

Research Paper

Vertical distribution, nutrient concentration and seasonal changes of fine root mass in a semi-deciduous tropical dry forest and in two adjacent pastures in the Western Llanos of Venezuela

Distribución vertical, concentración de nutrientes y cambios estacionales en la masa de raíces finas en un bosque seco tropical semicaducifolio y dos pastizales adyacentes en los Llanos Occidentales de Venezuela

ANA FRANCISCA GONZÁLEZ-PEDRAZA^{1,2,3} AND NELDA DEZZEO³

¹Universidad de Pamplona, Facultad de Ciencias Agrarias, Pamplona, Colombia. unipamplona.edu.co/fagrarias

²Universidad Nacional Experimental Sur del Lago “Jesús María Semprum”, Santa Bárbara, Venezuela. unesur.edu.ve

³Instituto Venezolano de Investigaciones Científicas (IVIC), Altos de Pipe, Venezuela. ivic.gob.ve

Abstract

With the objective to contribute to a better understanding of ecological consequences of deforestation on the below-ground system in the Western Llanos of Venezuela, we evaluated the vertical distribution, nutrient concentration and seasonal changes of total fine root mass (FRM) (<2 mm diameter) in a semi-deciduous tropical dry forest and in 2 adjacent pastures of *Cynodon nlemfuensis*: a young pasture (YP, 5 years old) and an old pasture (OP, 18 years old) in the Obispo municipality, Barinas State. This evaluation included measurements at the end of the rainy season, during the dry season and during the subsequent early rainy season in 2005/2006. Highest FRM was recorded during the dry season, which probably indicates a plant water-stress response mechanism. The highest proportion (63–88%) of FRM was concentrated in the 10–20 cm soil layer at all studied sites, probably due to a higher nutrient and moisture content at that depth. Non-significant differences ($P>0.05$) were observed in the total concentrations of organic carbon, nitrogen, phosphorus, calcium and magnesium in the FRM in soils supporting forest, OP and YP at the evaluated depths. Non-significant changes in the total FRM and nutrient concentrations were observed between the sampling periods and the 3 study sites. YP soils showed a slight increase in FRM that could be associated with the root growth of secondary vegetation, which is considered a weed and is periodically removed. Our results suggest that the land use change from tropical forest to pastures has not significantly affected the mass of fine roots and their carbon and nutrient concentrations. Further studies are needed to determine if these findings apply to other ecosystems.

Keywords: *Cynodon nlemfuensis*, root distribution, soil C, soil N, tropical pastures.

Resumen

Con el objetivo de contribuir a entender mejor las consecuencias ecológicas de la deforestación en el sistema suelo-raíces en los Llanos Occidentales de Venezuela, evaluamos la distribución vertical, concentración de nutrientes y los cambios estacionales en la masa total de raíces finas (MRF) (<2 mm de diámetro) en un bosque seco tropical semicaducifolio y en dos pasturas adyacentes de *Cynodon nlemfuensis*: una pastura de 5 años (PJ) y una de 18 años (PV). Esta evaluación se realizó en 2005/2006 en el municipio Obispo, estado Barinas, e incluyó mediciones al final del período de lluvias, durante el período seco y al inicio del período de lluvias subsiguiente. La mayor MRF se registró durante el período seco, lo que probablemente indica un mecanismo de respuesta al estrés hídrico de la planta. La mayor proporción (63–88%) de MRF se concentró en la capa de suelo de 10–20 cm en todos los sitios estudiados, probablemente debido a una mayor concentración de nutrientes y humedad a esa profundidad. No se observaron diferencias significativas ($P>0.05$) en las concentraciones totales de carbono orgánico, nitrógeno, fósforo, calcio y magnesio en la MRF en suelos de bosque, PJ y PV a las profundidades evaluadas. No se observaron cambios significativos en la MRF total y en las concentraciones de nutrientes entre los períodos de muestreo en

Correspondence: Ana Francisca González-Pedraza, Universidad de Pamplona, Facultad de Ciencias Agrarias, Pamplona, Norte de Santander, Colombia. Email: anagonzalez11@gmail.com

los 3 sitios de estudio. Los suelos en PJ mostraron un ligero aumento en la MRF que podría estar asociado con el crecimiento de raíces de la vegetación secundaria, que se considera una maleza y se elimina periódicamente. Nuestros resultados indican que la conversión del bosque a pasturas no afectó significativamente la masa de raíces finas y sus concentraciones de carbono y nutrientes. Se requieren estudios adicionales para determinar si los resultados son aplicables a otros ecosistemas.

Palabras clave: C en el suelo, *Cynodon nlemfuensis*, distribución de raíces, N en el suelo, pastos tropicales.

Introduction

Fine root mass in tropical forests is the most important component of below-ground C dynamics and can contribute significantly to global net primary production (Malhi et al. 2011). In tropical dry forests, fine root production is high, constituting an important source of carbon (C) and nutrients in the soil (Fiala et al. 2017). It has been suggested that the roots in these forests provide more N, P and K than the above-ground biomass (Singh et al. 1989).

Several environmental factors affect production of fine roots in tropical dry forests, such as the marked climatic seasonality (Murphy and Lugo 1986; Singh et al. 1989), soil nutrients (Blair and Perfecto 2001) and forest disturbances and land use history (Castellanos et al. 2001; Jaramillo et al. 2003). The clearing of dry forests for the establishment of pastures can have important effects on the production and distribution of roots within the soil profile and on the contributions of C and nutrients (Jaramillo et al. 2003).

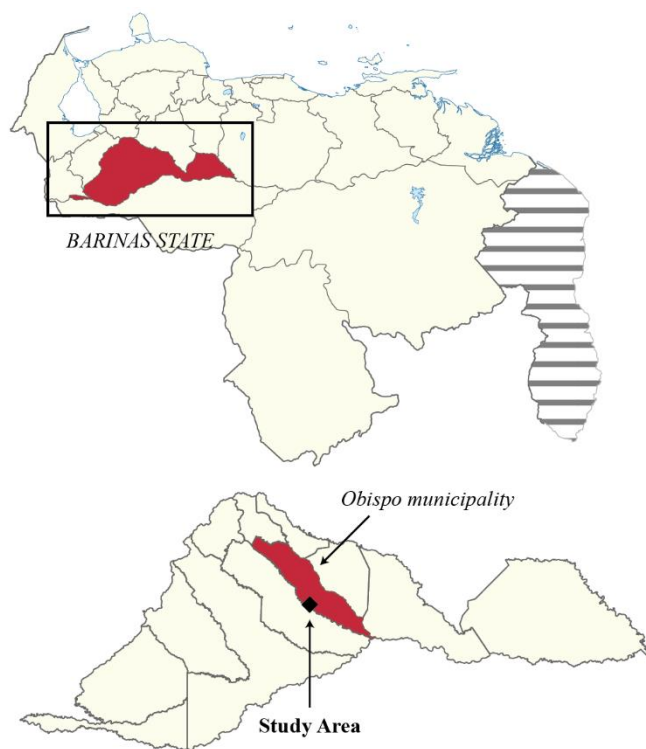
In Venezuela, large areas of tropical dry forests have been cleared and replaced by pastures. It is likely that this conversion has had impacts on the mass and distribution of fine roots within the soil profile. Studies on the replacement of tropical deciduous forests with pastures have shown important effects on C and nutrients in the soil profile (Crespo 2015), and pastures have the potential to store significant amounts of C in soils (Rodríguez et al. 2013; Crespo 2015). The dense and deep root system of grasses contributes to the formation of soil aggregates and provides protection to the soil C, making it least susceptible to oxidation and eventual loss to the atmosphere (Cambardella and Elliot 1993).

