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SOIL CARBON, NUTRIENTS, AND MYCORRHIZAE DURING CONVERSION OF DRY TROPICAL FOREST TO GRASSLAND

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Abstract. Wildfires and alien grass invasion threaten dry tropical forests throughout Central America. Efforts to preserve and restore these forests will require a better understanding of how conversion to grassland changes key belowground processes and organisms such as soil organic matter, nutrient cycling, and mycorrhizae. We studied forest, edge, and grassland soils from five 60-m transects perpendicular to abrupt forest–grassland boundaries in Guanacaste Province, Costa Rica. Nutrient concentrations, N mineralization dynamics, and mycorrhizal fungal communities were compared across vegetation type (forest, edge, and grassland). The dynamics of N mineralization were measured in year-long laboratory incubations, and the diversity of mycorrhizal fungal communities was assessed from populations of soil-borne spores. Soil C, N, and K were lower, while many base cations and micronutrients were higher in grassland plots than in forest plots. Although differences in the *quantity* of total soil C and N occurred mainly in the forest-to-edge transition, differences in the *quality* of soil organic matter, as reflected by soil C:N ratios and mineralization rates, occurred in the edge-to-grassland transition. Beta diversity of mycorrhizal spore communities (measured by Sorenson's similarity index) was lower in the grassland plots than in the forest plots, indicating that grass invasion had caused some convergence. However, total spore density and alpha diversity of mycorrhizal spore communities (measured by species richness and Simpson's diversity index) were not altered by wildfires and grass invasion. These results suggest that persistence and regeneration of forest plant species in the grasslands may not be constrained to a significant degree by the lack of mycorrhizal symbionts. These grasslands appear to be sustainable, alternative stable states for these areas. Positive feedbacks between the alien grassland vegetation and both fire and nutrient cycling maintain and reinforce this alternative state.

Key words: Costa Rica; deforestation; dry tropical forests; fire; grass invasion; Hyparrhenia rufa; *mycorrhizae; nitrogen mineralization; nutrient dynamics; soil organic matter; species diversity.*

INTRODUCTION

Dry tropical forests once covered more than half of the tropics but today only small fragments remain (Murphy and Lugo 1986). In Pacific Mesoamerica roughly 0.1% of these dry forests are currently intact, and accelerating rates of deforestation, wildfires, and invasion of alien grasses threaten remaining forest remnants (Janzen 1988). Aboveground changes during deforestation and grass invasion are generally obvious. However, understanding unseen belowground changes is equally important to efforts to preserve and restore dry tropical forests. Deforestation and the consequent loss of biodiversity may alter key processes, such as nutrient cycling and soil organic matter (SOM) development, on which sustainable ecosystem functioning (e.g., maintenance of SOM and nutrient pools, and resiliency of primary production) depends. Furthermore, the loss of critical organisms, such as mycorrhizal fungi, has been linked to altered ecosystem function elsewhere (Amaranthus 1992, Perry et al. 1989).

Mycorrhizae have long been recognized as important symbioses in tropical forest interactions (e.g., McLean 1919, St. John 1980). Most plant species rely on mycorrhizae for uptake of nutrients and water; these associations are obligate for many tropical plants (Janos 1980*a*). Janos (1980*b*) hypothesized that disturbance of lowland tropical forests reduces mycorrhizal fungal populations and inhibits forest regeneration. However, the effects of fires and grass invasion on mycorrhizae in dry tropical forests have not been well studied.

Species richness of mycorrhizal fungal communities has been correlated with the species richness of plant communities in temperate grasslands (Johnson et al. 1991) and tropical agroecosystems (Sieverding 1990). Because vascular plant species richness is radically reduced when dry forests are replaced by anthropogenic communities such as pastures, woodlots, and arable land, grass invasion could cause a parallel decline in the species richness of mycorrhizal fungal communities. Alternatively, since mycorrhizal associations are ubiquitous in tropical savannas and grasslands as well

