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Microbial activity in contrasting conditions of soil C and N availability in a tropical dry forest

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Abstract: We studied the relationships between soil nutrient availability and microbial biomass and activity of two contrasting soil conditions in a tropical deciduous forest in western Mexico. Hilltops have higher pH, water, dissolved organic C, and ammonium concentrations than hillslopes. Our main hypothesis was that soil microbial biomass, microbial activity and bacterium species richness would be higher in soils with high availability of nutrients. Fifteen soil cores, 0–5 cm depth, were taken in the dry, early rainy and rainy season, from each of the ten replicate plots in hilltop and hillslope positions located on three contiguous small watersheds. We measured moisture, C, N and P availability, potential C mineralization, net nitrification, microbial biomass and culturable heterotrophic and nitrifying bacteria in composite samples from each plot. Microbial biomass, species richness of culturable heterotrophic bacteria and C mineralization were significantly higher on hilltops than on hillslopes. Net nitrification was, in contrast, significantly higher on hillslopes than on hilltops and counts of culturable nitrifying bacteria were also significantly higher in the rainy-season samples. Hilltops and hillslopes had low similarity in composition of culturable heterotrophic bacterial species, particularly during the rainy season. The results suggested that C and N availability and seasonal changes in soil moisture are important controlling factors for some soil culturable-bacterial species, which may affect both C mineralization and nitrification in these tropical deciduous forest soils.

Key Words: C mineralization, culturable bacteria, dissolved organic carbon, microbial biomass, nitrification, tropical deciduous forest

INTRODUCTION

Water and nutrients are basic resources for growth and activity of soil microbial communities (Atlas & Bartha 2002). The availability of C and N favours heterotrophic micro-organisms specialized on labile nutrients, whereas low availability in these resources favours microbes that are able to break down more recalcitrant soil organic matter (Fontaine & Barot 2005, Fontaine *et al.* 2003, Hu *et al.* 1999). Consequently, microbial succession during soil organic matter decomposition depends on the enzymatic capabilities or resource specificity of the different micro-organisms involved in this process (Balser *et al.* 2002, Paul & Clark 1989). Other micro-organisms such as ammonia-oxidizing bacteria do not depend on organic matter directly, but differences in the availability of organic resources for heterotrophs may mediate N mineralization that provides them with ammonium (Booth *et al.* 2005, Verhagen & Laanbroek 1991). Altogether this suggests that both type and supply of resources may determine the structure of soil microbial communities.

The diversity and functioning of soil microbial communities is still poorly understood, despite the critical role of soil microbes in the regulation of nutrient cycling and ecosystem functioning (Balser *et al.* 2002). Some studies indicate that soil micro-organisms are ubiquitous (Finlay 2002, Finlay & Clark 1999), which may suggest that resource availability has little effect on microbial diversity and function, while other studies show that the size and composition of the microbial communities vary according to resource availability (Balser & Firestone

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2005, Carney & Matson 2005, Carney *et al.* 2004, Cookson *et al.* 2005, 2007; Waldrop *et al.* 2000). Microbial communities are therefore likely dependent on the environmental context and major limiting factors of each ecosystem.

Rainfall seasonality and habitat heterogeneity alter the availability of resources (water and nutrients) in tropical deciduous forests by affecting soil moisture and organic matter input (García-Oliva *et al.* 2003, Roy & Singh 1994). It has been suggested that water limits C and N mineralization and nitrification in these forests (García-Méndez *et al.* 1991, García-Oliva *et al.* 2003, Singh & Kashyap 2006, Singh *et al.* 1989), and recently that C availability is critical for C and N transformations (Montaño *et al.* 2007). Despite the fact that tropical deciduous forest covers around 42% of the world's tropical areas and around 47% of the forested area in Latin America (Murphy & Lugo 1986) there are few studies on bacterial ecology (Jha *et al.* 1996, Noguez *et al.* 2005, 2008; Singh & Kashyap 2006) in this highly threatened ecosystem (Miles *et al.* 2006). Noguez *et al.* (2005) reported, using TRFLP, that neighbouring hilltops and hillslopes within the tropical deciduous forest at the Chamela-Cuixmala Biosphere Reserve in Jalisco, Mexico shared only 54% of their bacterial Operational Taxonomic Units (OTU). Additionally, Noguez *et al.* (2008) found correlations between numbers of OTUs and soil N transformation in this ecosystem associated with two soil-aggregate size fractions. This suggested that the richness and composition of bacterial communities could be related to the availability of nutrients, which has been found to be different in these topographic positions (Montaño *et al.* 2007). However, there is little information in tropical deciduous forests about the links between resource availability and how variation in microbial communities may regulate soil biogeochemical processes in tropical forests. Despite it being well established that culturable bacteria represent only a small percentage (1–10%) of the bacteria species inhabiting soil (Rothschild 2006, Torsvik & Øvreås 2002), bacterial cultivation techniques in combination with biochemical (fatty acids) measurements could be an inexpensive, complementary approach to TRFLP in order to identify bacterial species and make comparative studies of species distribution (Nichols 2007).

This research was conducted to study some potential links among microbial activity, culturable bacterial communities and resource availability in two topographic positions with known differences in nutrient availability (hilltops and hillslopes) in a tropical deciduous forest in western Mexico. This approach provided an experimental setup to assess the response of microbial activity to natural differences in soil resources without soil disturbance effects or artificial manipulations. Our main hypothesis was that soil microbial biomass, as well as culturable heterotrophic and nitrifying bacteria would be higher in soils with high availability of soil resources and that the variation in bacterial communities would correlate with C mineralization and nitrification processes.