Considering that the rate of deforestation of tropical dry forests is increasing rapidly, it is important to improve the understanding of the ecological consequences of forest disturbance on the below-ground system. Detailed information on the changes that have occurred in fine root production once forests have been cleared and converted into pastures can be very useful in predicting the consequences of deforestation and to design effective pasture management strategies. The objective of this study was to evaluate the fine root mass and its nutrient composition in a tropical dry forest and in 2 adjacent pastures (5- and 18-years-old) planted following the logging and burning of forest in the Western Llanos of Venezuela.

Materials and Methods

Study site

The study area was in the El Mangón farm, located in the Obispo municipality, Hurtado sector of Barinas State in the Western Llanos of Venezuela (40°01'10"–40°59'10" N, 91°57'30"–91°25'18" W; 120 masl) (Figure 1). Average annual rainfall is 1,244 mm, with a rainy season from April to December and a dry season from January to March. Average annual temperature is 26.8 °C, and the relief is flat with a slope between 0 and 2% (Ewel et al. 1976; SIRA-INIA-CENIAP 2010).



Disclaimer: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of *Tropical Grasslands-Forrajes Tropicales* concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries.

Figure 1. Study area in the Western Llanos of Venezuela (SIRA-INIA-CENIAP 2010).

The landscape corresponds to an alluvial overflow plain, influenced by the fluvial dynamics of an old bed of the Santo Domingo River (Schargel and Strebin 1970).

Table 1. Soil characteristics of the study sites (mean ± SD) (Source: [González-Pedraza and Dezzeo 2011, 2014a, 2014b](#)).

Characteristic	Depth (cm)	Forest	5-years-old pasture (YP)	18-years-old pasture (OP)
pH (H ₂ O)	0–5	5.4±0.4Ba	5.0±0.5Cab	4.8±0.5Db
	5–10	5.8±0.4Ba	5.5±0.2BCa	5.5±0.4Ca
	10–20	6.0±0.4ABa	5.9±0.2Aa	6.1±0.3Ba
	20–30	5.7±0.7Bab	5.3±0.1BCb	5.9±0.4BCa
	30–40	6.6±1.1Aab	5.9±0.2Ab	6.9±0.7Aa
Total organic carbon (g/m ²)	0–5	1,390±251.9Aa	1,473±400.2Ba	1,517±249.9Ba
	5–10	1,379±228.5Ab	2,232±287.9Aa	1,904±436.1Aa
	10–20	916±143.5Bc	1,675±196.4Ba	1,364±229.4BCb
	20–30	1,002±133.6Bb	1,018±118.6Cb	1,123±117.3Ca
	30–40	493±59.9Ca	529±145.5Da	494±84.8Da
Total nitrogen (g/m ²)	0–5	173±59.6Ba	209±99.8Ba	184±55.2Ba
	5–10	184±33.2Ba	173±35.7Ba	205±28.3Ba
	10–20	641±465.5Ab	838±710.2Aab	1,404±811.1Aa
	20–30	204±89.2Ba	147±12.5Ca	215±114.8Ba
	30–40	137±43Ba	104±25.7Ca	126±23.3Ba
Total phosphorus (µg/g)	0–5	588.5±206.2Aa	926.3±329.9Aa	656.5±67.2Aa
	5–10	442.8±85.8Bb	776.1±177.3Ba	512.3±70.6Bb
	10–20	59.0±36.9Db	163.4±76.8Ca	99.0±68.4Dab
	20–30	295.5±115.4Cb	594.4±120.1Ba	309.9±68.5Cb
	30–40	321.4±65.7BCb	487.3±101.4Ba	298.3±15.4Cb
Calcium (meq/100 g)	0–5	11.0±3.9Aa	12.5±4.6Aa	9.1±1.8Aa
	5–10	6.1±3.0Cc	14.9±3.1Aa	11.4±3.0Ab
	10–20	9.2±1.6ABb	12.7±3.7Aa	10.6±2.1Aab
	20–30	9.0±1.3ABab	8.2±1.4Bb	10.3±1.8Aa
	30–40	7.3±0.7BCb	7.3±1.0Bb	9.2±2.7Aa
Magnesium (meq/100 g)	0–5	4.1±1.1ABa	5.0±1.2Aa	5.2±1.8Aa
	5–10	3.4±1.1Ba	4.5±0.9ABa	4.5±2.2Aa
	10–20	3.9±1.2ABa	3.9±0.9ABa	4.8±2.1Aa
	20–30	4.7±1.0Aab	3.4±1.0Bb	5.3±1.8Aa
	30–40	4.8±1.1Aa	3.4±0.8Bb	4.7±1.2Aa
Potassium (meq/100 g)	0–5	0.5±0.2Ab	1.2±0.7Aa	0.6±0.3Ab
	5–10	0.2±0.2Bb	0.8±0.4ABa	0.3±0.2Bb
	10–20	0.2±0.1Bb	0.5±0.3BCa	0.2±0.1Bb
	20–30	0.1±0.0Bb	0.4±0.2BCa	0.2±0.0Bb
	30–40	0.2±0.2Ba	0.3±0.2Ca	0.2±0.1Ba
Sodium (meq/100 g)	0–5	0.1±0.0Ca	0.1±0.0Ca	0.1±0.1Ba
	5–10	0.1±0.1BCa	0.1±0.0Ca	0.1±0.1Ba
	10–20	0.1±0.1BCa	0.1±0.0Ca	0.2±0.3Ba
	20–30	0.3±0.2Ba	0.2±0.1Ba	0.4±0.3Ba
	30–40	1.2±0.4Aa	0.8±0.1Ab	1.1±0.3Aab
Aluminum (meq/100 g)	0–5	1.7±0.1Aa	2.0±0.2Aa	1.8±0.6Aa
	5–10	0.5±0.1CDb	0.6±0.0Ba	0.5±0.0Bab
	10–20	0.6±0.1Ca	0.6±0.1Ba	0.6±0.1Ba
	20–30	0.7±0.1Ba	0.6±0.1Bb	0.6±0.1Bb
	30–40	0.5±0.1Da	0.4±0.1Ca	0.3±0.1Cb
Cation exchange capacity (meq/100 g)	0–5	17.2±3.8Aa	20.3±5.5Aa	16.8±3.3Aa
	5–10	10.3±2.4Cc	20.8±3.9Aa	16.8±3.1Ab
	10–20	13.9±1.3Bb	17.7±4.3Aa	16.2±3.7Aab
	20–30	14.7±1.7ABab	12.7±1.9Bb	16.5±2.9Aa
	30–40	13.5±1.7Bab	12.3±1.1Bb	15.2±2.9Aa
Base saturation (%)	0–5	90.5±3.8Ba	90.8±5.4Ba	88.9±4.7Ba
	5–10	95.4±2.1Bb	97.1±0.6Aa	96.7±0.7Aa
	10–20	96.2±1.4Ba	96.5±1.0Aa	96.2±1.1Aa
	20–30	95.7±1.4Ba	95.7±1.6Aa	96.5±1.2Aa
	30–40	96.9±1.2Aab	96.6±1.3Ab	98.1±0.9Aa

Different lower-case letters indicate significant differences between sites for the same depth (P<0.05). Different upper-case letters indicate significant differences between depths for the same site (P<0.05).