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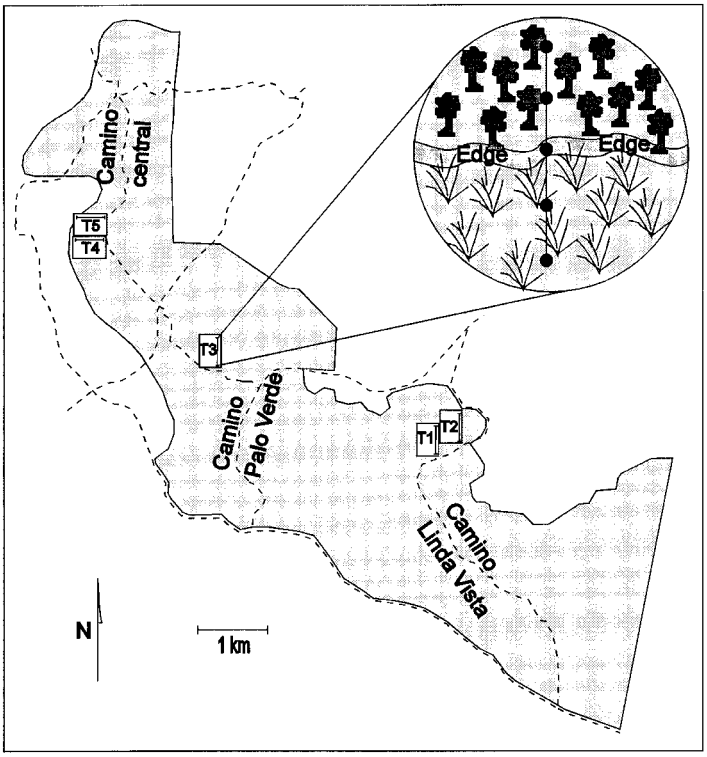

FIG. 1. Transect locations within the Lomas Barbudal Biological Reserve in Guanacaste, Costa Rica. Inset shows a schematic diagram of a 60-m transect with sampling plots at the forest edge, at 15 m and 30 m into the forest from that edge, and at 15 m and 30 m into the grassland.

as tropical forests (Redhead 1977, Newman et al. 1986), grass invasion may not cause a significant reduction in these fungi.

In this study, we examined soils from Costa Rican dry forests, forest edges, and adjacent grasslands to better understand how fires and grass invasion affect (1) pools of nutrients and SOM, (2) dynamics of N mineralization, and (3) population sizes and species diversity of mycorrhizal fungal spores. We partitioned total diversity into alpha (within-plot) and beta (between-transect) components (Whittaker 1972) to help elucidate the relationship between sampling scale and mycorrhizal fungal diversity in forest and grassland ecosystems.

METHODS

Site background

This study was conducted at the Lomas Barbudal Biological Reserve, a 2400-ha tract in southern Guanacaste Province (10°30′ N, 85°21′ W). Soils in Lomas Barbudal are developed from volcanic tuffs and are classified as Tropepts (Vásquez Morera 1983, Gómez 1986). Annual rainfall ranges from 1000 to 2200 mm, and there are two dry seasons: a short period generally from July to August and a more severe period from November through May (Frankie et al. 1988). The longer dry season corresponds with the highest temperatures. During March, April, and May, normal daytime temperatures range from 33° to 38°C (Frankie et al. 1988). Lomas Barbudal Reserve contains remnant stands of dry deciduous forests. Common tree species in this habitat include *Astronium graveolens, Spondias mombin, Luehea* spp., *Tabebuia* spp., *Bombacopsis quinata, Cordia alliodora, Bursera simaruba, Licania arborea, Lonchocarpus* spp., *Casearia aculeata, Chomelia spinosa, Lysiloma seemannii, Enterolobium cyclocarpum*, and *Calycophyllum candidissimum* (Frankie et al. 1988).

Forests at Lomas Barbudal are rapidly being damaged and destroyed by wildfires and subsequent invasion by the African grass *Hyparrhenia rufa* (Nees) Stapf. This grass, known in Latin America as jaraguá, was introduced to Costa Rica ≈1900 and began aggressively invading forest preserves in Guanacaste ≈30 yr ago (Parsons 1972; G. W. Frankie, *personal communication*). Jaraguá is a pyrophyte, prospering with annual burning; during the dry season it is extremely combustible (Daubenmire 1972). The 6–7 mo dry season coupled with strong easterly trade winds create conditions highly conducive to fire. The Lomas Barbudal Reserve is almost completely surrounded by alien grasslands, making jaraguá invasion the major threat to forest conservation and restoration efforts in the reserve.

