classification). The forest is dominated by deciduous trees, and 90-95% of the leaf area is lost during the dry season that extends for six months between May and October (Madeira, Espírito-Santo, Sanz D'Angelo, Nunes, Sánchez-Azofeifa, Fernandes & Quesada, 2009). The average temperature of the study area is 24.4 °C, with a maximum of 32 °C, and a mean annual precipitation of 871 mm (300-1300 mm range), which is concentrated in the rainy season from October to April.

Experimental design

A total of 18 permanent sampling plots was established in MSSP, (6 plots/stage) for three successional stages: early, intermediate, and late. The plots were established following the protocol of the Tropi-Dry Project (Alvarez, Avila-Cabadilla, Berbara, Calvo-Alvarado, Cuevas-Reyes, Espírito-Santo, Fernández, Wilson Fernandes, Herrera, Kalácska, Lawrence, Monge Romero, Nassar, Quesada, Quesada, Rivard, Sanz D'Angelo, Stoner, 2008) and are monitored by the Faculty of Biology of Unimontes University and the University of Alberta, Canada. Each plot has an area of 1,000 m² (50 m x 20 m).



Figure 1. Geographic location of MSSP in the North of Minas Gerais, Brazil

Figura 1. Ubicación geográfica del Parque Nacional Mata Seca en el Norte de Minas Gerais, Brasil.

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In each plot, all individual trees with a diameter greater than 5 cm at breast height (DBH=1.3 m) were measured annually. Each tree circumference was recorded in cm using metric tapes and tree heights were estimated in meters. Furthermore, the genus and species of each individual were identified with the help of a taxonomist based on samples collected in the field.

Data analysis

With data from each successional stage, we proceeded to calculate the diameter in mm for each individual. Then the mean annual increment in mm/year (MAI) was calculated only for those individuals present for the measurements in 2006 and 2011. We estimated MAI for each individual with equation 1 (Marín, Nygard, Rivas, Oden, 2005).

$$MAI = \frac{DBH11(mm) - DBH06(mm)}{T}$$
(1)

Data with inconsistencies were eliminated from the analysis. To perform the statistical comparison among successional stages, the increments by diameter class and species were calculated using the median instead of the arithmetic average, as the diameter increments do not follow a normal distribution and the use of this statistic (median) decreases the bias caused by outliers (Ortiz and Carrera, 2002). When comparing medians it is necessary to use a nonparametric test, so we used the Kruskal-Wallis test (1952) with α =0.05 to determine significant differences between increments, using the Statistica 6.1 program (StatSoft, 2004).

Results

Diameter increments per successional stage

In the analysis of the mean annual increment (MAI) using the medians per successional stage (Table 1), the largest

Table 1. Annual increments (median in mm*year-1) and standard deviations with their range and number of individuals in three successional stages in MSSP, Minas Gerais, Brazil.

Cuadro 1. Incrementos medios anuales (mediana en mm * año-1) y desviaciones estándar con su rango y número de individuos en tres estados de sucesión en el Parque Estatal Mata Seca, Minas Gerais, Brasil.

Successional Stage	MAI (mm*year¹)	Range (mm*year¹)	n individuals
Early	5.02 ± 6.41	0-19.68	173
Intermediate	2.55 ± 2.69	0-14.26	370
Late	1.91 ± 2.62	0-11.77	514

increments were in the early successional stage (5.02 \pm 6.41 mm/year), and this differed statistically (p<0.00) from the intermediate and late successional stages. Among the intermediate (2.55 \pm 2.69 mm/year) and late stages (1.91 \pm 2.62 mm/year), we found no significant differences (p>0.05).

Increments by diameter class

In the early successional stage, the highest diameter increments were concentrated in the 15-20 cm diameter class (Figure 2). The intermediate stage showed a maximum increment between 30-35 cm in diameter, although all categories showed increments between 2-5 mm/year, with no major differences between classes. The late stage had the largest increments between 45-50 cm with a maximum of 6.6 mm/year. The lowest MAI values for the late stage were between 50 to 65 cm, which was the highest diameter class for the late stage.