METHODS

Study area

The study area is located at the Chamela-Cuixmala Biosphere Reserve, near the Pacific Coast of Mexico (19° 29′ N, 105° 01′ W). Mean annual temperature is 24.6 °C and mean annual rainfall is 746 mm (1983–2004). Rainfall is mainly concentrated in a clearly marked wet season that lasts from June to October, and peaks in September (García-Oliva *et al.* 2002). The soils are poorly developed sandy clay loams, classified as Eutric Regosols in the FAO system (Cotler *et al.* 2002). The soil parent material is Tertiary rhyolite and the dominant clay is kaolinite (Campo *et al.* 2001). Soil organic matter (SOM) content is $< 5\%$ and is mainly concentrated in the top 5 cm (García-Oliva & Maass 1998). The vegetation is a highly diverse tropical deciduous forest (Lott 1993), where most tree species are leafless during the 7-mo dry season (Martínez-Yrízar *et al.* 1996).

Soil sampling

Soil samples were collected from an undisturbed forest located in three contiguous small watersheds that have been extensively studied for a long-term project on ecosystem function (Maass *et al.* 2002). These watersheds have the same geological age, parent material and different topographic units (slope and aspect; López-Blanco *et al.* 1999). We collected soil from two topographic positions (sites): hilltops (slope $= 1.2° \pm 0.7°$) and south-facing hillslopes (slope $= 26° \pm 3°$), distributed in the three watersheds. Soils have different concentrations of organic C (hilltop: 37 mg C g^{-1}, hillslope: 24 mg C g^{-1}) and dissolved organic C (244 μg C g^{-1} and 92 μg C g^{-1} for hilltop and hillslope, respectively; Montaño *et al.* 2007). Both sites have similar vegetation (Balvanera *et al.* 2002), annual solar radiation index (4356 MJ m^{-2} y^{-1} and 4426 MJ m^{-2} y^{-1} for hilltop and hillslope, respectively; Galicia *et al.* 1999), soil (Eutric Regosol) with similar texture, and water-holding capacity (Galicia *et al.* 1999).

Ten replicate sampling plots (10 × 15 m) were established in each of the two topographic positions (sites). The plots were located at least 300 m apart. Soil samples were collected in each plot on three sampling dates, in the dry (April), early rainy (June) and rainy (September) seasons in 2004, which had an annual precipitation

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of 578 mm. Fifteen undisturbed topsoil samples (0–5 cm depth), where most root and microbial activity is concentrated, were randomly collected from each plot at each sampling date. The samples were thoroughly mixed to form a composite soil sample per plot. Each soil sample was passed through a 2-mm sieve and one subsample was oven dried at 75 °C to determine soil moisture gravimetrically. The remaining soil was refrigerated at 10 °C until processing to prevent microbial proliferation and was processed in the laboratory within 10 d of sampling.

Soil chemical analyses

Soil pH was measured in deionized water (w:v 1:2) with an electric digital pH meter (Corning). Dried soil samples were ground with a pestle and mortar prior to total soil nutrient analyses. Total C was determined by combustion and coulometric detection. Dissolved organic carbon (DOC) was extracted in deionized water, filtered through a Whatman No. 42 paper (Jones & Willett 2006), and determined with a C analyser. Total N and P were determined after acid digestion by a macro-Kjeldahl method. Total N was determined by colorimetrical analysis and total P by the molybdate colorimetric method after ascorbic acid reduction (Murphy & Riley 1962). Inorganic N (NH_4^+ and NO_3^-) was extracted with 2 M KCl, followed by filtration through a Whatman No. 1 paper filter (Robertson *et al.* 1999), and determined colorimetrically by the phenol-hypochlorite method. Inorganic phosphorus was extracted with sodium bicarbonate (Pi; pH 8.5), and was determined by the molybdate-ascorbic acid method (Murphy & Riley 1962). All C forms were determined with a Carbon Analyser UIC Mod. CM5012, while N and P forms were determined colorimetrically using a Bran-Luebbe Auto Analyser III (Norderstedt, Germany).

Soil functional processes

Two microbial functional processes were considered: potential C mineralization and net nitrification. These microbial processes were measured in 16-d laboratory aerobic incubations. Samples of homogenized fresh soil were wetted to field capacity, placed in polyvinyl-chloride (PVC) tube cores and incubated in jars at 26 °C. The jars were regularly aerated for 1-h periods and every 48 h they were watered by weight to field capacity with deionized water (Robertson *et al.* 1999). Potential C mineralization was estimated as evolved CO_2-C collected in 1 M NaOH traps, which were changed every 2 d. Carbonates were precipitated by adding 1.5 M $BaCl_2$ and then titrated with 1 M HCl. Net nitrification during each incubation period was estimated as the difference between initial and final nitrate concentrations, which were analysed using the method described above.

Soil microbiological analyses

Microbial biomass C was determined with the chloroform fumigation-extraction method (Vance *et al.* 1987). Fumigated and non-fumigated samples were incubated for 24 h at 25 °C and constant moisture (Brookes *et al.* 1985). Microbial C was extracted from both fumigated and non-fumigated samples with 0.5 M K_2SO_4, filtered through a Whatman No. 42 paper, and measured using a C analyser (UIC, mod. CM5012). Microbial C was calculated by subtracting the extracted C in non-fumigated samples from that of fumigated samples and dividing by a *KEC* value of 0.45 (Joergensen 1996).

Culturable heterotrophic and nitrifying bacteria were quantified using 10 g of fresh soil from each composite sample and processing under sterile conditions. The soil was shaken with 90 ml of sterile deionized water, and aliquots (0.1 ml) of three ten-fold dilution series were used as inoculum to determine the culturable heterotrophic bacteria with the plate count method (Zuberer 1994), and the nitrifying bacteria with the most probable number method (MPN; Alexander 1982). For the quantification of culturable heterotrophic bacteria, 0.1 ml of the extract was transferred to plates with sterile Tryptic-Soy-Agar medium (TSA; Bioxon). Plates were incubated at 25 °C and colony-forming units (CFU) were counted after 3 d. Size, shape, colour, concavity, consistency and edge type of colonies of heterotrophic bacteria were used to characterize and group isolates morphologically, which allowed us to identify morphotypes in each plate. Colonies of each morphotype found were streaked repeatedly on TSA medium and incubated again at 25 °C for 80 h to obtain pure cultures. Pure cultures were then transferred into tubes containing solid TSA medium and stored at −40 °C until further biochemical identification based on fatty acid profiles. The ammonium oxidizer bacteria were quantified and determined using ammonium-calcium carbonate ($(NH_4)_2SO_4$, 0.5 g; K_2PO_4, 1.0 g; $FeSO_4 \cdot 7H_2O$, 0.03 g; NaCl, 0.3 g; $MgSO_4 \cdot 7H_2O$, 0.3 g; $CaCO_3$, 7.5 g; deionized sterile water) in agar culture medium (Bioxon). Five replicate culture tubes were used for each dilution. Each tube was inoculated with an extract of 0.1 ml and incubated for 6 wk at 30 °C. After the incubation period, each tube was tested for nitrite using Griess–Ilosvay reagent. The number of positive and negative tubes was used to calculate the CFU using a MPN table (Alexander 1982). We were not able to isolate nitrifying bacteria for identification by fatty acid methyl-esters (FAME).