Study design

We located five sites with negligible topographic relief and with abrupt forest–grassland transitions and positioned 60-m transects perpendicular to the forest boundary (edge). The transects were all ≥100 m but

≤7000 m apart (Fig. 1). The grassland side of the transects was completely covered by dense, essentially monotypic stands of tall (2.5–3.5 m), dry jaraguá. These grasslands are estimated to be 5–15 yr old (G. W. Frankie, *personal communication*). Edge sites were vegetated with a sparse cover of forest plants mixed with jaraguá. The forest side of the transects contained high diversity dry-forest vegetation dominated by seasonally deciduous trees and a herbaceous ground cover.

Sample collection

An Oakfield soil sampler was used to collect soil samples from five 1-m^2 plots along each of the five transects. Plots were located at the forest edge, 30 m and 15 m into the forest, and 30 m and 15 m into the grassland (Fig. 1). Ten soil cores (2.2 cm diameter by 15 cm deep) were collected from each plot, combined in sterile plastic bags, and allowed to air dry thoroughly (soils were initially quite dry). The samples were collected 18 January 1989 and transported to the University of Minnesota where they were stored dry at 4°C until they were processed 7 mo later.

Soil analysis

A subsample of the soils from each of the 25 plots was dried at 60°C, passed through a 1-mm sieve, and ground with a coffee mill prior to chemical analyses. Total soil C and N were measured with a Carlo-Erba NA1500 N/C analyzer. The Research Analytical Laboratory at the University of Minnesota (Crops Research Building, St. Paul, Minnesota 55108) analyzed the soils for extractable P (Bray-1 method as in Dahnke 1988), exchangeable K, Ca, Mg, and Na (following extraction with ammonium acetate), and Cu, Zn, Fe, Pb, and Ni (following extraction with DTPA [diethylenetriaminepentaacetic acid]). To measure pH, dried soils were mixed with deionized water to form a saturated paste that was measured after 1.5 h.

Laboratory incubations

One-year aerobic soil incubations were performed in the laboratory using the methods of Nadelhoffer (1990). Complete details of the methods are given in Wedin and Pastor (1993) and are only summarized here. For each plot, ≈20 g of soil was mixed with 20 g of acid-washed silica sand to facilitate drainage during leaching and placed on top of a layer of glass wool and a glass-fiber filter in the upper portion of a two-chambered plastic filter unit (150 mL Falcon Filter Model 7102). On each sampling date, the samples were leached with 100 mL of 0.01 mol/L $CaCl_2$ followed by 25 mL of a dilute nutrient solution containing all nutrients except N. The samples were leached on days 1, 17, 39, 66, 130, 164, 220, 295, and 367. The first leaching (day 1) removed initial mineral N in the air-dried samples and these results were not used in the calculation of net N mineralization. Soil extracts were analyzed colorimetrically for NO_3^- and NH_4^+ with an Alpkem autoanalyzer. Solution concentrations were converted to mass of N per unit mass of dry soil, and net N mineralization for each sampling period was estimated as the sum of leached NO_3^--N and NH_4^+-N. Only net N mineralization, in contrast to gross N mineralization, was measured and all references to mineralization imply net mineralization.

We performed two measures of N mineralization. Cumulative N mineralized at each sampling date was the sum of N mineralized in that period and all previous periods. For each sampling period we also calculated a daily N mineralization rate by dividing N mineralization during that period by the number of the days in the period. The cumulative N mineralization results are presented both per unit soil mass (absolute) and per unit total soil N mass (relative). Treatment differences in absolute N mineralization reflect differences in both the quantity and quality of the soil organic matter (SOM), while relative N mineralization reflects differences in only SOM quality. Daily N mineralization rates are presented on a relative basis only.