Figure 3 shows the diameter increments for the three most dominant and abundant species in the early stage of succession. *Handroanthus ochraceus* (Bignoniaceae) was only found among the diameter classes of 5 to 15 cm and did not exceed an increment of 7 mm/year, while *Mimosa hostilis* (Fabaceae Mimosoideae) and *Myracrodruon urundeuva* (Anacardiaceae) were found in all diameter classes in the early stage from 5 cm to 20 cm and reached diameter increments up to 13 mm/yr and 15 mm/year, respectively (Figure 3). They were also two of the fastest growing species in the early stage.

Figure 4 shows the diameter increments for the 3 most dominant and abundant species in the intermediate successional stage. *Combretum duarteanum* (Combretaceae) was found only in the diameter classes of 5-20 cm and reappeared in the 25-30 cm class. where



Figure 2. Mean annual increment MAI (in mm per year) by diameter classes for three successional stages in MSSP, Minas Gerais, Brazil.

Figura 2. Incremento medio anual IMA (en mm por año) por clases de diámetro para tres estados de sucesión en el Parque Nacional Mata Seca, Minas Gerais, Brasil.





Figure 3. Mean annual increment MAI (in mm per year) by diameter classes for three species with greatest abundance in the early successional stage in MSSP, Minas Gerais, Brazil.

Figura 3. Incremento medio anual IMA (en mm por año) por clases de diámetro para tres especies con la mayor abundancia en el estado temprano en el Parque Nacional Mata Seca, Minas Geraiss, Brasil.



Figure 4. Incremento medio anual IMA (en mm por año) por clases de diámetro para tres especies con la mayor abundancia en el estado intermedio en el Parque Nacional Mata Seca, Minas Gerais, Brazil.

Figura 4. Incremento medio anual IMA (en mm por año) por clases de diámetro para tres especies con la mayor abundancia en el estado tardío en el Parque Nacional Mata Seca, Minas Gerais, Brasil.

it had the greatest diameter increments. *Commiphora leptophloeus* (Burseraceae) was found in the intermediate stage from 15-30 cm in diameter and was also in the class of 35-40 cm. Its greatest increments did not exceed 5 mm/year. *Handroanthus reticulatus* (Bignoniaceae) was located in all diameter classes and had increments up to 7.5 mm/year in the 35 and 40 cm diameter class.



Figure 5. Mean annual increment MAI (in mm per year) by diameter classes for three species with greatest abundance in the late successional stage in the MSSP, Minas Gerais, Brazil.

Figura 5. Incremento medio anual IMA (en mm por año) por clases de diámetro para tres especies con la mayor abundancia en el estado tardío en el Parque Nacional Mata Seca, Minas Gerais, Brasil.

Figure 5 shows the diameter increments for the most dominant and abundant species in the late successional stage. *Combretum duarteanum* was found only in the diameter classes of 5 to 20 cm and had no higher diameter increments in the intermediate forest. Handroanthus chrysotrichus was in the diameter classes of 5 to 40 cm and had no major increments more than 3.5 mm/year. *Myracrodruon urundeuva* was found in the diameter classes of 10 to 55 cm and was it had the highest increments in the late stage.

Species with lower and higher increments

Most of the lowest MAI's (average) were found in the late successional stage, only three in the intermediate stage, and one in the early stage (Table 2).

Most of the species with higher MAIs (average) were from the early successional stage, only three were found in the intermediate stage, and two in the late stage (Table 3).

Discussion

For the three successional stages evaluated, diameter increments were highest in the early stage, while the smallest increments occurred in the late stage; there was no statistical difference between the increments in the intermediate and late stages. Diameter increments for the intermediate and late stages were within the range reported for neotropical dry forests at 1-2 mm/year (Murphy and Lugo, 1986). The similarity in the growth rates for the late and intermediate successional stages is probably because the sites considered as mature forests in some studies (including ours) are more similar in structure and diversity to intermediate successional

Table 2. Species with lowest MAI (mm*year1) for the three successional stages in MSSP, Minas Gerais, Brazil.