Whole-cell FAMEs were used for biochemical identification of heterotrophic bacterial isolates. Gram

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positive and negative bacteria were estimated from the content of branched-chain or monoenoic and cyclopropane fatty acids, respectively. A loop full of cell material of late-log-phase cells of each isolate was transferred to a glass tube and fatty acids were extracted using standard and recommended procedures for gas chromatographic FAME analysis as described by Sasser (1990). Analysis was performed with an Agilent 6890 Plus Chromatograph and the Sherlock system software using the method TSBA41 and the library TSBA41 (Microbial Identification System MIDI Inc, Delaware, USA). A similarity index threshold of 0.30 was applied for acceptance of identification as recommended by the MIDI manual. Some isolates were not found in the identification library, but were considered as different bacterial morphotypes since they had a different composition of fatty acids. All bacterial isolates were incorporated to the bacteria strain collection of the Research Centre Flakkebjerg in Denmark.

Culturable bacterial-species richness was estimated in terms of the observed species and morphotypes number (S_{obs}; Magurran 2004), which had different composition of fatty acids but rendered no species name using MIDI. We used a dissimilarity index by cluster analysis of the species composition between sites (hilltop and hillslope) and sampling dates (seasons) to estimate the proportion of bacterial species shared between sites. For this analysis we used Ward´s Method with Euclidean distances based on species presence-absence data. The index is equal to 0 in cases of complete similarity, that is when two sets of species are identical, and 100% if the sites have no species in common (Magurran 2004).

Statistical analyses

All data were expressed on a dry-weight basis unless otherwise stated. Data were subjected to a repeated-measures analysis of variance (RMANOVA), where site (hilltop or hillslope) was considered as the main effect and sampling dates were treated as repeated measures. A Greenhouse–Geisser correction was estimated for the sphericity assumption of the time factor (von Ende 1993), but it did not modify the significance of any P values. A Tukey's HSD multiple comparison test was used when statistical differences were observed with RMANOVA (Sokal & Rohlf 1995). The data were transformed (logarithm or square root) to satisfy ANOVA assumptions when required (Sokal & Rohlf 1995), however, results are reported in their original scale of measurement. A stepwise regression analysis was used to assess the importance of available nutrients in relation to microbial biomass and bacterial communities and of both nutrients and bacterial communities on soil C mineralization and nitrification. All statistical analyses were performed with Statistica ver. 6.0 software (StatSoft, Tulsa, USA), and a $P \leq 0.05$ was considered significant.

RESULTS

Soils had a slightly acid pH and hillslope soils had a lower pH than the hilltop soils in the dry and the early rainy seasons (Table 1). Hilltop soils had higher soil moisture than the hillslope soils. In both sites, the maximum soil moisture was recorded in the early rainy season (Table 1). Hilltop soils had higher total C than the hillslope soils. The total N and P concentrations and C:P ratios were not affected by site or sampling date, but the hilltops had higher C:N ratios than the hillslopes (Table 1).

Dissolved organic carbon (DOC) concentrations were in general higher at the hilltop soils than at the hillslope soils (Table 2). A significant date × site interaction indicated that DOC was more variable among sampling dates in the hilltop than in the hillslope soils (Table 2) though it showed the same trend decreasing from the dry to the early rainy season and increasing to the middle of the rainy season. Ammonium concentrations were also higher in the hilltop than in the hillslope soils on the three sampling dates, and decreased progressively from the dry towards the rainy season in both sites. In contrast, nitrate concentrations did not vary between sites and were lowest in the dry season. The hillslope soils had higher NO_3:NH_4 ratios than the hilltop soils, with the highest NO_3:NH_4 ratios in the rainy season (Table 2). There was a significant interaction for extractable phosphorus concentration indicating that the P_i availability changed in a different way with time for both soils, with no clear trend suggesting more P availability in a given site or sampling date (Table 2). Hilltop soils had higher potential C mineralization (CO_2-C evolved) than the hillslope soils, and the samples collected in the dry season had the highest potential C mineralization (Figure 1a). Net nitrification was consistently greater for the hillslope soils than for the hilltop soils, and the highest nitrification was recorded in samples collected in the early rainy and rainy seasons (Figure 1b).

Microbial C was higher in the hilltop soils than at the hillslope soils, and decreased from the dry season to the rainy season in both sites (Figure 2a). The colony-forming units (CFU) of culturable heterotrophic bacteria were higher in the hilltop than in the hillslope soils in the early rainy season. In both sites the CFU of heterotrophic bacteria were lowest in the rainy season, and only in the hilltop soils a peak was observed in the early rainy season (Figure 2b). In contrast, the most probable number (MPN) of nitrifying bacteria was higher in the hillslope than in the hilltop soils only in the rainy season, and increased from the dry season to the rainy season in both sites (Figure 2c).

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Table 1. Mean ± SE for pH, moisture, total nutrients, and C:nutrient ratios for hilltops and hillslopes in a tropical deciduous forest of Chamela Jalisco, Mexico. Values followed by a different uppercase letter (A and B) indicate that means are significantly different ($P \leq 0.05$) between sites (hilltop vs hillslope) within sampling date. Similarly, different lowercase letters (a, b, c) indicate that means are significantly different ($P \leq 0.05$) among sampling dates within a site. RMANOVA F-ratios with: ns = not significant. * $P < 0.05$; ** $P < 0.01$ and *** $P < 0.001$.