Analysis of mycorrhizal fungal communities

To assess the species composition of arbuscular mycorrhizal (AM, previously called vesicular–arbuscular mycorrhizal: for explanation of this terminological change, see Morton and Benny 1990) fungal communities in the forest–grassland transects, spores were extracted, counted, and identified from each of the 25 soil samples. Soils were thoroughly mixed and spores were extracted from 25-g subsamples using a modification of McKenney and Lindsey's (1987) technique; we used a smaller mesh screen (25 μm) to minimize loss of the smallest spores. Spores were spread onto a membrane filter and a dissecting microscope (30× magnification) and fine forceps were used to remove the spores and place them in polyvinyl-alcohol on permanent slides. A compound microscope (100–1000×) was used to identify (Schenck and Pérez 1990) and count the spores. The relative density (% of spores) of each species in each sample was calculated as: $100(n_i/N)$, where n_i = the number of spores from the i^{th} species and N = the total number of spores examined from the sample (N averaged 3209 spores).

Alpha diversity of mycorrhizal fungal communities in forest, edge, and grassland plots was estimated from species richness (mean number of species) and the Simpson diversity index (Brower and Zar 1977:136–137). Beta diversity was estimated using Sorenson's similarity index based on presence-absence: $[C_s = 2j/(a + b)]$, where j = number of species found in both sites, a = number of species in site A, and b = number of species in site B. This index was calculated for all pairwise comparisons of the grassland, edge, and forest plots to calculate the across-transect similarities of the AM fungal communities in the three vegetation types.

TABLE 1. Mean values of soil parameters by vegetation type in a Costa Rican dry forest and adjacent grassland, and *F* ratios from ANOVAs of these parameter values. Within rows, means followed by different superscript letters indicate that mean parameter values are significantly different ($P < 0.05$). N = number of soil cores.

Soil parameter	Vegetation type			Source of variation		
	Grass ($N = 10$)	Edge ($N = 5$)	Forest ($N = 10$)	Vegetation	Transect	Transect × Vegetation
Carbon and nitrogen						
Carbon†	4.26[a]	4.09[a]	5.23[b]	8.83**	11.90***	0.51
Nitrogen†	0.31[a]	0.33[a]	0.43[b]	16.68***	19.68***	0.46
C:N ratio	14.1[b]	12.4[a]	12.5[a]	5.40*	10.27***	2.55
Cumulative N mineralized in laboratory incubations						
Day 17 absolute N mineralized (μg N/g soil)	5.94[a]	15.62[ab]	23.52[b]	50.34***	2.55	0.42
Day 17 relative N mineralized (mg N/g N)	1.67[a]	5.05[b]	5.65[b]	18.08***	5.17*	2.87
Day 367 absolute N mineralized (μg N/g soil)	214[a]	213[a]	316[b]	15.52***	1.88	0.31
Day 367 relative N mineralized (mg N/g N)	72.9[a]	70.9[a]	77.8[a]	0.86	6.02**	0.32
Other Nutrients						
Phosphorus (μg/g)‡	2.7[a]	2.4[a]	2.7[a]	0.24	0.58	0.66
Potassium (μg/g)‖	105.0[a]	245.0[b]	274.5[b]	6.45*	3.25*	3.83*
Calcium (μg/g)‖	4,435[a]	3,369[a]	3,872[a]	0.73	28.51***	4.60**
Magnesium (μg/g)‖	674[a]	519[a]	536[a]	1.28	12.53***	1.49
Sodium (μg/g)‖	31.9[b]	14.3[a]	8.9[a]	12.34**	0.90	1.25
Iron (μg/g)§	55.0[b]	27.2[a]	36.3[a]	18.37***	0.37	0.28
Zinc (μg/g)§	1.58[a]	0.86[a]	1.31[a]	0.86	5.64*	2.02
Copper (μg/g)§	4.58[b]	2.84[a]	2.76[a]	6.88*	35.07***	2.49
Lead (μg/g)§	0.55[b]	0.38[ab]	0.25[a]	13.55***	1.86	0.59
Nickel (μg/g)§	0.48[b]	0.25[a]	0.28[a]	15.34***	6.44**	0.69
Soil pH	5.97[a]	6.08[a]	6.22[a]	0.94	2.91	3.00

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (significance level of *F* ratios from mixed-model two-way ANOVAs of vegetation and transect effects on soil parameters).
† Total N and C (% dry mass).
‡ Extractable P, determined by the Bray-1 method.
‖ Extractable element in equilibrium with ammonium acetate.
§ Element extracted with DTPA (diethylenetriaminepentaacetic acid).

