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Slash-and-burn effects on fine root biomass and productivity in a tropical dry forest ecosystem in México

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Abstract

We examined the effects of slash-and-burn of a tropical dry forest (TDF) and pasture establishment on fine root (≤1 mm) biomass and productivity. We also determined the seasonal changes of fine roots. The study was conducted in the coast of Jalisco, México where the dominant vegetation is tropical dry forest. Two 33 m×100 m experimental plots with undisturbed TDF were slashed-and-burned by local farmers. Two adjacent plots with TDF were established as control sites. After slash-and-burning of the experimental plots, these were seeded with three pasture grasses along with two local maize varieties. Root sampling was initiated in March 1993 and roots were collected monthly until February 1994. Eight soil samples were collected randomly in each plot at each sampling date to a depth of 10 cm with a soil corer. Each soil core was divided in three depths: 0–2, 2.1–5, and 5–10 cm. Roots were separated in two size categories: fine (≤1.0 mm) and small (1.1–5 mm). Fine roots were separated into live and dead. Productivity of fine roots for each depth was estimated from the biomass data. Live fine root biomass in the 0–10 cm profile decreased due to burning but 47% of the fine root mass loss was at the 0–2 cm depth. Dead fine root biomass diminished significantly only at this depth. Total fine root productivity and mortality was 42–45% higher in TDF than in pasture in the first 5 cm of soil. About 86 and 76% of the fine root productivity in TDF and pasture, respectively, occurred in the first 5 cm of soil. Fine root turnover rates were high and similar in both ecosystems. Live fine root biomass in TDF and pasture increased in response to rainfall, particularly in the first 5 cm of soil. Mean annual live fine root biomass was significantly greater in TDF than in pasture only at the 0–2 cm depth. Mean biomass per cm of soil was greater in the first 2 cm of the profile in both TDF and pasture and it represented one-third of the fine root biomass in the 0–10 cm profile. There were no significant differences of small roots (1.1–5.0 mm in diameter) due to treatment, seasonality or dynamics. Based on root turnover and root production, our results indicate that the relative importance of belowground processes for C supply to the soil in this TDF is greater than the aboveground return.

Keywords: Slash-and-burn; Fine roots; Tropical dry forest; Root biomass; Root productivity; México

1. Introduction

The fine root fraction is a large and dynamic portion of forest root systems and may account for a significant percentage of primary production (Nadelhoffer

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and Raich, 1992; Cuevas, 1995). For example, Nadelhoffer et al. (1985) reported that 27% of net primary production in nine temperate forests was allocated to fine roots, which was similar to that allocated to leaf litter (26%). Overall, root production may represent between 40 and 85% of net primary production (Fogel, 1985). Considerable effort has concentrated on prediction of C allocation to fine roots (Raich and Nadelhoffer, 1989) and, more recently for global modeling purposes, on understanding the abiotic factors that may control fine root growth (Vogt et al., 1996). Fine roots may contribute more carbon than aboveground parts to soil organic matter accumulation due to their higher annual inputs and faster decay rates (Vogt et al., 1991).

Tropical dry forests (TDF) have some of the highest rates of deforestation and conversion to cropland and pasture often follows slash-and-burn forest conversion (Houghton et al., 1991). The immediate effects of burning are superficial heating of the soil, partial or total destruction of the humus and surface soil organic matter (SOM), and alteration of the physical and chemical properties of the soil and of microbial populations (Sánchez, 1976; Raison, 1979, 1980; Kauffman et al., 1993; Maass, 1995; García-Oliva et al., 1999; Giardina et al., 2000). One long-term consequence of frequent burning is the reduction of site productivity (Lal, 1987; Srivastava and Singh, 1989).