The soil parent material is of alluvial origin, a sandy clay loam with kaolinite as dominant clay mineral (Ewel et al. 1976). In general terms, the soils have been described as deep, moderately fertile, with moderate concentrations of organic matter, nitrogen and phosphorus, high cation exchange capacity and base saturation (Table 1), with clay loam and silty clay loam textures (Table 2) (Schargel and Strebin 1970; González-Pedraza and Dezzeo 2011, 2014a, 2014b). The main soil orders found in this area correspond to Inceptisols and Vertisols, among them Tropaquepts, Usterts and Aquerts (Mogollón and Comerma 1994).

According to González-Pedraza and Dezzeo (2011), soils at the study site are fine-textured with a predominance of silt. Forest and OP soils show similar clay and sand contents, while YP soils have significantly higher clay content (up to 18% more than forest and OP soils). In general, the soil properties at the studied sites tended to be similar (Table 2).

The predominant vegetation in the region is semi-deciduous, periodically flooded forest (Ewel et al. 1976). These forests consist of 2 strata, the upper one consisting of deciduous and semi-deciduous trees with heights of 15–20 m, and the lower one consisting of deciduous and evergreen trees with heights less than 15 m (Table 3) (Aymard 2015).

Table 2. Particle size distribution (mean \pm SD) in the 0–40 cm of forest and pasture soils (Source: González-Pedraza and Dezzeo (2011)).

Particle size distribution	Depth (cm)	Forest	5-years-old pasture	18-years-old pasture
% Sand	0–5	19.8 \pm 5.9Aa	12.5 \pm 7.8ABb	22.3 \pm 5.6Aa
	5–10	20.8 \pm 7.6Aa	10.0 \pm 7.4ABb	22.7 \pm 7.6Aa
	10–20	15.6 \pm 4.4Aa	5.6 \pm 1.8Bb	18.3 \pm 8.0Aa
	20–30	15.8 \pm 2.6Aa	15.4 \pm 6.8Aa	13.5 \pm 5.5Aa
	30–40	17.1 \pm 2.5Aa	12.9 \pm 3.3ABb	15.4 \pm 4.3Ab
% Silt	0–5	49.7 \pm 6.2Ba	44.8 \pm 6.1Ba	47.1 \pm 4.5Ca
	5–10	53.9 \pm 5.6ABa	46.8 \pm 5.7Bb	47.1 \pm 3.0Cb
	10–20	57.5 \pm 4.1Aa	60.0 \pm 3.5Aa	52.7 \pm 3.6Bb
	20–30	57.5 \pm 4.2Aa	60.4 \pm 5.3Aa	57.0 \pm 4.1ABa
	30–40	58.3 \pm 2.0Ab	66.3 \pm 4.4Aa	60.0 \pm 2.7Ab
% Clay	0–5	30.5 \pm 9.6Ab	42.7 \pm 10.6Aa	30.6 \pm 6.4Ab
	5–10	25.2 \pm 6.9Ab	43.2 \pm 8.3Aa	30.2 \pm 6.2Ab
	10–20	26.9 \pm 1.6 Ab	34.4 \pm 3.2ABa	28.9 \pm 5.1Ab
	20–30	26.7 \pm 2.0Aab	24.2 \pm 3.4BCb	29.5 \pm 3.3Aa
	30–40	24.6 \pm 1.0Aa	20.8 \pm 2.0Cb	24.6 \pm 2.5Aa

Different lower-case letters indicate significant differences between sites ($P < 0.05$). Different upper-case letters indicate significant differences between depths for the same site ($P < 0.05$).

Table 3. Main species of trees present in the semi-deciduous forest. (Source: Adapted from Figueroa 2006).

Family	Botanical name	Common name	Phenology
Acanthaceae	<i>Trichanthera gigantea</i> (Bonpl.) Nees	Naranjillo	Evergreen
Anacardiaceae	<i>Spondias mombin</i> L.	Jobo	Deciduous
Annonaceae	<i>Rollinia exsucca</i> (DC.) A. DC.	Anoncillo	Semi-deciduous
	<i>Annona jahnii</i> Saff.	Manidito	Semi-deciduous
Bixaceae	<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	Bototo	Deciduous
Cordiaceae	<i>Cordia collococca</i> L.	Caujaro	Semi-deciduous
Euphorbiaceae	<i>Sapium glandulosum</i> (L.) Morong	Lechero	Semi-deciduous
Fabaceae	<i>Samanea saman</i> (Jacq.) Merr.	Samán	Deciduous
	<i>Inga</i> sp.	Guamo	Evergreen
	<i>Albizia</i> sp.	Carabali	Semi-deciduous
	<i>Pterocarpus acapulcensis</i> Rose	Drago	Facultatively deciduous
Malvaceae	<i>Ceiba pentandra</i> (L.) Gaertn.	Ceiba	Facultatively deciduous
	<i>Sterculia apetala</i> (Jacq.) H. Karst.	Camuruco	Deciduous
	<i>Luehea candida</i> (DC.) Mart.	Guácimo cimarrón	Facultatively deciduous
	<i>Guazuma ulmifolia</i> Lam.	Guácimo	Evergreen
Moraceae	<i>Maclura tinctoria</i> (L.) D. Don ex Steud. subsp. <i>tinctoria</i>	Mora	Deciduous
	<i>Brosimum alicastrum</i> Sw.	Charo	Evergreen
Rubiaceae	<i>Genipa americana</i> L.	Caruto	Deciduous
Sapindaceae	<i>Sapindus saponaria</i> L.	Paraparo	Deciduous
Urticaceae	<i>Cecropia peltata</i> L.	Yagrumo	Evergreen

In this region in the last 50 years, large areas of natural forest have been converted into pasture using the slash-and-burn method. Estrella grass (*Cynodon nlemfuensis* Vanderyst) is grown for grazing by cattle (Truter et al. 2015).

Field work was carried out in an area of tropical dry forest with dominant deciduous vegetation and in 2 adjacent areas, where the original forest had been cut down manually and burnt, and Estrella grass had been planted (5- and 18-years-old, YP and OP, respectively). The pastures have never been fertilized, but have been mowed annually to control weeds and to promote grass growth. At sampling time, species from the original forest that could not be cut by hand, as well as vegetation of secondary growth, like palms and some species of legumes, were observed in the pasture. Cattle were introduced into YP for grazing during the dry season and early and late in the rainy season. On each occasion the cattle remained in this pasture until they consumed all available grass. Every 1–2 months cattle were introduced to the old pasture (OP) and remained for 3–7 days, while consuming all available grass.

Fine root sampling

At each selected site (forest, YP and OP), soil samples were taken from a 600 m² plot (20 × 30 m). The distance between the 3 sites was 1–3 km. At each plot, soil samples

for determining the vertical distribution of the fine root mass (<2 mm) and their nutrient concentrations were collected at 12 points arranged along 3 transects with 4 sampling points per transect. The samples were collected with a soil core at 0–5, 5–10, 10–20, 20–30 and 30–40 cm depths at the end of the rainy season 2005 (November). For determining the seasonal changes in mass of fine roots, soil samples at 0–5 and 5–10 cm depths were collected at 12 points in each study plot along 3 transects on 3 occasions: end of rainy season 2005 (November), during the dry season (March 2006) and early rainy season (May 2006) (Figure 2).