Statistical analysis

Mixed-model two-way ANOVA was used to evaluate the *fixed effect* of vegetation type (grass, edge, or forest) and the *random effect* of transect location on soil properties and total spore densities, species richness, and species diversity of the mycorrhizal fungal communities. Mixed-model two-way ANOVA was also used to evaluate the effects of vegetation type and transect location on the relative densities of 15 species that occurred in ≥30% of the samples. One-way ANOVA was used to assess the variance accounted for by vegetation type in the pairwise across-transect comparisons of Sorenson's similarity index. Multiple comparisons of means were made using Tukey's test. Spearman rank correlations were performed to assess the relationships between individual spore populations and soil properties. Total spore population data were $\ln(x + 1)$ transformed, and relative spore densities were arcsine transformed (Zar 1984) prior to statistical analysis. All analyses were performed using Statgraphics (STSC 1986).

RESULTS

Soil carbon and nitrogen

Total soil C was 17% lower in the grassland plots and 21% lower in the edge plots compared to plots in the intact forest (vegetation effect on total soil C was significant at $P < 0.01$, Table 1). Differences in total soil N between the forest, edge, and grassland plots were comparable to soil C differences, although relative differences were larger for N than for C in the grassland plots. The net effect of C and N differences among vegetation types was that the soil C:N ratio did not differ between forest and edge sites (means of 12.5 and 12.4, respectively), but was significantly higher (mean ratio = 14.1) in grassland sites (Table 1). Thus, the quantity of SOM (i.e., total soil C) differed between the forest and the edge plots, but not between the edge and the grassland plots. In contrast, the quality of SOM, as estimated by soil C:N ratio, differed between the edge and the grassland plots, but not between the forest and the edge plots. There were also large and highly significant ($P < 0.001$) transect effects on total soil C, N, and C:N ratio (Table 1).

In our laboratory incubations, there were highly significant ($P < 0.001$) differences among vegetation types for both absolute N mineralized (sum of NO_3^--N and NH_4^+-N released per unit dry soil mass) and relative N mineralized (sum of mineral N released per unit soil N) at day 17, the first leaching (Table 1, Fig. 2). Absolute N mineralized (g N/g soil) in grassland plots was 25% and in edge plots 66% of that in intact