In general, soils have poor thermal conductivity and the heat flux generated by wild fires diminishes rapidly with depth (Zinke et al., 1978; Ewel et al., 1981; Kauffman et al., 1993). However, heat flux from slash burning may be substantially greater than during natural fires resulting in increased temperatures that penetrate deeper in the soil profile (Raison, 1979). Although fine roots in tropical forests tend to concentrate in the upper layers of the soil, a large fraction of the root biomass may be protected from the effects of fire (Jenik, 1971; Stark and Spratt, 1977; Sanford, 1989; Castellanos et al., 1991; Ramakrishnan, 1992; Rentería, 1997). The protected biomass, along with the above-ground material that does not burn totally (e.g. stumps, trunks, coarse branches), constitutes the main source of organic matter for the soil after burning. Decomposition of remnant forest roots may contribute significantly to soil organic matter up to 11 years after pasture establishment (García-Oliva et al., 1994).

The use of slash-and-burn for converting TDF to cattle pastures is common in the Chamela region of Jalisco, México (González-Flores, 1992). As part of a larger study on the effects of slash-and-burn on TDF biomass and nutrient dynamics (see description in Miller and Kauffman, 1998), the objectives of this study were: (1) to determine the short-term changes in fine root biomass and productivity as a result of the slash-and-burn of a tropical dry forest and (2) to measure and contrast seasonal changes of fine roots in an undisturbed tropical dry forest and a pasture, seeded after slash-and-burning part of the undisturbed forest.

2. Materials and methods

2.1. Study site

This study was carried out in the Ejido San Mateo, municipality of La Huerta, in the coast of Jalisco, México (19°30′N;105°03′W). The dominant vegetation of the region is the tropical dry forest with about 1120 species of vascular plants in 544 genera and 124 families. Leguminosae, Euphorbiaceae and Compositae are the richest families (Lott, 1993). The study site, previous to slash-and-burn, included 104 woody species (>dbh 1 cm) but with only 13 species having a relative abundance >4% (Miller and Kauffman, 1998). Prior to cutting, the forest had an estimated height of 10 m and an aboveground biomass of ca. 118 Mg ha^{-1} (Kauffman et al., 1992). The air temperature in the region fluctuates very little during the year with a mean of 24.9°C. The rainy period extends from July to November with a mean of 679 mm (García-Oliva et al., 1995) and a dry period of 5–8 months, which gives the region a marked seasonality. Leaf flush is synchronous among most tree species and occurs after the start of the rainy season (Bullock and Solís-Magallanes, 1990). Rainfall during the study period (1993–1994) recorded at the nearby Estación de Biología Chamela (10 km from the study site) was 959 mm (Fig. 1), well above the mean. The soils at Chamela have been described as sandy-loams and sandy-clay-loams entisols (Solís, 1993), commonly with rocks in the superficial horizons and rhyolite parent material (Campo, 1995).

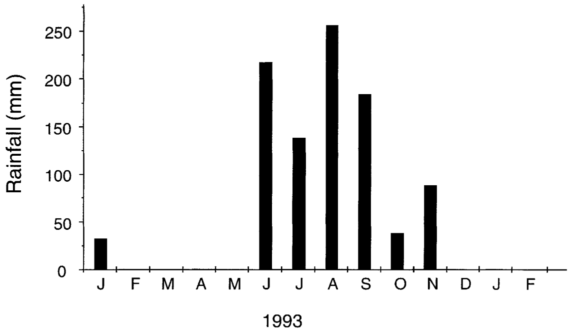

Fig. 1. Monthly distribution of rainfall during the study period at the Estación de Biología Chamela, Jalisco, México.

2.2. Treatment plots

The experimental plots were located on a 30% slope with a west aspect at 200 m.a.s.l. Two 33 m×100 m treatment plots with undisturbed TDF were slashed between 2 and 6 February 1993 by local farmers. The slashed vegetation was burned on April 23. In an adjacent, undisturbed TDF, two plots of similar size were established as control sites. Transformation of the TDF was completed in the first 15 days of June when three pasture grasses (*Cenchrus ciliaris* L., *Panicum maximum* Jacq. and *Andropogon gayanus* Kunth) were seeded along with two local maize (*Zea mays* L.) varieties. Following maize harvest, at the end of October and early November, cattle were allowed into the pasture.