Cuadro 2. Especies con IMA más bajos (mm * año⁻¹) para los tres estados de sucesión en Parque Nacional Mata Seca, Minas Gerais, Brasil.

Successional Stage	Species	n individuals	MAI (mm*year-1)	Std dev
Late	Goniorrhachis marginata	2	0.92	1.94
Late	Auxemma oncocalyx	6	1.86	1.79
Late	Eugenia florida	2	1.86	3.95
Late	Syagrus oleracea	5	1.86	1.91
Late	Eugenia uniflora	1	1.06	0.00
Late	Ptilochaeta glabra	1	1.06	0.00
Late	Luetzelburgia andradelimae	7	1.59	3.00
Late, intermediate	Aralia excelsa	4	1.76	3.29
Intermediate	Cyrtocarpa caatingae	3	0.97	3.29
Intermediate	Lonchocarpus campestris	2	1.33	3.29
Early	Aspidosperma pyrifolium	2	0.16	2.57

Table 3. Species with lowest MAI (mm*year1) for the three successional stages in MSSP, Minas Gerais, Brazil.

Cuadro 3. Especies con IMA más altos (mm * año⁻¹) para tres estados sucesionales en Parque Nacional Mata Seca, Minas Gerais, Brasil.

Successional Stage	Species	n individuals	MAI (mm*year1)	Std dev
Early	Senegalia polyphylla	5	8.35	3.38
Early	Mimosa hostilis	13	10.35	8.02
Early	Ruprechtia fagifolia	1	11.28	0.00
Early	Schinopsis brasiliensis	4	9.39	1.52
Early	Platymiscium blanchetii	6	7.44	4.24
Early	Piptadenia viridiflora	2	11.08	4.47
Intermediate	Cnidosculus pubescens	1	8.02	0.00
Early, intermediate	Enterolobium contortisiliquum	6	8.84	5.98
Late	Plathymenia reticulate	5	7.30	7.92
Late, intermediate, Early	Myracrodruon urundeuva	87	9.33	5.66

forests than to mature forests (Madeira et al., 2009). The recovery time for tropical dry forests in the lowlands can take up to 150 years, but the late successional and intermediate stages in MSSP are approximately only 60 years old and 40 years old, respectively.

The diameter increments for early stages of succession were surprisingly high compared to that reported for other tropical dry forests. However, Monge et al., (2002) reported an increment of 4.13 mm/year in an undisturbed remnant dry forest in Palo Verde, Costa Rica. Uslar et al., (2004) found increments from 1.1 mm/year - 7.1 mm/ year for some species for a semi-deciduous dry forest in Santa Cruz, Bolivia. In another study conducted by Tropi-Dry (Carvajal-Vanegas and Calvo-Alvarado, 2013) in the dry forest at Santa Rosa, Costa Rica, using the same protocols as this study, we obtained the following results for MAI's per successional stage: early, intermediate, and late stages of 1.60 mm/year, 2.20 mm/

year, 1.20 mm/year, respectively. These results are in contrast to the high increments found for Brazil in this study. This is counterintuitive given that Santa Rosa has a less prolonged dry season with more rainfall. The differences may be related to soil moisture during the dry season or to a different species composition, although Carvajal-Vanegas and Calvo-Alvarado (2013) reported maximum increments in certain species of 19 mm/year. These differences between MSSP and other tropical dry forests may also be due to specific site characteristics, soil depth and texture, water table, and conditions that can favour tree growth that reduces the effect of the dry season.