	Sampling dates (season)			*F*-ratios: source of variation		
	Dry	Early rainy	Rainy	Site (S)	Date (D)	D × S
pH (water:soil 2:1)				9.7^{**}	4.6^{*}	3.3^{*}
Hilltop (high C)	6.6 ± 0.1^{Aa}	6.8 ± 0.1^{Aa}	6.6 ± 0.1^{Aa}			
Hillslope (low C)	6.2 ± 0.1^{Bb}	6.5 ± 0.1^{Ba}	6.5 ± 0.1^{Aa}			
Moisture (%)				18.2^{**}	195.6^{***}	2.6^{ns}
Hilltop (high C)	2.7 ± 0.8^{Ac}	15.9 ± 0.5^{Aa}	6.6 ± 0.4^{Ab}			
Hillslope (low C)	1.8 ± 0.6^{Bc}	12.3 ± 0.9^{Ba}	4.8 ± 0.3^{Bb}			
Total soil C (mg C g^{-1})				35.8^{***}	0.24^{ns}	0.31^{ns}
Hilltop (high C)	30.4 ± 2.4^{Aa}	31.7 ± 1.1^{Aa}	30.8 ± 1.8^{Aa}			
Hillslope (low C)	21.3 ± 1.8^{Ba}	21.5 ± 1.9^{Ba}	23.4 ± 1.6^{Ba}			
Total soil N (mg N g^{-1})				1.7^{ns}	0.59^{ns}	0.58^{ns}
Hilltop (high C)	3.3 ± 0.2^{Aa}	3.0 ± 0.2^{Aa}	3.3 ± 0.1^{Aa}			
Hillslope (low C)	2.9 ± 0.2^{Aa}	3.0 ± 0.2^{Aa}	3.2 ± 0.1^{Aa}			
Total soil P (mg P g^{-1})				3.6^{ns}	4.7^{ns}	0.20^{ns}
Hilltop (high C)	0.24 ± 0.02^{Aa}	0.23 ± 0.02^{Aa}	0.26 ± 0.02^{Aa}			
Hillslope (low C)	0.20 ± 0.02^{Aa}	0.20 ± 0.02^{Aa}	0.22 ± 0.02^{Aa}			
Total soil C:N				12.8^{**}	0.46^{ns}	0.76^{ns}
Hilltop (high C)	9.2 ± 0.9^{Aa}	11.1 ± 1.3^{Aa}	9.3 ± 0.6^{Aa}			
Hillslope (low C)	7.2 ± 0.5^{Ba}	7.3 ± 0.7^{Ba}	7.5 ± 0.5^{Ba}			
Total soil C:P				3.0^{ns}	1.1^{ns}	0.64^{ns}
Hilltop (high C)	137 ± 17^{Aa}	145 ± 15^{Aa}	118 ± 12^{Aa}			
Hillslope (low C)	111 ± 13^{Aa}	111 ± 11^{Aa}	107 ± 8^{Aa}			

Culturable bacterium species richness was higher at the hilltop than at the hillslope soils in the dry and early rainy seasons, but the sites had similar bacterial richness in the middle of the rainy season (Site × Date, $F = 5.3$, $P < 0.01$, Appendix 1). The highest culturable bacterium richness was found in the rainy season in both sites. We documented a total of 28 genera with 61 bacterial species in the two sites. Nineteen species were common to both sites and 47% of the total species was found only in the hilltop and 31% only in the hillslope soils. *Bacillus*, *Brevibacillus* and *Paenibacillus* species accounted for 31% of the bacterial isolates found. From the total

Table 2. Mean ± SE for seasonal variation in dissolved organic carbon, ammonium, nitrate, and bicarbonate extractable phosphorous concentrations, and nitrate:ammonium ratios for hilltops and hillslopes in a tropical deciduous forest of Chamela Jalisco, Mexico. Values followed by a different uppercase letter (A and B) indicate that means are significantly different ($P \leq 0.05$) between sites (hilltop vs hillslope) within sampling date. Similarly, different lowercase letters (a, b, c) indicate that means are significantly different ($P \leq 0.05$) among sampling dates within a site. DOC = dissolved organic carbon, Pi = inorganic phosphorus extracted with sodium bicarbonate. RMANOVA *F*-ratios with: ns = not significant. * $P < 0.05$; ** $P < 0.01$ and *** $P < 0.001$.

	Sampling dates (season)			*F*-ratios: source of variation		
	Dry	Early rainy	Rainy	Site (S)	Date (D)	D × S
DOC (μg C g^{-1})				54.4^{***}	70.7^{***}	10.7^{**}
Hilltop (high C)	522 ± 43^{Aa}	134 ± 8.0^{Ac}	246 ± 15^{Ab}			
Hillslope (low C)	278 ± 12^{Ba}	111 ± 9.0^{Ab}	147 ± 28^{Bb}			
NH_4 (μg N g^{-1})				11.7^{**}	40.1^{***}	1.7^{ns}
Hilltop (high C)	17 ± 1^{Aa}	11 ± 0.6^{Ab}	6 ± 1^{Ac}			
Hillslope (low C)	14 ± 1^{Ba}	6 ± 1.0^{Bb}	3 ± 1^{Bc}			
NO_3 (μg N g^{-1})				4.0^{ns}	5.1^{*}	0.23^{ns}
Hilltop (high C)	16 ± 2^{Ab}	26 ± 4^{Aa}	20 ± 5^{Aa}			
Hillslope (low C)	19 ± 1^{Ab}	29 ± 5^{Aa}	27 ± 3^{Aa}			
NO_3:NH_4 ratios				8.9^{***}	19.7^{***}	2.6^{ns}
Hilltop (high C)	1.0 ± 0.1^{Bc}	2.4 ± 0.4^{Bb}	6.1 ± 2^{Ba}			
Hillslope (low C)	1.4 ± 0.1^{Ac}	6.5 ± 2.1^{Ab}	11.4 ± 2^{Aa}			
Pi (μg P g^{-1})				3.1^{ns}	21.6^{**}	14.2^{***}
Hilltop (high C)	40 ± 2^{Aa}	29 ± 4^{Bb}	32 ± 3^{Ab}			
Hillslope (low C)	37 ± 3^{Aa}	42 ± 8^{Aa}	17 ± 3^{Bb}			