2.3. Root sampling

Root sampling started in March 1993, prior to burning of the slashed plots, and roots were collected monthly (except June and September) until February 1994. The April sampling took place 1 day after the burn. In each of the four plots (two in TDF and two burned), eight soil samples were randomly collected with a soil corer 4.2 cm inside diameter to a depth of 10 cm. Each soil core was divided in three depths: 0–2, 2.1–5 and 5.1–10 cm. These samples were taken to the laboratory and stored at −2°C until root separation. Roots were hand separated with the aid of sieves, a magnifying lens and tweezers, and were placed on Petri dishes. They were classified into two size categories: fine (diameter <1.0 mm) and small (1.1–5.0 mm). Only fine roots were further separated into live and dead using a stereoscopic microscope. Criteria utilized for separation included color, turgidity, harshness, and flexibility. Roots were oven-dried at 70°C until constant weights were obtained.

Productivity, mortality, and disappearance of live and dead fine roots for each depth were estimated with the biomass data based on Fairley and Alexander (1985). Statistically different values between successive collection dates were used in the calculations. Fine root biomass turnover was calculated as the quotient between annual production and mean annual live fine root biomass for the study period (Frisel, 1981).

2.4. Statistical analysis

To determine the effects of slash-and-burn on fine root biomass and to describe and compare its dynamics in TDF and pasture, a repeated-measures analysis of variance (ANOVAR cf. Potvin et al., 1990) was used with fixed factors and a split-plot design. The plots were the subjects, time was the within-subject factor, and treatment the between-subject factor (Von Ende, 1993). This analysis took into account the correlation between dates and allowed comparison and fitting of the response patterns (shape of the curve). We obtained the Huynh–Feldt corrected probability (Huynh and Feldt, 1970) to decide rejection or acceptance of the differences with time and the time by treatment interactions. Data were transformed to log $(X+1)$ when assumptions for normality of residuals and homoscedasticity were not met. Values are presented in their original scale of measurement. Polynomial contrasts by soil depth were used to compare the response patterns in time (trends analysis) between treatments (Winer et al., 1992).

The ANOVAR was performed for each root diameter class in the 0–10 cm profile and at each soil depth. An additional ANOVAR was performed for the dry season months (March-May) to compare the effects of the slash-and-burn treatment with the dry season dynamics of the TDF. This analysis was performed at each of the three depths and for the live and dead fine roots. All analyses were performed with SYSTAT (Wilkinson, 1990) and Statistica (StatSoft, 1992).

3. Results

Live fine root biomass in the 0–10 cm profile decreased from 53.3 in March to 39.4 g m^{-2} in April (p=0.013), 1 day after the burn. The analyses of roots at separate depths indicated that 47% of this biomass loss was at 0–2 cm depth, where it decreased from 12.0 to 5.4 g m^{-2} ($F_{1,2}$=18.2; p=0.05) (Fig. 2b). Dead fine root biomass also diminished from 17.4 to 11.8 g m^{-2} ($F_{1,2}$=203.1; p=0.005) at 0–2 cm depth, although root mortality increased after that ($F_{1,2}$=21.9; p=0.04; Fig. 2b). The other depths did not show (p>0.1) immediate significant effects of burning either in the live or dead root fractions, although in all cases post-fire biomass values were smaller than pre-burn levels (Fig. 2d,f). Live fine root biomass at the 2–5 cm depth continued to decrease until May, when it was significantly lower than pre-burn biomass ($F_{1,2}$=8.84; p=0.096). Fine dead roots showed a consistent response to burning at the three depths, with a biomass decrease immediately after the burn and an increase in May (Fig. 2b,d and f).