According to soil moisture data from the Tropi-dry project recorded by soil sensors during 2007-2012 obtained in the same plots as in this study, the average monthly soil moisture during the dry season was higher in the early stage than in the intermediate and late stage plots. This

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Revista Forestal Mesoamericana Kurú | Vol.14 Núm.35 (2017) pág.24-32 ISSN: 2215-2504 | DOI: 10.18845/rfmk.v14i35.3150 | <u>revistas.tec.ac.cr/kuru</u> could explain why the early stage had larger increments. Information obtained by interviewing the staff working in the park suggests that the plots in the early stage are located in a lower zone than the intermediate and late stages. It may be that these early stage plots were located in a topographic location where they could store more soil moisture and be more influenced by the water table than the higher zones of the park where the intermediate and late stages are located. Soil fertility could also be another factor that may influence differences in growth increments between stages (Chazdo, Letcher, van Breugel, Martinez-Ramos, Bongers & Finegan, 2007). Previous analyzes of soils taken by Unimontes University showed that the intermediate stage plots had a pH below 5.5, and base content not as high as the early and late plots, which indicates lower soil fertility and a higher percentage of Acidity Saturation (Calvo-Alvarado, 2008) in the intermediate stage. A high base content was observed in the early stage plots, which indicates good fertility and a low percentage of Acidity Saturation. The late stage plots showed the same soil fertility as the early stage, but had a greater amount of organic matter.

The high growth rate could also be favored by previous soil management. Vieira, Scariot & Holl (2007) found higher growth rates in a regenerating dry forest in Goiás, Brazil after burning, because there were higher levels of soil nutrients even 7.5 years after the fire compared to forests with less disturbance. In our study, early stage growth rates could have benefited from past fires that occurred before the creation of the park. The great capacity for resprouting in some species may be affected by the intensity of the practices used for pasture management in the past, such as fires, deforestation, and use of tractors or heavy equipment. In our study plots, the presence of abundant trees with multiple stems in early plots, and the presence of *M. urundeuva* in all three stages of succession in MSSP, suggest that regeneration by sprouts occurred widely and is related to previous land management (Madeira et al., 2009).

In the early successional stage, the highest diameter increments were in the 15 to 20 cm class, which represented the largest diameters in the early stage. This is because the number of individuals decreased in this class due to competition; therefore, the trees that survived to reach these diameters had a better root system, more light, and greater nutrient availability (Ghazoul and Sheil, 2010). Carvajal-Vanegas and Calvo-Alvarado (2013) also reported greater growth increments in the 15 to 20 cm class for early successional stages of succession in Santa Rosa, Costa Rica.

The intermediate successional stage showed a maximum increment between 30 to 35 cm in diameter and the late stage exhibited the largest increments in the 45 to 50 cm class with a maximum of 6.6 mm/year. Meza and Mora (2003) also found that the maximum MAI (2.6 mm/

year) was in the class of 45 to 50 cm for the dry forest of Guanacaste National Park in Costa Rica. Quirós (2002) explains that the increments in these classes in mature forest occur mainly because individuals manage to secure a place in the ecosystem (in any part of the strata) where they can capture fully the resources they need (mainly light), which results in an accelerated increment in their diameters. This explains why emergent trees generally have a greater increase in larger diameter classes (Ghazoul and Sheil, 2010); Carvajal-Vanegas and Calvo-Alvarado, 2013). Moreover, the lowest MAI values for the late stage are in the 50 to 65 cm class, given that trees with these dimensions are at a mature stage of flowering and fruiting where the allocation of nutrients is for reproduction and not growth (Fredericksen, Contreras & Pariona, 2001).

Species that have greater diameter increments are mostly found in the successional early stage dominated by *Myracrodruon urundeuva* (Anacardiaceae), *Handroanthus ochraceus* (Bignoniaceae), and *Mimosa hostilis* (Fabaceae Mimosoideae). High rates of growth in the early stage are influenced by the high number of individuals of these species. Carvajal-Vanegas and Calvo-Alvarado (2013) also found that species with high dominance and abundance in Santa Rosa, Costa Rica were the species with the greatest increments in the intermediate stage (*Swietenia macrophylla* and *Rehdera trinervis*).