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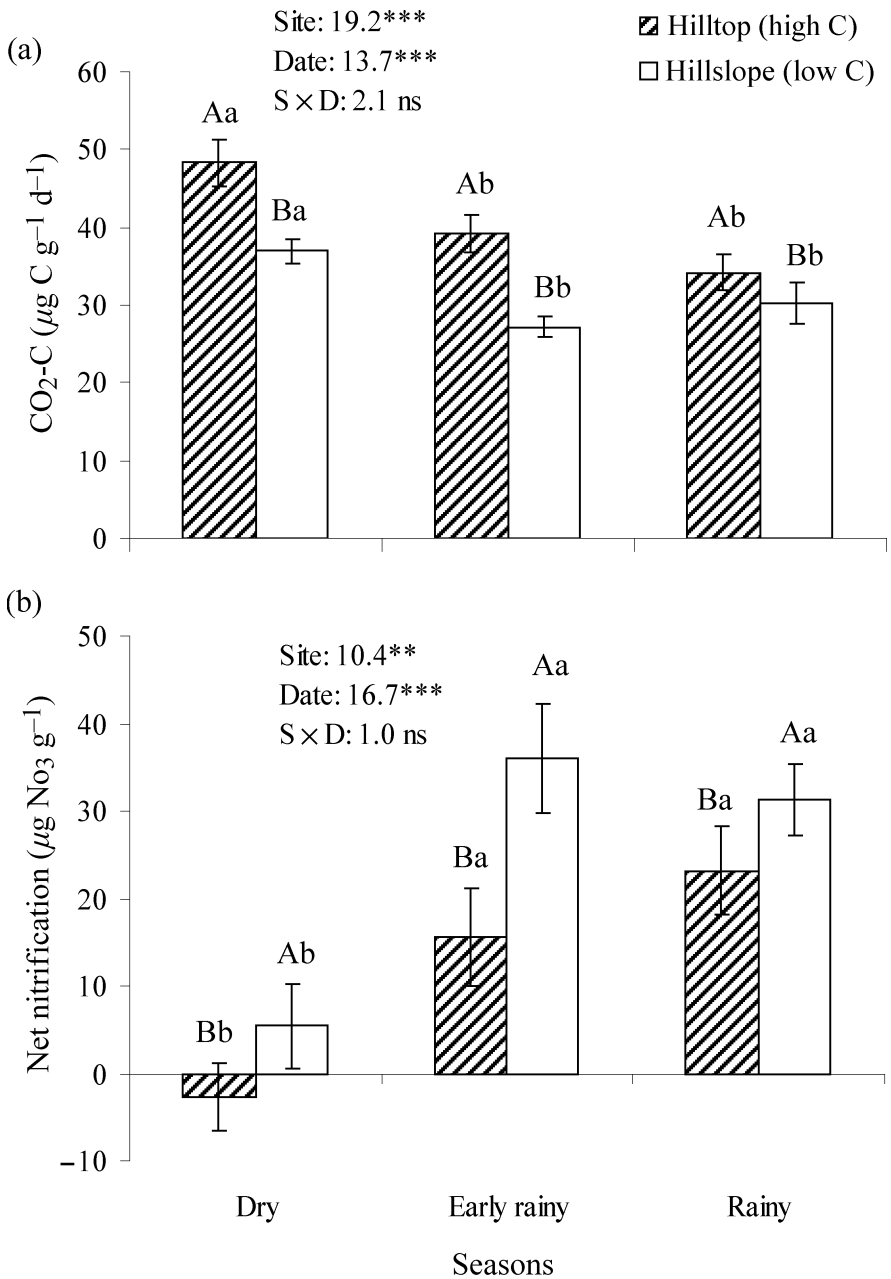

Figure 1. Seasonal variation (mean ± SE) of potential C mineralization rate (CO_2-C) (a), and net nitrification (b) after a 16-d incubation period in hilltop and hillslope soils (high C and low C respectively) from a tropical deciduous forest at Chamela, Mexico. Different uppercase letters (A and B) indicate that means are significantly different ($P \leq 0.05$) between sites (hilltop vs hillslope) within sampling date (season). Similarly, different lowercase letters (a, b, c) indicate significant differences ($P \leq 0.05$) among sampling dates within a site. RMANOVA F-ratios with: ns = not significant, * $P \leq 0.05$; ** $P \leq 0.01$, *** $P \leq 0.001$.

number of culturable heterotrophic bacterial species, 67% were Gram-positive and 33% were Gram-negative bacteria (Appendix 1). The lowest dissimilarity index values (23%) of the culturable bacterium composition were found at the hillslopes of the dry and early rainy seasons, while the hilltops of the early rainy and rainy seasons had the highest dissimilarity (58%; Figure 3).