Total fine root productivity and mortality were 42–45% higher in TDF than in pasture in the first 5 cm of

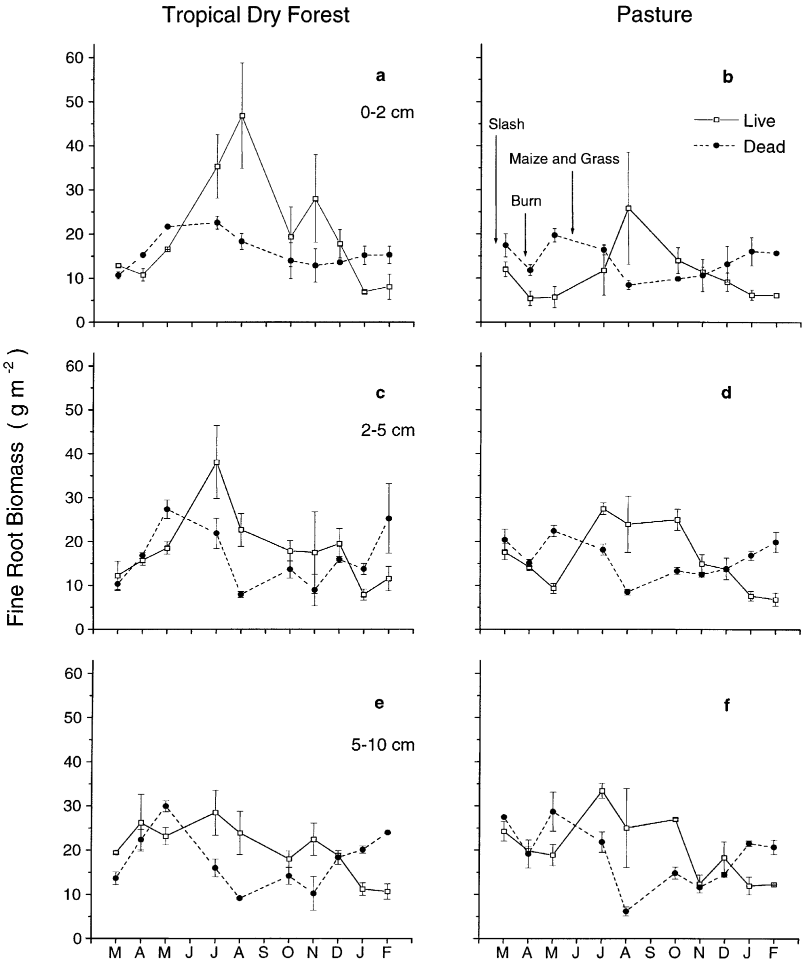

Fig. 2. Seasonal dynamics of live and dead fine root biomass (≤1 mm diameter) of tropical dry forest and pasture at three soil depths in the Chamela region, Jalisco, México: (a–b)=0–2 cm; (c–d)=2–5 cm, and (e–f)=5–10 cm. Each value represents the mean of two plots in which eight subsamples were collected per date. Vertical lines at each data point indicate S.E.=1.

Table 1
Fine root productivity (*P*), mortality (*M*), disappearance (*D*) and turnover (per year) in tropical dry forest and pasture of the Chamela region, Jalisco, México[a]

Depth (cm)	TDF				Pasture			
	P	*M*[b]	*D* (%)	Turnover	*P*	*M*[b]	*D* (%)	Turnover
0–2	75.8	66.7	90	3.8	41.6	39.3	95	3.9
2–5	71.2	72.5	59	3.9	41.1	46.4	92	2.6
5–10	33.5	48.9	69	1.7	34.8	41.3	100	1.7
Total	180.5	188.1	73		116.5	126	96	

[a] Values are given per depth increment and for the 0–10 cm profile. Productivity and mortality are in g m^{-2} per year.

[b] Mortality values greater than the productivity is an artifact of the calculations; it simply means that the live biomass died.

soil (Table 1). Approximately 86 and 76 of the productivity at the 0–10 cm depth in the TDF and pasture, respectively, occurred in the first 5 cm of soil. Root disappearance was higher overall in the pasture but turnover rates were similar in both ecosystems, except at the 2–5 cm depth, where TDF showed a 33% higher turnover than the pasture.