Some specific characteristics of these species can also influence their dominance and high MAI's. Handroanthus ochraceus is a species with phenolic compounds in the leaves and, according to Silva, Espírito-Santo & Melo (2011), the percentage of herbivory is higher in the intermediate and late stages and lower in the early stage for MSSP. Myracrodruon urundeuva produces a chemical barrier formed by tannins, which are compounds known to have fungicidal and insecticidal effects. These substances are mainly formed in the boundary between sapwood and heartwood (Amorim, Lemos de Morais & Nascimento, 2002). Leaves of Mimosa hostilis have highly hallucinogenic alkaloids due to the activity of DMT (N, N-dimethyltryptamine). This species is widely used in indigenous rituals (Carneiro, 2004). Also, data of Faccion (2011), who analyzed this same species (H. ochraceus, M. urundeuva, M. hostilis) in MSSP, demonstrated that the concentration of phenolic compounds decreases when advancing through the successional stages and that the concentration of these compounds is negatively related to leaf damage. These factors may influence the dominance and the diameter increment rate of these species in the early stages. In addition, is possible that these species were less predated by livestock in the previous years in which cattle was still present on these sites (Belem and Carvalho, 2013). That is, their survival rates may be higher because of their chemical defences against herbivores or other agents, which allows them to



reach greater diameters.

In conclusion, our data are a contribution on tropical dry forest successions given the scarcity of information for these forests in Brazil. There is a lack of information on growth rates in secondary dry forests in the early and intermediate stages of succession, which makes it difficult to judge the magnitude of these growth rates. Hence, our results must be supplemented with data from other sites to better understand the variations in diameter growth rates of trees in these forest ecosystems.

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References

- Alvarez M, Avila-Cabadilla LD, Berbara R, Calvo-Alvarado JC, Cuevas-Reyes P, Espírito-Santo MMDo, Fernández Á, Wilson Fernandes G, Herrera R, Kalácska M, Lawrence D, Monge Romero F, Nassar JM, Quesada M, Quesada R, Rivard B, Sanz D'Angelo V, Stoner K (2008) Ecology procedures. In: Nassar JM, Rodríguez JP, Sánchez-Azofeifa A, Garvin T, Quesada M (eds) Manual of Methods: Human, Ecological and Biophysical Dimensions of Tropical Dry Forests. Ediciones IVIC, Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela. pp 15-46.
- Amorim K, Lemos de Morais S, Nascimento E (2002) Caracterização dos Taninos da Aroeira-Preta (Myracrodruon urundeuva). R. Árvore 26(4):485-492.
- Bawa KS (1974) Breeding system of tree species of a lowland tropical community. Evolution 28: 85–92.
- Belem RA, Carvalho VL (2013) Zoneamento ambiental em uma unidade de conservação do bioma caatinga: um estudo de caso no Parque Estadual Mata Seca, Manga, Norte de Minas Gerais. Rev. Geogr (UFPE). 30(3): 44-57.
- Bullock SH, Mooney HA, Medina E (1995) Seasonally Dry Tropical Forests. Cambridge: Cambridge University Press.
- Calvo-Alvarado J, Sánchez-Azofeifa A, Portillo-Quintero C (2013) Neotropical Seasonally Dry Forests. In: Levin SA. (ed.) Encyclopedia of Biodiversity, second edition Waltham, MA: Academic Press. pp 488-500.