Stepwise regression analysis to assess the importance of available nutrients in relation to microbial biomass and bacterial communities and of both nutrients and bacterial communities on soil C mineralization and nitrification showed some significant but in general weak correlations among most variables (Table 3). In general, both DOC and ammonium were positively related to microbial biomass (C microbial), culturable heterotrophic bacteria,

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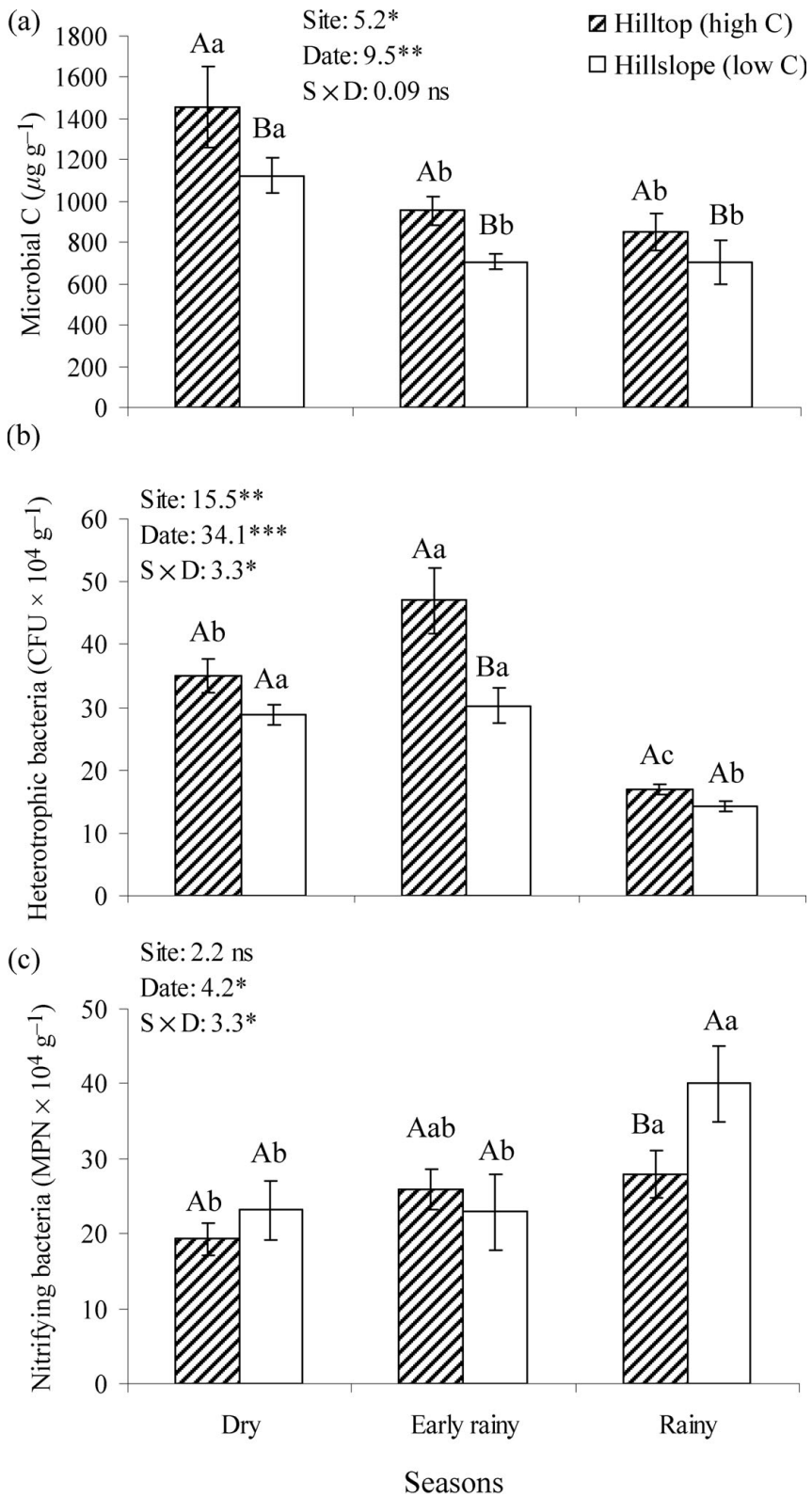

Figure 2. Seasonal variation (mean ± SE) in microbial carbon and culturable bacterium counts (CFU) (a), heterotrophs (b) and nitrifiers (c) in hilltop and hillslope soils (high C and low C respectively) in a tropical deciduous forest of Chamela, Mexico. Different uppercase letter (A and B) indicate that means are significantly different ($P \leq 0.05$) between sites (hilltop vs hillslope) within sampling date (season). Similarly, different lowercase letters (a, b, c) indicate significant differences ($P \leq 0.05$) among sampling dates within a site. RMANOVA F-ratios with: ns = not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

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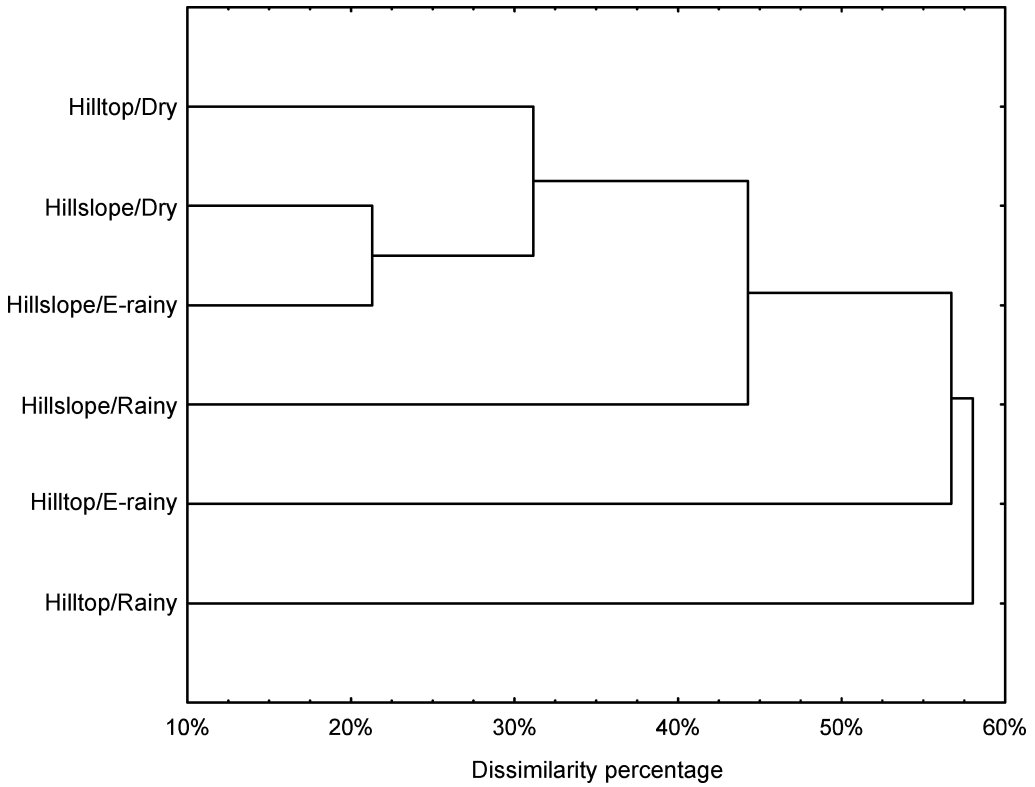