Fine root mass

All collected soil samples were dried and passed through a 2 mm soil sieve. The fine roots were extracted from the soil fraction which passed through the 2 mm sieve. From each sieved soil sample, 2 × 200 g subsamples were taken. In these subsamples all fine roots (both living and dead) were manually extracted and weighed. Mean weight of fine root mass from the 2 subsamples was used to calculate the dry matter (DM) of fine root mass from each soil sample. The data were converted to t DM/m² considering the area of the core, before being converted to a hectare basis according to the following equation:

$$\text{Fine root mass (t DM/ha)} = \text{weight of fine root mass (t DM/m}^2\text{)} \times \text{area of one hectare of soil (10,000 m}^2\text{/ha)}.$$

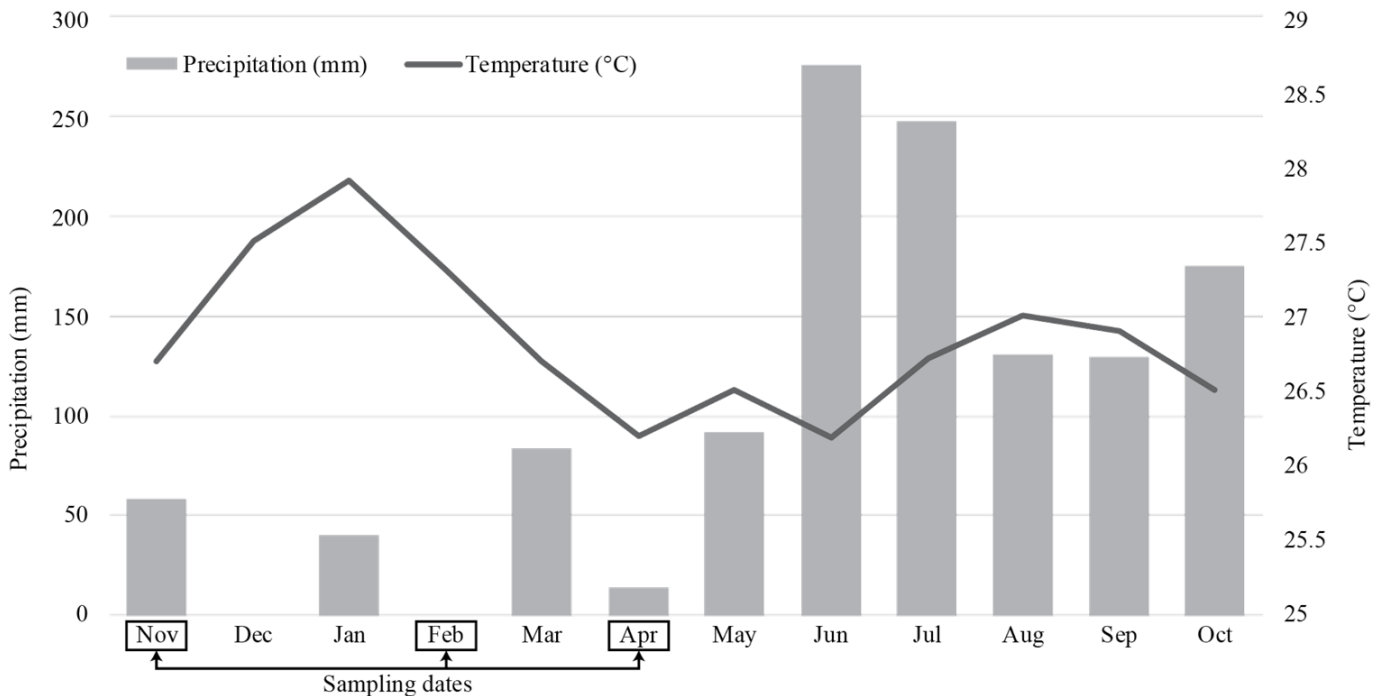


Figure 2. Distribution of precipitation and temperature during the sampling period. [Source: Barinas Agrometeorological Station (SIRA-INIA-CENIAP 2010)].

Laboratory analyses

Total organic carbon in fine roots (TOCr) was determined using the Loss on Ignition (LOI) method (Schulte and Hopkins 1996). It was assumed that 58% of the organic matter (OM) was organic carbon (Nelson and Sommers 1996) and %TOCr was calculated according to the following equation:

$$\%TOCr = [\text{pre-ignition weight (g)} - \text{post-ignition weight (g)}] \times 0.58 \times 100 / \text{pre-ignition weight (g)}.$$

Concentration of total organic carbon in the fine roots was multiplied by the respective root mass to give TOCr and the results were expressed in kg/ha based on dry weight and bulk density of the soil.

Total nitrogen (N), phosphorus (P), calcium (Ca) and magnesium (Mg) in the fine root mass was extracted by digestion with concentrated sulfuric acid and oxidation with hydrogen peroxide (Tiessen and Moir 1993). Total nitrogen in the roots (TNr) was determined by the colorimetric method of Keeney and Nelson (1982) on a Technicon Autoanalyzer II. Total phosphorus (TPr) was measured by the molybdenum blue method of Murphy and Riley (1962). Total Ca and total Mg were measured on an atomic absorption spectrophotometer (AA). Total N, P, Ca and Mg concentrations obtained in the fine root mass were multiplied by their respective root masses, and the results were expressed in kg/ha based on dry weight and bulk density of the soil.

Statistical analysis

Statistical analysis of data was carried out using one-way analysis of variance (ANOVA). Means were separated with Tukey's test when statistical differences ($P < 0.05$) were observed. When necessary, the data were transformed to homogenize variances, and when that did not meet this assumption ($P > 0.05$) according to Levenne's test, a non-parametric Mann-Whitney test was also applied. To determine relationships between variables at sites of interest, a simple linear regression analysis was used. All statistics were computed using STATISTICA for Windows 6.0 (Statistica 2001).

Results

Vertical distribution of fine roots

No significant differences ($P > 0.05$) between study sites (forest, YP and OP) were detected in the vertical distribution of the fine root mass. However, total mass of fine roots in the top 40 cm of soil was somewhat higher in YP ($5.95 \pm$

0.57 t DM/ha) than in forest ($5.27 \pm 0.68 \text{ t DM/ha}$) and OP ($4.57 \pm 0.54 \text{ t DM/ha}$). Distribution of fine root mass was not uniform down the soil profile as root mass in the 10–20 cm horizon was generally greater than in the other horizons at all study sites ($P < 0.05$; Figure 3).

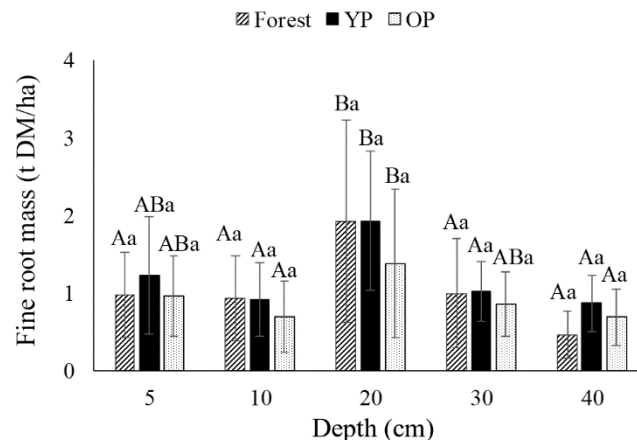


Figure 3. Vertical distribution of fine root mass in soils supporting dry semi-deciduous forest and 5-years-old (YP) and 18-years-old (OP) pasture. All points are mean values with standard error bars across forest and pastures. Different lower-case letters indicate significant differences between sites ($P < 0.05$). Different upper-case letters indicate significant differences between depths ($P < 0.05$).