A partial ANOVAR for the dry season months (March, April, and May) indicated that live (two upper depths; $p<0.1$) and dead (the three depths; $p<0.07$, Huynh–Feldt corrected) fine root dynamics differed significantly between TDF and pasture. That is, the tendency of live and dead fine root biomass to increase in the TDF prior to the onset of rains (Fig. 2a,c) differed from the dynamics shown by fine root biomass (live and dead) in pasture. Surprisingly, during the dry season, the biomass of live fine roots at 0–10 cm depth in TDF increased significantly ($p=0.04$) from 44.5 in March to 58.2 g m^{-2} in May.

Live fine root biomass in both TDF and pasture increased significantly ($p<0.1$) after the onset of the rainy season at the 0–2 and 2–5 cm depths, reaching their maximum values in July–August (Fig. 2). At the 5–10 cm depth, it increased to a July maximum ($p=0.02$) only in pasture. Live fine root biomass in TDF and pasture decreased to a minimum between January and February. Seasonal dynamics at all depths, except 5–10 cm in TDF, were adequately described by a second-degree polynomial ($p<0.01$). Dead root biomass decreased in both TDF and pasture after May, reaching a minimum generally in August.

Mean annual live and dead fine root biomass in the 0–10 cm profile was similar in TDF and pasture (Table 2). Comparisons by depth indicated a significantly greater ($p=0.017$) live fine root biomass in TDF (20.2±12.8 g m^{-2}; mean and S.D.) than in pasture (10.8±6.1 g m^{-2}) only at 0–2 cm. There were no significant differences ($p>0.1$) in mean dead root biomass between TDF and pasture at any of the three depths of soil.

Although the mean relative biomass distribution in TDF indicated that between 32 and 35% of the fine root biomass occurred at each of the three depths, mean biomass per cm of soil (root density) was greater in the first 2 cm of the profile (Table 3). Also at this depth, the difference between TDF and pasture was more pronounced. Except for the live fine roots in

Table 2
Mean annual biomass (g m^{-2}) of live and dead fine roots in tropical dry forest and pasture of the Chamela region, Jalisco, México[a]

Depth and category	Biomass	
	TDF	Pasture
0–2 cm		
Live	20.2 ± 12.8	10.8 ± 6.1[b]
Dead	15.9 ± 3.8	13.9 ± 3.7
2–5 cm		
Live	18.1 ± 8.2	16.1 ± 7.4
Dead	16.2 ± 6.7	16.1 ± 4.3
5–10 cm		
Live	20.2 ± 5.9	20.3 ± 7.1
Dead	17.8 ± 6.5	18.6 ± 7.0
0–10 cm		
Live	58.5 ± 24.2	47.2 ± 18.5
Dead	49.8 ± 15.0	48.6 ± 14.7

[a] Values are given per depth increment and for the 0–10 cm profile with S.D.=1.

[b] Denotes a significant ($p<0.05$) difference between TDF and pasture.

Table 3
Mean fine root biomass concentration (g m^{-2} cm^{-1}) by depth in tropical dry forest and pasture of the Chamela region, Jalisco, México[a]

Category and depth	Biomass concentration	
	TDF	Pasture
Live		
0–2 cm	10.1±6.4	5.4±3.1
2–5 cm	6.0±2.7	5.4±2.5
5–10 cm	4.0±1.2	4.1±1.4
Dead		
0–2 cm	8.0±1.9	7.0±1.8
2–5 cm	5.4±2.2	5.4±1.4
5–10 cm	3.6±1.3	3.7±1.4

[a] Values are given with S.D.=1.

Table 4
Small root (1.1–5 mm) mean annual biomass (g m^{-2}) in the top 10 cm of soil in tropical dry forest (TDF) and pasture of the Chamela region, Jalisco, México[a]

Soil depth (cm)	Biomass	
	TDF	Pasture
0–10	115.5±25.0	101.9±28.7
0–2	18.3±4.1	21.3±8.3
2–5	32.6±13.4	30.8±7.8
5–10	64.5±20.3	49.7±19.8

[a] Values include live and dead roots with S.D.=1, n=10.

pasture, there was a general decrease in fine root density with depth.