Figure 3. Dissimilarity cluster (Ward's method, based on Euclidean distances) showing differences in heterotrophic bacterial composition in the hilltop and hillslope soils (high C and low C respectively) collected in Dry, Early rainy (E-rainy) and Rainy seasons (sampling date) in a tropical deciduous forest of Chamela, Mexico.

and potential C mineralization, but inversely related to net nitrification and the culturable nitrifying bacteria.

DISCUSSION

The results suggested that resource availability is an important controlling factor for both microbial growth and culturable bacterial species richness in this tropical deciduous forest. Dissolved organic carbon and ammonium accumulation on the hilltops compared with hillslopes correlated with higher microbial growth most likely due to higher availability of organic C for heterotrophic micro-organisms as previously suggested (García-Oliva *et al.* 2003, Montaño *et al.* 2007). The increase in nitrifying bacterial colonies in soil with less ammonium and DOC in the rainy season suggests that low C availability reduced both growth and dominance of the heterotrophic bacteria and favoured nitrifiers. Nitrifiers obtain energy from ammonium oxidation, not

Table 3. Stepwise multiple regressions, correlation coefficients and significance levels to detect controls on microbial biomass, culturable bacterium communities and microbial activity in a tropical deciduous forest of Mexico. Regression analyses were performed on pooled data across the sites and seasons (forward procedure with n = 60). In the analyses all soil variables were incorporated in the model to detect the main controls on Y-variable with two exceptions: for microbial variables both mineralization and nitrification were excluded and for both C mineralization and nitrification the manipulated variables during the incubation were not considered. [a]DOC = dissolved organic carbon, HB = culturable heterotrophic bacteria. Significant: * $P < 0.05$; ** $P < 0.01$ and *** $P < 0.001$.

Y-variable	Log X-variable	r	r^2
Microbial biomass	DOC	0.64	0.44***
Heterotrophic bacterial colonies	Ammonium	0.53	0.39*
	DOC	0.20	
Nitrifying bacterial colonies	DOC	−0.32	0.19*
Potential C-mineralization	DOC	0.59	0.41***
	HB counts	0.24	
Net nitrification	DOC	−0.46	0.29*
	HB counts	−0.18	

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from organic C (Booth *et al.* 2005, Verhagen & Laanbroek 1991), and this could explain the decline in ammonium and the increase in the NO_3:NH_4 ratio and net nitrification in the hillslope soils, as suggested in a previous study conducted in this forest (Montaño *et al.* 2007). However, there were no significant differences in nitrate concentrations, and this might be explained by leaching or denitrification increasing variability. Additionally, it is also possible that our results did not reflect total nitrate production due to the limitation of net measurements. Overall, it seems that, as hypothesized, the differences in C mineralization and nitrification between our study sites could be due to the presence of different bacteria, which in turn could be regulated by C availability (Cleveland *et al.* 2007, Cookson *et al.* 2007, Fierer *et al.* 2007).

Similarly, the higher richness of culturable heterotrophic bacterial species on the hilltops could be also associated to the abundance of resources, because it may provide a broader range of different niches to be occupied by more bacterial species (Begon *et al.* 1986, Diamond 1988, Torsvik *et al.* 2002). This agrees with studies in other contexts showing that soils with more resource availability have higher microbial diversities (Bossio *et al.* 1998, Torsvik & Øvreås 2002, Zhou *et al.* 2002). Nevertheless, further work is required to test this hypothesis because our measurements cannot resolve if DOC and nutrients were a substrate or a product of bacterial richness and microbial activity, in order to establish causation.

Bacterial richness showed an opposite seasonal trend to microbial biomass that may be explained in different ways: (1) a few active and fast-growing bacteria are able to use available nutrients when water availability is low, and (2) bacterial richness increases in the rainy season but growth is limited by low DOC and nutrient availability, and reduced by grazing. The increase in microbial C in the dry season, when an accumulation of DOC, P and NH_4^+ also occurs, has already been documented in tropical deciduous forests (Campo *et al.* 1998, Montaño *et al.* 2007, Singh *et al.* 1989). This may be due to the presence of fast-growing bacteria that are resistant to drought conditions and have high efficiency in the utilization of labile resources (Atlas & Bartha 2002). The rainy-season samples with lower labile resource availability, in contrast, showed higher species richness but lower growth. It is likely that these bacteria use most of their resources for complex organic matter decomposition to obtain nutrients at the expense of growth and reproduction (Atlas & Bartha 2002, Fontaine *et al.* 2003, Waldrop *et al.* 2000). The main functional implication of the impairment of microbial biomass and bacterial richness is that the conservation of nutrients in microbial biomass during the dry season (Singh *et al.* 1989) would depend on a few bacterial species functioning well under high nutrient, but low water availability.

The predominance of Gram-positive bacteria in our study sites could be explained by the seasonal fluctuations in water and nutrients that occur in this forest, which may act as stress factors that select spore-forming Gram-positive bacteria, more resistant to high stress and heterogeneous, unpredictable conditions (Atlas & Bartha 2002, Paul & Clark 1989, Williams & Rice 2007). Gram-positive bacteria are considered as more capable of metabolizing complex C substrates than Gram-negative bacteria, which are known for being fast-growing and highly competitive for simple substrates (Paul & Clark 1989, Waldrop *et al.* 2000). The higher abundance of Gram-positive bacteria in these soils is supported by data obtained using fatty acid biomarkers, a culture-independent quantitative measure of soil microbial groups, in a microbial community study conducted later in the same plots (Gavito *et al.* unpubl. data).