Seasonal changes in fine root mass

Within each sampling period, no significant differences ($P > 0.05$) between forest, YP and OP were observed in the mass of fine roots in both 0–5 cm and 5–10 cm horizons. Differences between seasons in mass of fine roots occurred in the 0–5 cm horizon, with root mass increasing during the dry season to values exceeding those in the early or late rainy season for all sites ($P < 0.05$; Table 4).

Table 4. Seasonal variation in mass of fine roots (mean \pm SD) in the top 10 cm of soils supporting forest and pastures of 2 ages.

Season	Depth (cm)	Fine root mass (t DM/ha)		
		Forest	YP ¹	OP
End rainy season	0–5	0.9 \pm 0.5ABa	1.0 \pm 0.4Ba	1.0 \pm 0.5Ba
	5–10	0.7 \pm 0.3Aa	0.9 \pm 0.4Aa	0.5 \pm 0.5Ba
Dry season	0–5	1.4 \pm 0.7Aa	2.1 \pm 0.8Aa	1.6 \pm 0.7Aa
	5–10	0.8 \pm 0.6Aa	1.1 \pm 0.5Aa	1.0 \pm 0.4Aa
Early rainy season	0–5	0.7 \pm 0.4Ba	1.1 \pm 0.6Ba	1.1 \pm 0.4Ba
	5–10	0.7 \pm 0.4Aa	0.9 \pm 0.4Aa	0.6 \pm 0.3ABb

¹YP: 5-years-old pasture; OP: 18-years-old pasture.

Different lower-case letters indicate significant differences between depths ($P < 0.05$). Different upper-case letters indicate significant differences between seasons ($P < 0.05$).

Total carbon and nutrients in the fine root mass

The total concentrations of carbon and nutrients in fine roots in the top 40 cm of soil was determined only in soil samples collected at the end of the rainy season. No significant differences ($P>0.05$) in total organic carbon (TOCr) and total nitrogen (TNr) in fine roots were found between Forest, YP and OP except for the 30–40 cm soil depth, where YP contained significantly ($P<0.05$) more TOCr than forest soil (Table 5). TOCr was highest ($P<0.05$) in the 10–20 cm horizon in all soils. In contrast, TNr tended to decrease steadily with increasing soil depth, with levels in the top 5 cm exceeding those in the 30–40 cm horizon (Table 5).

No significant differences ($P>0.05$) between forest and pasture soils were found in total phosphorus, calcium and magnesium in the mass of fine roots in the top 40 cm of soil (Table 6). However, there were changes in concentrations down the profile. A significant increase ($P<0.05$) in total phosphorus in roots in the forest soil in the 10–20 cm horizon was observed. Total calcium and magnesium in fine roots tended to decline with depth but differences were inconsistent and rarely significant.

Significant positive relationships existed between fine root mass and nutrient content in 0–40 cm soil horizons in forest and pasture (Table 7).

Table 5. Total organic carbon and total nitrogen (mean \pm SD) in fine roots (<2 mm) in the top 40 cm of soils supporting forest and 5-years-old and 18-years-old pastures.

Nutrient (kg/ha)	Depth (cm)	Forest	5-years-old pasture	18-years-old pasture
Total organic carbon in the fine root mass (TOCr)	0–5	455 \pm 246.3Ba	466 \pm 227.9Ba	381 \pm 204.9Ba
	5–10	403 \pm 234.4Ba	360 \pm 177.5Ba	305 \pm 196.5Ba
	10–20	864 \pm 542.8Aa	894 \pm 421.9Aa	706 \pm 480.9Aa
	20–30	424 \pm 309.9Ba	390 \pm 130.5Ba	430 \pm 228.5Ba
	30–40	182 \pm 148.7Bb	357 \pm 160.3Ba	304 \pm 147.6Bab
Total nitrogen in the fine root mass (TNr)	0–5	7.2 \pm 3.5Aa	9.0 \pm 3.7Aa	8.0 \pm 4.4Aa
	5–10	4.8 \pm 1.2Aa	5.9 \pm 3.2ABa	4.2 \pm 2.5Ba
	10–20	5.9 \pm 4.3Aa	6.8 \pm 4.2Aa	4.8 \pm 1.9Ba
	20–30	3.5 \pm 2.5Ba	2.4 \pm 0.6BCa	3.2 \pm 1.7Ba
	30–40	2.6 \pm 2.5Ba	1.8 \pm 1.4Ca	2.9 \pm 2.5Ba

Different lower-case letters indicate significant differences between sites ($P<0.05$). Different upper-case letters indicate significant differences between depths ($P<0.05$).

Table 6. Vertical distribution of total nutrients (mean \pm SD) in fine root mass in soils supporting forest and 5-years-old and 18-years-old pastures.

Nutrient (kg/ha)	Depth (cm)	Forest	5-years-old pasture	18-years-old pasture
Phosphorus	0–5	0.7 \pm 0.4Ba	1.2 \pm 0.6Aa	0.8 \pm 0.5Aa
	5–10	0.4 \pm 0.2Ba	0.6 \pm 0.4Aa	0.4 \pm 0.2Aa
	10–20	1.5 \pm 1.4Aa	1.4 \pm 0.7Aa	0.8 \pm 0.6Aa
	20–30	0.5 \pm 0.4Ba	0.7 \pm 0.4Aa	0.6 \pm 0.3Aa
	30–40	0.5 \pm 0.3Ba	0.4 \pm 0.1Aa	0.3 \pm 0.1Aa
Calcium	0–5	8.3 \pm 4.9Aa	10.0 \pm 6.6Aa	7.0 \pm 4.9Aa
	5–10	6.5 \pm 3.1Aa	9.4 \pm 6.5Aa	5.6 \pm 4.2Aa
	10–20	8.2 \pm 6.2Aa	4.2 \pm 2.6ABab	1.9 \pm 0.8Bb
	20–30	7.3 \pm 2.6Aa	6.6 \pm 4.7Aab	5.7 \pm 2.8Aa
	30–40	4.2 \pm 2.3Aa	3.2 \pm 2.8Ba	3.9 \pm 2.4ABa
Magnesium	0–5	4.6 \pm 1.9Aa	6.1 \pm 3.1Aa	5.9 \pm 2.6Aa
	5–10	4.1 \pm 1.8Aa	4.9 \pm 3.3ABa	3.9 \pm 1.8Aa
	10–20	4.7 \pm 2.5Aa	6.5 \pm 3.4Aa	4.4 \pm 2.3Aa
	20–30	4.7 \pm 2.1Aa	3.3 \pm 1.3ABa	4.9 \pm 3.9Aa
	30–40	2.5 \pm 1.8Aa	1.8 \pm 1.2Ba	2.6 \pm 2.0Aa

Different lower-case letters indicate significant differences between sites ($P<0.05$). Different upper-case letters indicate significant differences between depths ($P<0.05$).

Table 7. Linear correlation coefficients (Pearson; r) for relationships between fine root mass (<2 mm) and nutrient concentrations in fine roots in the top 40 cm of soils supporting forest and 5-years-old (YP) and 18-years-old (OP) pasture.

Nutrient	Forest	YP	OP
TOCr	0.99	0.96	0.93
TNr	0.94	0.94	0.92
P	0.77	0.82	0.76
Ca	0.80	0.76	0.68
Mg	0.96	0.82	0.88

TOCr: total organic carbon; TNr: total nitrogen; P: phosphorus; Ca: calcium; Mg: magnesium.