The statistical analysis did not reveal significant differences of small roots (1.1–5.0 mm in diameter) due to treatment, seasonality or dynamics (Table 4). Mean annual biomass to 10 cm was 115.5±25.0 in TDF and 101.9±28.7 g m^{-2} in pasture (mean and S.D.).

4. Discussion

Soil temperatures after slash burning are substantially higher than in natural fires, so high temperatures are recorded up to several cm below the soil surface (Raison, 1979). Soil temperatures reached 200°C at 2 cm depth during our experimental burns in Chamela (Giardina et al., 2000). Fine root biomass (live and dead) showed a nearly 30% reduction in the 10 cm profile immediately after burning, but the most important changes were in the top 2 cm of soil where fine roots were largely combusted, resulting in a 41% decrease in fine root biomass. Slash-and-burn at this site also reduced colony forming units of fungi, yeast, and bacteria at this depth (García-Oliva et al., 1999). The changes in the dead-root fraction at the three depths before the onset of rains showed the effects of slash-and-burn clearly, with an immediate decline in root mass due to incineration and a subsequent increase due to root mortality as a secondary effect of burning.

Root productivity has been reported between 2000 and 5000 kg ha^{-1} per year in TDF (Murphy and Lugo, 1986). More recently, fine root productivities between 2180 and 4880 kg ha^{-1} per year have been estimated for TDF sites in India (0–15 cm soil depth; Singh and Singh, 1993; Roy and Singh, 1994). Fine root productivity of the Chamela TDF lies within the reported range: 1805 kg ha^{-1} per year in the 0–10 cm profile (this study) and 4230 kg ha^{-1} per year for a 40 cm depth (Kummerow et al., 1990). These results also indicate that about 35% of fine root production in the 40 cm profile or between 70 and 81% in the 10 cm profile occur in the first 5 cm of soil. Our productivity value may represent an underestimate since we did not consider subterranean herbivory, exudation, and exfoliation of root tissues (Fogel, 1985). On the other hand, the sequential core method employed may overestimate fine root productivity (Hendricks et al., 1993; Sundarapandian and Swamy, 1996). Nevertheless, our results for the first year allowed us to estimate that the conversion of TDF to pasture through slash-and-burn resulted in a 56% decrease of fine root productivity in the uppermost 5 cm of soil. Given the relevance of fine root inputs for soil organic matter (Vogt et al., 1991), this may represent a substantial decrease in organic C flow into the soil or at least a major relocation of production from the surface layers to deeper layers in the soil profile. The duration of the change in C inputs is an important land use issue that deserves further quantification.

The variability and periodicity of root growth are due to environmental causes, among which water availability is one of the most important (Vogt et al., 1991), particularly in dry forests (Kavanagh and Kellman, 1992). Fine roots at the 0–5 cm depth responded strongly to seasonality of rainfall. Live fine root biomass appeared to respond to the water and nutrient pulses that occur in dry seasonal ecosystems after initiation of rains (Lodge et al., 1994; Campo et al., 1998). Such a seasonal response of fine roots is well documented in tropical and subtropical forests (Kavanagh and Kellman, 1992; Silver and Vogt, 1993; Singh and Singh, 1993; Roy and Singh, 1995; Arunachalam et al., 1996; Sundarapandian and Swamy, 1996). At Chamela, proliferation of fine roots occurred 3 days after initiation of rains (Kummerow et al., 1990). We do not find, however, an adequate explanation for the increase in fine root biomass during the dry season months prior to the onset of rains. The lack of a seasonal biomass response from small roots (1.1–5 mm) in TDF and pasture is consistent with results of a previous study in the Chamela TDF (Kummerow et al., 1990). However, roots <25 mm have shown seasonal variations in other TDF sites (Singh and Singh, 1981).