- Calvo-Alvarado J (2008) Curso de suelos Forestales. Serie de apoyo académico. Escuela de Ingeniería Forestal. p 98.
- Carneiro HS (2004) As plantas sagradas na história da América. Varia Historia nº 32, São Paulo, pp 102-119.
- Carvajal-Vanegas D, Calvo-Alvarado J (2013) Chapter 19: Tree diameter growth of three successional stages of tropical dry forests, Santa Rosa National Park, Costa Rica. In: Sanchez-Azofeifa GA and Powers J (eds.) Tropical Dry Forests in the Americas: Ecology, Conservation and Management. CRC Press. Pp: 351-366.
- Cascante A, Quesada M, Lobo JA, Fuchs EJ (2002) Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree Samanea saman. Conserv. Biol. 16:137–47.
- Chazdon RL, Letcher SG, van Breugel M, Martinez-Ramos M, Bongers F, Finegan B (2007) Rates of change in tree communities of secondary neotropical forests following major disturbances. Philos. T. R. Soc. B 362(1478): 273-289.
- Clark DA, Clark DB (1992) Life-history diversity of canopy and emergent trees in a neotropical rain-forest. Ecol monogr 62: 315-344.
- Enquist BJ, Leffler J (2001) Long term tree ring chronologies from sympatric tropical dry-forest trees: Individualistic responses to climatic variation. J. Trop. Ecol 17: 41–60.
- Espírito-Santo MMDo, Cássio A, Anaya F, Barbosa R, Fernandes W, Sánchez-Azofeifa A, Scariot A, Eustáquio de Noronha S, Andrade C (2009) Sustainability of tropical dry forests: Two case studies in southeastern and central Brazil. For Ecol Manag. 258: 922–930.
- Ewel J (1980) Tropical succession: Manifold routes to maturity. Biotropica 12: 2–7.
- Faccion G (2011) Caracteristicas foliares e grupos funcionais de árvores ao longo de um gradiente sucessional em uma floresta tropical seca (dissertation) UNIMONTES (MG): Universidade Estadual de Montes Claros.
- Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in lowlands of Costa Rica. J. Ecol 62: 881–919.
- Fredericksen T, Contreras F, Pariona W (2001) Guía de Silvicultura para Bosques Tropicales de Bolivia. Proyecto de Manejo Forestal Sostenible (BOLFOR). Santa Cruz, Bolivia. p 77.
- Fuchs EJ, Lobo JA, Quesada M (2003) Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns on the tropical dry forest tree, Pachira quinata (Bombacaceae). Conserv. Biol. 17: 149–57.
- Ghazoul J, Sheil D (2010) Tropical rain forest ecology, diversity, and conservation. Oxford University Press. UK. p 515.
- Giraldo JP, Holbrook M (2011) Physiological Mechanisms Underlying the Seasonality of Leaf Senescence and Renewal in Seasonally Dry Tropical Forest Trees. In: Dirzo R, Young H, Mooney H, Ceballos G (eds.) Seasonally Dry Tropical Forests: Ecology and Conservation 129-140. Island Press. London. UK. 408 p.
- Hamrick JL, Murawski DA (1990) The breeding structure of tropical tree populations. Plant Spec Biol. 5: 157–165.