Discussion

The total fine root mass in the top 40 cm of soil was higher than those reported by Jaramillo et al. (2003) for semi-deciduous dry forests (3.6–4.3 t DM/ha in the top 60 cm) and for pastures of *Panicum maximum*, *Cenchrus ciliaris* and *Andropogon gayanus* (3.1–3.7 t DM/ha in the top 60 cm). However, the values for YP and OP can be considered low compared with that reported by Crespo and Lazo (2001) for a pasture of *Cynodon nlemfuensis* (10 t DM/ha in the top 15 cm of soil).

While no significant differences in total fine root mass were found between sites, the top 20 cm of soil accounted for 72.5, 68.4 and 66.2% of the total in Forest, YP and OP, respectively. Accordingly the fine root mass declined with depth as reported by Du et al. (2019) in 4 vegetation types (grassland, shrubland, secondary forest and primary forest) in a karst area, Southwest China during vegetation restoration. In that study the fine roots were concentrated in the top 10 cm of soil, which accounted for more than 57% of the root biomass, and decreased with increasing soil depth (soil samples from 0 to 30 cm deep). In karst ecosystems, fine roots contribute to the regulation of nutrient cycling in terrestrial ecosystems and the high density of fine roots within the top few centimeters of soil is crucial for acquiring nutrients.

According to Du et al. (2019), although fine root biomass of all vegetation types decreased with soil depth, the decrease was more rapid in forests (especially in secondary forests) than in other vegetation types. They suggested that the vertical distribution patterns of fine roots showed a more rapid decline in species-rich communities than in species-poor communities, which probably reflected changes in soil water content, nutrient concentration and bulk density in the soil profile.

Fiala et al. (2017) also measured a reduction in fine root mass (diameter <1 mm) with increasing soil depth in 6 Cuban forests (submontaneous evergreen broad-leaved

forest, submontaneous evergreen narrow-leaved forest, semi-deciduous narrow-leaved forest, semi-deciduous broad-leaved forest and 2 species of mangroves, *Rhizophora mangle* and *Avicennia germinans*). Fifty-seven percent of the dry mass of fine live roots was concentrated in the upper 0–5 cm soil layer in the semi-deciduous forests. Semi-deciduous narrow-leaved forest had live (87 g DM/m²) and dead (284 g DM/m²) fine roots and semi-deciduous broad-leaved forest had live (200 g DM/m²) and dead (210 g DM/m²) (range 371–410 g DM/m²) fine roots in the top 15 cm of soil, which exceeded those in evergreen forests. The authors concluded that fine root biomass is better predicted by nutrients in litterfall. The mangrove stands had 554 g live fine roots DM/m² (*A. germinans*) and 758 g DM/m² (*R. mangle*) in the top 15 cm of soil.

Variations in root dry mass and percentage distribution of roots of Florico grass (*Cynodon nlemfuensis*) in the 0–40 cm soil layer under 4 different grazing strategies and seasons were evaluated by Barros et al. (2017). High concentrations of roots were observed in the 0–10 cm layer (51.8–65.6%) for all grazing strategies in all seasons. This concentration of roots near the soil surface was explained by the branched architecture of the root system, common in forage grasses and the ability of the plant to acquire water and nutrients. According to Barros et al. (2017) the root system has less need to go deeper to acquire water and nutrients when grazing is less severe.

Similarly, Rodríguez et al. (2013) reported more than 80% of the below-ground root biomass was present in the 0–5 cm soil layer in different grasslands of Mayabeque province, Cuba.

Despite *C. nlemfuensis* being easy to establish, persistent, highly productive and adapted to different climate and soil conditions, this species does not withstand high-intensity grazing for long periods. After defoliation by grazing the plants consume organic reserves for restoration of tissues lost and then physiological activity is adjusted as the stocks of reserves are gradually restored (Sollenberger 2008; Truter et al. 2015).

The significant increase in root mass detected in the 10–20 cm soil horizon at all study sites could be associated with the highest nutrient concentrations in soil at that depth (González-Pedraza and Dezzeo 2011; 2014a; 2014b). A further hypothesis may be that plant roots explore deeper soil in search of water, particularly during the dry season, in order to survive during periods of water stress, as shown by Snyman (2009) in pastures under different drying conditions in semi-arid regions of southern Africa. A high concentration of roots at this same depth of soil was also reported for savannas in tropical dry forest areas of India (Tripathi et al. 1999).

In this region the soils have been described as deep, moderately fertile, with moderate concentrations of organic matter, nitrogen and phosphorus, high capacity for cation exchange (CEC) and saturation with bases, with clay loam and silty clay loam textures ([Schargel and Strebin 1970](#); [González-Pedraza and Dezzio 2011](#)). Schargel and Strebin ([1970](#)) described a buried horizon at a depth of close to 50 cm, where increases in the percentages of clay, CEC, calcium, potassium, carbon and nitrogen were observed.

Fine roots are usually quick to respond to changes in vegetation type, soil temperature, moisture and nutrient content ([Du et al. 2019](#)). The increase in fine root mass during the dry period at 0–5 cm soil depth (Table 4) is contrary to the results found by Singh et al. ([1989](#)), Kummerow et al. ([1990](#)) and Trujillo et al. ([2006](#)). However, other studies have reported small increases in root biomass with decreased water availability in the soil ([Castellanos et al. 2001](#); [Snyman 2009](#); [Barros et al. 2017](#); [Du et al. 2019](#)), and this has been considered as an adaptive strategy of plants under significant water stress ([Snyman 2009](#)).

For example in temperate grasslands, Walter et al. ([2012](#)) demonstrated that root length was highest when rainfall variability was intermediate and was 43 and 24% shorter with extreme and low rainfall variability. According to this author, although enhanced root growth under drought conditions is viewed as an adaptive feature of many species, sometimes grassland roots may not respond to dryness with enhanced root growth.

During the dry season, Barros et al. ([2017](#)) reported a higher concentration (65.6%) of fine roots of *C. nlemfuensis* near the surface (0–10 cm) in more severe grazing treatments than in less severe ones. This may be associated with the renewal of the root system, also known as “turnover”, during the favorable dry season growth period and with the accumulation of organic reserves. The lower densities of root dry mass in winter, relative to the other seasons, would reflect the fast recovery of the aerial parts of plants in the rainy season and redirection of organic reserves to restore the root system reserves.

Pastures under grazing tend to accumulate more reserves in their roots, as a mechanism of adaptation to defoliation ([Barros et al. 2017](#)). This aspect, combined with the water shortage during the dry season, could be contributing to the increased mass of fine roots during this time of year. On the other hand, the significant reduction in the mass of fine roots with increasing soil depth that occurred during the dry season could be related to a higher concentration of nutrients in the first 5 cm of soil, as was noted by Castellanos et al. ([2001](#)) for tropical dry forests and pastures.

The TOCr and TNr results obtained in the forest and pastures of this study are similar to those reported by Trujillo et al. ([2006](#)), Jaramillo et al. ([2003](#)) and Crespo and Lazo ([2001](#)) for other tropical dry forests and pastures. The similarity between the studied forest and pastures in the C and N concentrations in the mass of fine roots is also consistent with the results found by Jaramillo et al. ([2003](#)). The high values for TOCr and TNr in fine roots within the 10–20 cm soil horizon are closely related to the high root mass present at that depth of soil. A positive and significant correlation ($P < 0.05$) was found between the mass of fine roots and the amounts of TOCr and TNr throughout the soil profile (Table 4).