Interestingly, despite 41% higher than average rainfall during the study period, a clear, seasonal biomass response was not evident at 5–10 cm in TDF, and productivity was only 44% of the productivity measured in the uppermost 2 cm of soil. High water and nutrient retention in the litter layer and in the first 5 cm of soil (Campo et al., 1998) may reduce root production at the lower 5–10 cm depth. Experimental evidence has shown that substantial water percolation (40%) below the first 5 cm of soil in the Chamela TDF requires the equivalent of 30 mm of rainfall reaching the litter layer, regardless of previous litter and soil moisture contents (Campo et al., 1998). However, 30 mm rainfall events have only a 20% probability in Chamela (García-Oliva et al., 1995) and nearly 28% of the annual precipitation is intercepted by the canopy and soil litter layers (J.M. Maass, unpublished). Thus, substantial water movement through the soil profile may not be a frequent episode in this TDF. We propose that the removal of the tree canopy and the soil litter layer through slash-and-burn may have caused a slight response to rainfall by fine roots at the 5–10 cm depth in pasture.

The accumulation of litter and soil organic matter on level microsites and topographic depressions, the standing dead trees or their remains and the channels created by the decaying thick roots, may create nutrient patches where fine roots proliferate (Roy and Singh, 1994). Fine root proliferation in fertile patches has been shown in different ecosystems (St. John et al., 1983; Cuevas and Medina, 1988; Jackson and Caldwell, 1989; Caldwell, 1994). Similarly, on a vertical gradient, the accumulation of litter on the surface soil promotes nutrient concentration and thus fine root accumulation in the upper layers of the soil (Berish, 1982; St. John, 1983; Bowen and Nambiar, 1984; Cuevas, 1995). In the nearby TDF at the Chamela Biological Station, the first 12 cm of soil hold 30.1 Mg ha^{-1} of SOM and approximately 80% of that occur in the top 6 cm (García-Oliva and Maass, 1998). Also, the first 5 cm of soil show higher concentrations of microbial C and N and inorganic P and N than the 5 cm immediately below (González-Ruiz, 1997). The larger variance of live fine root biomass during the rains than in the dry season in this study may reflect a horizontal spatial heterogeneity in the availability of nutrients, probably generated through the mechanisms outlined above. Moreover, fine root biomass, particularly in the undisturbed TDF, presented a well differentiated stratification with one-third of the biomass occurring in the upper one-fifth of the 10 cm soil profile. This vertical distribution, at a finer scale, agrees with that reported at another TDF site in Chamela (Kummerow et al., 1990), where more than 50% of the fine roots occurred in the first 10 cm of a 40 cm profile. It is also consistent with a more general pattern of root biomass concentration in the upper soil in tropical forests (Gower, 1987; Sanford, 1989; Arunachalam et al., 1996; Jackson et al., 1996; Sundarapandian and Swamy, 1996). Fine root concentration in the top 2 cm of soil should allow plants to respond to the short and erratic rains, so common in the Chamela region (García-Oliva et al., 1995) as well. Small roots (1.1–5 mm), however, did not show evident biomass concentration at this scale of the soil profile.

The mean turnover rates (k) for TDF (3.1 per year) and pasture (2.7 per year) in the top 10 cm of soil suggest that fine roots are an important source of soil carbon and nutrients in Chamela, even if we allowed for an overestimate in productivity. The turnover rate for leaf litterfall in the Chamela TDF is 0.72 per year (estimated from Martínez-Yrízar, 1995). Thus, mean residence time ($1/k$) of leaf litterfall is about four times longer than that of fine roots. In addition, the total litterfall production in Chamela is 3564 kg ha^{-1} per year (Martínez-Yrízar et al., 1996) approximated the estimated fine root productivity of 4230 kg ha^{-1} per year (Kummerow et al., 1990). Hence, based on root turnover and root production values, the relative importance of belowground processes for C supply to the soil in TDF is greater than the aboveground return. Therefore, a decrease in fine root production coupled to the decrease in aboveground productivity due to forest transformation may have important consequences for C sequestration, nutrient availability and recovery of TDF.

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