The low similarity between sites in bacterial species composition may indicate that not all heterotrophic bacteria respond in the same way to resource availability. Studies conducted in the same forest, revealed also that hilltops had higher bacterial diversity than hillslopes, and had 36% and 26%, respectively, of unique bacterial Operational Taxonomic Units (OTU) using terminal restriction fragment-length polymorphism (TRFLPs) (Noguez *et al.* 2005, 2008). The results from Noguez *et al.* (2005) suggest that soil bacteria are non-ubiquitous and respond to resource distribution in this forest. The presence and activity of some species of bacterium in a given site could depend on adaptations to specific resource limitations, as shown in other studies (Belotte *et al.* 2003, Cleveland *et al.* 2007, Goddard & Bradford 2003). However, an experimental labelling approach to link unequivocally diversity and function and further studies testing resource use by specific species or functional groups of micro-organisms are still needed to understand nutrient cycling controls in tropical dry forest soils. In conclusion, our study provides a data set that suggests that C and N availability and seasonal changes in soil moisture may control microbial community dynamics, and consequently C mineralization and nitrification in these tropical deciduous forest soils.

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Appendix 1. List of heterotrophic bacterial species identified in the hilltop and hillslope soils of a tropical deciduous forest of Chamela, Mexico. Total relative frequencies (F %) per species at each site and date in which a species was recorded: D = dry, ER = early rainy, R = rainy seasons, as well as bacterial species richness and total common species between sites are showed. Bacterial identification was performed with the commercial Sherlock Microbial Identification System (MIDI) based on fatty acid profiling. MIDI bacteria names are based on the List of Prokaryotic names with Standing in Nomenclature (LPSN), available at the public website http://www.bacterio.cict.fr

	Hilltop (high C)				Hillslope (low C)				
Species	F (%)	D	ER	R	F (%)	D	ER	R	Common species
Gram-positive									
Arthrobacter globiformis	3.6	×			0.0				
Arthrobacter mysorens	4.5			×	0.0				
Bacillus cereus	14.1		×	×	40.7	×	×	×	×
Bacillus cereus kurstakii	2.3			×	0.0				
Bacillus circulans	15.5	×	×		6.1			×	×
Bacillus lentimorbus	9.5	×	×		0.0				
Bacillus megaterium	23.5	×	×	×	47.7	×	×	×	×
Bacillus simplex	0.0				5.3		×		
Bacillus thuringiensis canadensis	0.0				3.0			×	
Bacillus thuringiensis israelensis	0.0				10.5		×		
Bacillus thuringiensis kurstakii	7.0		×	×	16.6		×	×	×
Bacillus thuringienesis dendrolium	0.0				16.7	×			
Brevibacillus brevis	9.4	×		×	3.0			×	×
Brevibacillus epidermidis	6.8			×	3.0			×	×
Brevibacillus laterosporus	16.7	×	×		36.4	×		×	×
Brevibacillus laterosporus linens	0.0				3.0			×	
Brevibacterium epidermidis	0.0				3.0			×	
Brevibacterium iodinum	0.0				3.0			×	
Brochothrix campestris	2.4		×		0.0				
Brochothrix thermosphacta	0.0				3.0			×	
Cellulomonas cartae	9.4		×	×	0.0				
Cellulomonas turbata	10.6	×	×	×	0.0				
Kocuria varians	10.4	×		×	9.1			×	×
Micrococcus luteus	6.8			×	6.1			×	×
Microbacterium imperiale	0.0				5.3		×		
Nocardia asteroides	2.4		×		0.0				
Paenibacillus glucanolyticus	2.4		×		0.0				
Paenibacillus macerans	6.0	×	×		5.3		×		×
Paenibacillus pabuli	2.3			×	6.1			×	×
Paenibacillus polymyxa	7.1		×		3.0			×	×
Paenibacillus thiaminolyticus	3.6	×			6.1			×	×
Rathayibacter rathayi	0.0				3.0			×	
Salmonella bongori	4.5			×	0.0				
Staphylococcus saprophyticus	9.4	×		×	8.3		×	×	×
Staphylococcus xylosus	0.0				8.3		×	×	
Streptoverticillium reticulum	2.4		×		0.0				
morphotype 18	2.4		×		0.0				
morphotype 19	2.4		×		0.0				
morphotype 21	2.4		×		0.0				
morphotype 51	6.9		×	×	0.0				
morphotype 56	7.0		×	×	0.0				
Gram-negative									
Acinetobacter baumannii	9.5	×	×		0.0				
Acinetobacter haemolyticus	9.5	×	×		0.0				
Bergeyella zoohelcum	0.0				3.0			×	
Cedecea neteri	2.3			×	0.0				
Chryseobacterium balustinum	2.4		×		6.1			×	×
Enterobacter cancerogenus	2.3			×	0.0				
Escherichia coli	4.5			×	0.0				
Gordona amarae	4.7		×	×	0.0				
Klebsiella pneumoniae	4.5			×	5.3		×	×	×
Klebsiella pneumoniae ozaenae	6.8			×	0.0				
Klebsiella trevisanii	2.3			×	0.0				
Kluyvera ascorbata	2.3			×	10.5		×		×
Pseudomonas putida Biotype A	0.0				3.0			×	
Salmonella choleraesuis	2.3			×	5.3		×	×	×
Salmonella choleraesuis diarizonae	2.3			×	5.3		×	×	×

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Appendix 1. Continued.

	Hilltop (high C)				Hillslope (low C)				
Species	F (%)	D	ER	R	F (%)	D	ER	R	Common species
Sphingobacterium multivorum	18.9	×	×	×	0.0				
Sphingobacterium spiritivorum	2.3			×	0.0				
Xanthobacter agilis	2.4		×		0.0				
morphotype 22	2.4		×		0.0				
morphotype 42	4.8		×		0.0				
Seasonal bacterial richness		14	27	28		4	13	26	
Exclusive species per site		29				13			
Total species per site		48				32			19

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