While the sites were not contiguous, soils on which the various sites were located were very similar. Our data suggest that conversion of forests to pasture did not change carbon and nutrient levels in the soil to any significant degree. Several factors can influence these outcomes such as the land cover, post-conversion land management, climate and soil type and texture ([Dengiz et al. 2019](#)).

Dengiz et al. ([2019](#)) analyzed the spatial variability of soil organic carbon density under different types of land cover within different soil types in a subhumid terrestrial ecosystem and found that soil type and land cover were critical factors influencing spatial variation of soil organic carbon (SOC) density. Land cover was the primary factor affecting variation in SOC density, while soil properties like texture, genetic horizons and soil depth also had an important influence. The observation that organic carbon concentration decreases with increasing soil depth under all land cover types has been generally observed in most situations.

Soil fertility may have a direct influence on fine root mass production. In this study, soil fertility affected the quantities of fine roots in these soils (high correlation between fine root mass and nutrient content in the top 40 cm of forest and pasture soils). Reynolds and D’Antonio ([1996](#)) indicated the possibility that nutrient availability has direct effects on root mass because fine roots are generally plastic organs and plants can deploy photosynthate below-ground to gather growth-limiting resources. Similarly, Hutchings and de Kroom ([1994](#)) said that root proliferation in fertile soils promotes extensive exploration of the soil and increases root surface area for greater water and nutrient uptake.

Tropical pastures can accumulate large stores of C in the soil. Chaplot et al. ([2016](#)) evaluated the potential of grassland rehabilitation through high density-short duration grazing to sequester atmospheric carbon and found a significant increase in SOC stocks with increasing grass biomass and grass cover to rates as high as 12%/year. Amongst the proposed explanations were

increased root biomass production, greater soil aggregate stability and associated greater organic matter protection from decomposers.

Our findings suggest that the quantities of fine roots, soil carbon and other nutrients in soils supporting tropical pastures can be equal to or exceed those in soils supporting tropical forest trees. However, the values reported here were recorded at 3 specific times of the year from 3 relatively similar sites but not strictly the same soils. Nevertheless, the data do add to the increasing database of soil C storage information under various types of vegetation.

Conclusions

According to the results of this study, the land use change from forest to pastures has not significantly affected the mass of fine roots (<2 mm) and their carbon and nutrient concentrations in the soil. Additionally, the changes in distribution of fine root mass down the soil profile were closely related to the changes in the nutrient content of the soil at the considered depths.

The moderate increase in the mass of fine roots in the young pasture (YP) may be associated with additional root inputs from the growth of secondary forest vegetation, which is considered a weed and therefore removed periodically. Further studies in other regions are needed to determine if these findings apply to other ecosystems.

Further studies are needed to clarify the effects of climate seasonality and soil nutrients on magnitude and distribution of fine root mass within the soil profile and its contribution to C storage in soil under both forest and pastures.

References

(Note of the editors: All hyperlinks were verified 4 April 2020.)

- Aymard G. 2015. Bosques de los Llanos de Venezuela: Estructura, composición florística, diversidad y estado actual de conservación. En: López R; Hétier JM; López D; Schargel R; Zinck A, eds. Tierras Llaneras de Venezuela. 2nd Edn. p. 241–268. IRD-CIDIAT, Mérida, Venezuela.
- Barros ACC de; Almeida JCC; Camargo Filho ST; Carvalho CAB de; Campana LL; Morais LF de. 2017. Root dry matter mass and distribution of Florico grass under different grazing strategies. Pesquisa Agropecuária Brasileira 52:1276–1285. doi: [10.1590/s0100-204x2017001200017](https://doi.org/10.1590/s0100-204x2017001200017)
- Blair BC; Perfecto I. 2001. Nutrient content and substrate effect on fine root density and size distribution in a Nicaraguan rain forest. Biotropica 33:697–701. doi: [10.1111/j.1744-7429.2001.tb00227.x](https://doi.org/10.1111/j.1744-7429.2001.tb00227.x)
- Cambardella CA; Elliot ET. 1993. Carbon and nitrogen distribution in aggregates from cultivated and native grassland soils. Soil Science Society of America Journal 57:1071–1076. doi: [10.2136/sssaj1993.03615995005700040032x](https://doi.org/10.2136/sssaj1993.03615995005700040032x)
- Castellanos J; Jaramillo VJ; Sanford RL; Kauffman JB. 2001. Slash-and-burn effects on fine root biomass and productivity in a tropical dry forest ecosystem in Mexico. Forest Ecology and Management 148:41–50. doi: [10.1016/S0378-1127\(00\)00523-5](https://doi.org/10.1016/S0378-1127(00)00523-5)
- Chaplot V; Dlamini P; Chivenge P. 2016. Potential of grassland rehabilitation through high density-short duration grazing to sequester atmospheric carbon. Geoderma 271:10–17. doi: [10.1016/j.geoderma.2016.02.010](https://doi.org/10.1016/j.geoderma.2016.02.010)
- Crespo G. 2015. Factores que influyen en el reciclaje de nutrientes en pastizales permanentes, avances en el desarrollo de su modelación. Revista Cubana de Ciencia Agrícola 49:1–10. bit.ly/2yBUrCY
- Crespo G; Lazo J. 2001. A study on the root biomass of *C. nlemfuensis* cv. Panamanian, *P. maximum* cv. Likoni and *D. annulatum* and their nutrient contribution. Cuban Journal of Agricultural Science 35(3):259–263.
- Dengiz O; Saygin F; İmamoğlu A. 2019. Spatial variability of soil organic carbon density under different land covers and soil types in a sub-humid terrestrial ecosystem. Eurasian Journal of Soil Science 8:35–43. doi: [10.18393/ejss.486582](https://doi.org/10.18393/ejss.486582)
- Du H; Liu L; Su L; Zeng F; Wang K; Peng W; Zhang H; Song T. 2019. Seasonal changes and vertical distribution of fine root biomass during vegetation restoration in a karst area, Southwest China. Frontiers in Plant Science 9, article 2001. doi: [10.3389/fpls.2018.02001](https://doi.org/10.3389/fpls.2018.02001)
- Ewel JJ; Madriz A; Tosi Jr JA. 1976. Zonas de vida de Venezuela: Memoria explicativa sobre el mapa ecológico. Segunda Edn. Ministerio de Agricultura y Cría, Fondo Nacional de Investigaciones Agropecuarias, Caracas, Venezuela.
- Fiala K; Hernández L; Holub P. 2017. Comparison of vertical distribution of live and dead fine root biomass in six types of Cuban forests. Journal of Tropical Forest Science 29:275–281. [jstor.org/stable/44272905](https://www.jstor.org/stable/44272905)
- Figuerola C. 2006. Plan de manejo simplificado y de impacto ambiental, aprovechamiento de productos forestales. Fundo Agropecuario El Mangón, C.A., superficie 1821 hectáreas, Parroquia La Luz, municipio Obispos, Estado Barinas. Venezuela. Informe técnico. (Unpublished.)
- González-Pedraza AF; Dezzeo N. 2011. Efecto del cambio de bosque a pastizal sobre las características de algunos suelos en los Llanos Occidentales de Venezuela. Interciencia 36:135–141. bit.ly/2xP8Nzp
- González-Pedraza AF; Dezzeo N. 2014a. Changes in the labile and recalcitrant organic matter fractions due to transformation of semi-deciduous dry tropical forest to pasture in the Western Llanos, Venezuela. In: Greer FE, ed. Dry forests: Ecology, species diversity and sustainable management. Nova Science Publishers Inc., New York, USA. p. 105–132.
- González-Pedraza AF; Dezzeo N. 2014b. Effects of land use change and seasonality of precipitation on soil nitrogen in a dry tropical forest area in the Western Llanos of Venezuela.