- Jaimes I, Ramirez N (1999) Breeding systems in a secondary deciduous forest in Venezuela: the importance of life form, habitat, and pollination specificity. Plant Systemat. Evol. 215: 23–36.
- Janzen DH (1988) Tropical dry forests: The most endangered major tropical ecosystem, In: Wilson EO (ed.) Biodiversity, National Academy Press, Washington DC, pp 130-137.
- Jaramillo V, Martínez-Yrízar A, Sanford R (2011) Primary Productivity and Biogeochemistry of Seasonally Dry Tropical Forests. In: Dirzo R, Young H, Mooney H, Ceballos G (eds.) Seasonally Dry Tropical Forests: Ecology and Conservation. Island Press. London p 408.
- Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variable analysis. J. Am Stat Assoc. 47(260): 583-621.
- Madeira B, Espírito-Santo MMDo, Sanz D'Angelo V, Nunes YRF, Sánchez-Azofeifa A, Fernandes W, Quesada M (2009) Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. Plant Ecol. 201:291–304.
- Marín GC, Nygard R, Rivas BG, Oden PC (2005) Stand dynamics and basal area change in a tropical dry forest reserve in Nicaragua. For. Ecol. Manag. 208 (3):63-75
- Meza V, Mora F (2003) Dinámica y Crecimiento Diamétrico del Bosque Seco Tropical no manejado. Parque Nacional Guanacaste, Costa Rica. Propuesta de ponencia presentada al XII Congreso Forestal Mundial. Quebec, Canadá.
- Monge A, Quesada R, Gonzalez E (2002) Estudio de la dinamica del bosque seco tropical a partir de parcelas permanentes de muestreo en el parque nacional Palo Verde, Bagaces, Costa Rica. In: Chaverri A, Quesada R, Chaves E, Fonseca W, Sanabria E (eds.) Ecosistemas forestales de bosque seco tropical: investigaciones y resultados en Mesoamerica. Heredia, CR, Universidad Nacional / INISEFOR. pp 175-184.
- Murphy PG, Lugo AE (1986) Ecology of tropical dry forests. Annu Rev Ecol Syst 17:67-88.
- Neves F, Braga R, Espírito-Santo MMDo, Delabie J, Fernandes W, Sánchez-Azofeifa A (2010) Diversity of Arboreal Ants in a Brazilian Tropical Dry Forest: Effects of Seasonality and Successional Stage. Sociobiology. 56(1): 1-18.
- Ortiz E, Carrera F (2002) Estadística básica para inventarios forestales. In: Orozco, L; Brumér, C. Inventarios forestales para bosques latifoliados en América Central. CATIE, Turrialba, CR. pp 71-99.
- Phillips L, Nuñez VP, Timana ME (1998) Tree mortality and collecting botanical vouchers in tropical forests. Biotropica 30:298-305.
- Portillo-Quintero C, Sánchez-Azofeifa A (2010) Extent and conservation of tropical dry forests in the Americas. Biol. Conserv. 143(1):144-155.
- Quesada M, Sánchez-Azofeifa A, Alvarez-Añorve M, Stoner K.E, Avila-Cabadilla L, Calvo-Alvarado J, Castillo MM, Espírito-Santo MMDo, Fagundes M, Fernandes GW, Gamon J, Lopezaraiza-Mikel M, Lawrence D, Cerdeira Morellato LP, Powers JS, de S. Neves F, Rosas-Guerrero V, Sayago R, Sánchez Montoya G (2009) Succession and management of tropical dry forests in the Americas: Review and new

perspectives. For Ecol Manag 258: 1014-24.

- Quirós BK (2002) Composición florística y estructural para el bosque primario del Hotel La Laguna Lagarto Lodge, Boca Tapada de Pital, San Carlos, Alajuela, Costa Rica. Informe de práctica de especialidad. ITCR. Cartago, Costa Rica. pp. 14-15, 46-62.
- Sánchez-Azofeifa A, Portillo-Quintero C (2011) Extent and Drivers of Change of Neotropical Seasonally Dry Tropical Forests. In: Dirzo R, Young H, Mooney H, Ceballos G (eds.) Seasonally Dry Tropical Forests: Ecology and Conservation. Island Press. London. UK. pp 45-57.
- Sánchez-Azofeifa A, Kalácska M, Quesada M, Calvo-Alvarado J, Nassar JM, Rodriguez JP (2005) Need for integrated research for a sustainable future in tropical dry forests. Conserv. Biol. 19: 285-286.
- Silva JO, Espírito-Santo MMDo, Melo GA (2011) Herbivory on Handroanthus ochraceus (Bignoniaceae) along a successional gradient in a tropical dry forest. Arthropod-Plant Interact. 6:45–57.
- StatSoft Inc (2004) STATISTICA 6.1 (data analysis software system), version 6. www.statsoft.com.
- Uslar Y, Mostacedo B, Saldias M (2004) Composición, estructura y dinámica de un bosque seco semideciduo en Santa Cruz, Bolivia. Ecol. Boliv 39:25-43
- Vieira D, Scariot A (2006) Principles of natural regeneration of tropical dry forests for restoration. Restoration Ecol 14: 11–20.
- Vieira D, Scariot A, Holl K (2007) Effects of Habitat, Cattle Grazing and Selective Logging on Seedling Survival and Growth in Dry Forests of Central Brazil. Biotropica. 39: 269–274.
- Whigham DF, Zugasty Towle P, Cabrera Cano E, O'Neill J, Ley E (1990) The effect of annual variation in precipitation on growth and litter production in a tropical dry forest in the Yucatan of Mexico. Trop Ecol. 31(2): 23-34.

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