- The Scientific World Journal 2014, Article 514204. doi: [10.1155/2014/514204](https://doi.org/10.1155/2014/514204)
- Hutchings MJ; de Kroom H. 1994. Foraging in plants: The role of morphological plasticity in resource acquisition. *Advances in Ecological Research* 25:159–238. doi: [10.1016/S0065-2504\(08\)60215-9](https://doi.org/10.1016/S0065-2504(08)60215-9)
- Jaramillo VJ; Ahedo-Hernández R; Kauffman JB. 2003. Root biomass and carbon in a tropical evergreen forest of Mexico: changes with secondary succession and forest conversion to pasture. *Journal of Tropical Ecology* 19:457–464. doi: [10.1017/S0266467403003493](https://doi.org/10.1017/S0266467403003493)
- Keeney DR; Nelson DW. 1982. Nitrogen-Inorganic forms. In: Page AL, ed. *Methods of soil analysis: Part 2 Chemical and microbiological properties*. Agronomy Monograph No. 9. ASA and SSSA, Madison, WI, USA. p. 643–698. doi: [10.2134/agronmonogr9.2.2ed.c33](https://doi.org/10.2134/agronmonogr9.2.2ed.c33)
- Kummerow J; Castellanos J; Mass M; Larigauderie A. 1990. Production of fine roots and the seasonality of their growth in a Mexican deciduous dry forest. *Vegetatio* 90:73–80. doi: doi.org/10.1007/BF00045590
- Malhi Y; Doughty C; Galbraith D. 2011. The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:3225–3245. doi: [10.1098/rstb.2011.0062](https://doi.org/10.1098/rstb.2011.0062)
- Mogollón L; Comerma J. 1994. *Suelos de Venezuela*. Editorial Ex Libris C.A., Caracas, Venezuela.
- Murphy J; Riley JP. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27:31–36. doi: [10.1016/S0003-2670\(00\)88444-5](https://doi.org/10.1016/S0003-2670(00)88444-5)
- Murphy PG; Lugo AE. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17:67–88. doi: [10.1146/annurev.es.17.110186.000435](https://doi.org/10.1146/annurev.es.17.110186.000435)
- Nelson DW; Sommers LE. 1996. Total carbon, organic carbon, and organic matter. In: Sparks DL; Page AL; Helmke PA; Loeppert RH; Soltanpour PN; Tabatabai MA; Johnston CT; Sumner ME, eds. *Methods of soil analysis. Part 3. Chemical methods*. SSSA Book Series No. 5. SSSA, Madison, WI, USA. p. 961–1010. doi: [10.2136/sssabookser5.3.c34](https://doi.org/10.2136/sssabookser5.3.c34)
- Reynolds HL; D'Antonio C. 1996. The ecological significance of plasticity in root weight ratio in response to nitrogen: Opinion. *Plant and Soil* 185:75–97. doi: [10.1007/BF02257566](https://doi.org/10.1007/BF02257566)
- Rodríguez I; Hernández L; Crespo G; Sandrino B; Fraga S. 2013. Performance of the below ground root biomass in different grasslands of Mayabeque province, Cuba. *Cuban Journal of Agricultural Science* 47:201–207. bit.ly/2JJ07gA
- Schargel R; Strebin S. 1970. Estudio agrológico preliminar. Sector Obispos, Estado Barinas. Ministerio de Obras Públicas, Guanare, Estado Barinas, Venezuela.
- Schulte EE; Hopkins BG. 1996. Estimation of soil organic matter by weight loss-on-ignition. In: Magdoff FR; Tabatabai MA; Hanlon Jr. EA, eds. *Soil organic matter: Analysis and interpretation*. SSSA Special Publication No. 46. SSSA, Madison, WI, USA. p. 21–31. doi: [10.2136/sssaspecpub46.c3](https://doi.org/10.2136/sssaspecpub46.c3)
- Singh JS; Raghubanshi AS; Singh RS; Srivastava SC. 1989. Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. *Nature* 338:499–500. doi: [10.1038/338499a0](https://doi.org/10.1038/338499a0)
- SIRA-INIA-CENIAP. 2010. *Sistemas de información en recursos agroecológicos, estación meteorológica Barinas*. Instituto Nacional de Investigaciones Agrícolas, Ministerio del Poder Popular para la Agricultura y Tierras, Maracay, Estado Aragua, Venezuela.
- Snyman HA. 2009. Root studies on grass species in a semi-arid South Africa along a soil-water gradient. *Agriculture, Ecosystems & Environment* 131:247–254. doi: [10.1016/j.agee.2009.01.023](https://doi.org/10.1016/j.agee.2009.01.023)
- Sollenberger LE. 2008. Sustainable production systems for *Cynodon* species in the subtropics and tropics. *Revista Brasileira de Zootecnia* 37:85–100. doi: [10.1590/S1516-35982008001300011](https://doi.org/10.1590/S1516-35982008001300011)
- Statistica. 2001. *Basic statistical analysis methods*. Version 6.0. StatSoft, Tulsa, OK, USA.
- Tiessen H; Moir JO. 1993. Characterization of available P by sequential extraction. In: Carter MR; Gregorich EG, eds. *Soil sampling and methods of analysis*. Taylor & Francis Group, Boca Raton, FL, USA. p. 75–86.
- Tripathi SK; Singh KP; Singh PK. 1999. Temporal changes in spatial pattern of fine-root mass and nutrient concentrations in Indian bamboo savanna. *Applied Vegetation Science* 2:229–238. doi: [10.2307/1478986](https://doi.org/10.2307/1478986)
- Trujillo W; Fisher MJ; Lal R. 2006. Root dynamics of native savanna and introduced pastures in the Eastern Plains of Colombia. *Soil and Tillage Research* 87:28–38. doi: [10.1016/j.still.2005.02.038](https://doi.org/10.1016/j.still.2005.02.038)
- Truter WF; Botha PR; Dannhauser CS; Maasdorp BV; Miles N; Smith A; Snyman HA; Tainton NM. 2015. Southern African pasture and forage science entering the 21st century: Past to present. *African Journal of Range & Forage Science* 32:73–89. doi: [10.2989/10220119.2015.1054429](https://doi.org/10.2989/10220119.2015.1054429)
- Walter J; Grant K; Beierkuhnlein C; Kreyling J; Weber M; Jentsch A. 2012. Increased rainfall variability reduces

biomass and forage quality of temperate grassland largely independent of mowing frequency. Agriculture,

Ecosystems & Environment 148:1–10. doi: [10.1016/j.agee.2011.11.015](https://doi.org/10.1016/j.agee.2011.11.015)

(Received for publication 7 August 2019; accepted 17 January 2020; published 31 May 2020)

© 2020



Tropical Grasslands-Forrajes Tropicales is an open-access journal published by *International Center for Tropical Agriculture (CIAT)*, in association with *Chinese Academy of Tropical Agricultural Sciences (CATAS)*. This work is licensed under the Creative Commons Attribution 4.0 International ([CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)) license.