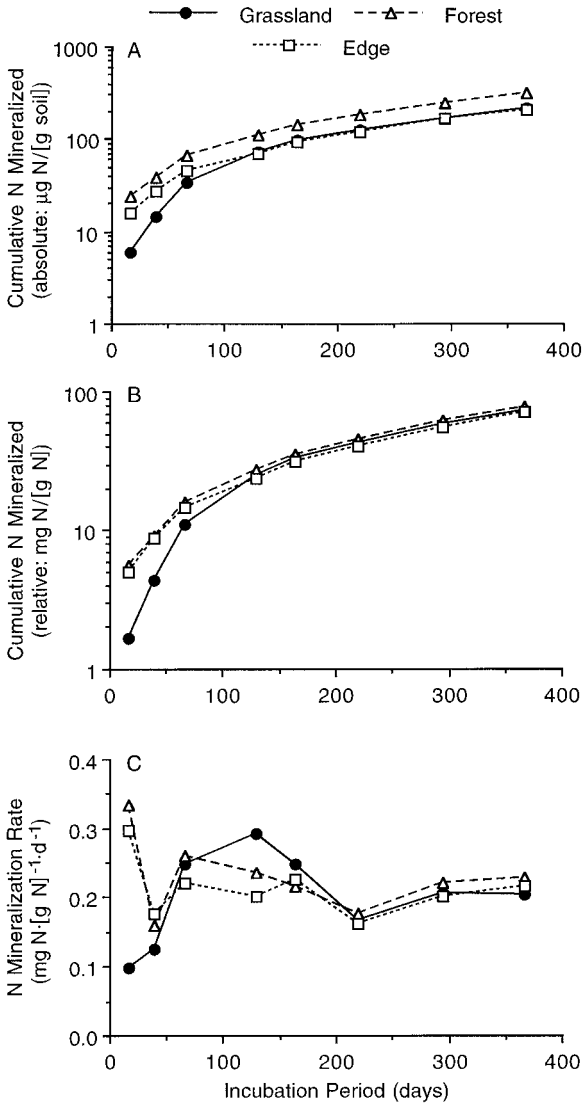

FIG. 2. N mineralization in the grassland, edge, and forest soils of the dry-forest study site (results of year-long N mineralization incubations): cumulative N mineralized per unit soil mass (absolute N mineralized) (A) and per unit soil N (relative N mineralized) (B) and daily N mineralization rates (C).

TABLE 2. *F* ratios from mixed-model two-way ANOVA tests of spatial and vegetation effects on the mycorrhizal fungal community of a Costa Rican dry forest and adjacent grassland.

Variable	Source of variance: Vegetation	Transect	Transect × Vegetation
Total spore count	0.53	31.10***	5.79**
Species richness	0.15	2.55	1.90
Simpson diversity index	0.99	14.77***	2.25
Spore types (% of spores)			
Acaulospora foveata	1.02	1.81	0.56
A. scrobiculata	1.47	5.97**	1.51
A. spinosa	0.22	9.95***	8.31***
Acaulospora no. 1	1.85	10.14***	2.11
Acaulospora no. 3	0.30	23.41***	0.74
Acaulospora no. 4	0.98	18.00***	3.75*
Glomus aggregatum	0.19	9.42**	2.08
G. clavispora	3.21	3.99*	1.39
G. etunicatum	0.38	5.25**	1.66
G. leptotichum	1.71	6.37**	2.86
G. microcarpum	8.25**	2.34	0.79
Glomus no. 1	0.16	6.09**	6.75**
Glomus no. 2	0.14	15.83***	2.99*
Glomus no. 3	0.25	0.15	1.32
Glomus no. 4	0.49	4.89*	3.56*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (significance level of *F* ratios).

forest plots. Relative N mineralized (mg N/g N) in edge plots was similar to that in forest plots, but grassland plots had lower values. Thus, both short-term *absolute* N mineralized and total SOM were lower in edge plots than forest plots, while *relative* N mineralized in forest and edge plots did not differ.

Nitrogen mineralized in the first period (day 17) was significantly correlated with soil C:N ratios ($y = -4.48x + 73.84$, $R^2 = 0.476$, $P < 0.001$, N [number of soil samples] = 25). Grassland plots had relatively high C:N ratios and low N mineralization, while forests plots had low C:N ratios and high N mineralization. The correlation between soil C:N ratio and day-17 N mineralization was also significant for forest plots ($R^2 = 0.54$, $P = 0.016$, $N = 10$) and grassland plots ($R^2 = 0.78$, $P < 0.001$, $N = 10$) considered separately. In contrast, cumulative N mineralized during the entire 1-yr incubation was not significantly correlated with soil C:N ratio ($R^2 = 0.143$, $P = 0.063$).

After the initial incubation period, relative daily mineralization rates increased sharply for grassland soils (Fig. 2C). From approximately day 100 through day 164 of the incubations, grassland soils had the highest daily mineralization rates. After 200 d, daily mineralization rates from soils of all vegetation types converged on ≈ 0.2 mg N·(g N)$^{-1}$·d^{-1}. Cumulative N mineralized per unit soil mass (i.e., absolute N mineralization) at the end of the incubation (day 367) differed significantly among vegetation types, with high levels in the forest soils reflecting their greater SOM and total soil N (Table 1, Fig. 2A). However, cumulative N mineralized per unit soil N mass (i.e., relative N mineralization) on day 367 did not differ significantly among vegetation types (Fig. 2B).

The effect of transect on cumulative N mineralized (absolute) was not significant on either day 17 or day 367. When considered on a relative basis, however, both short-term (day 17) and long-term (day 367) cumulative N mineralized was significantly different among transects. In no case did the interaction of transect and vegetation type have a significant effect on any of the N mineralization parameters analyzed (Table 1).

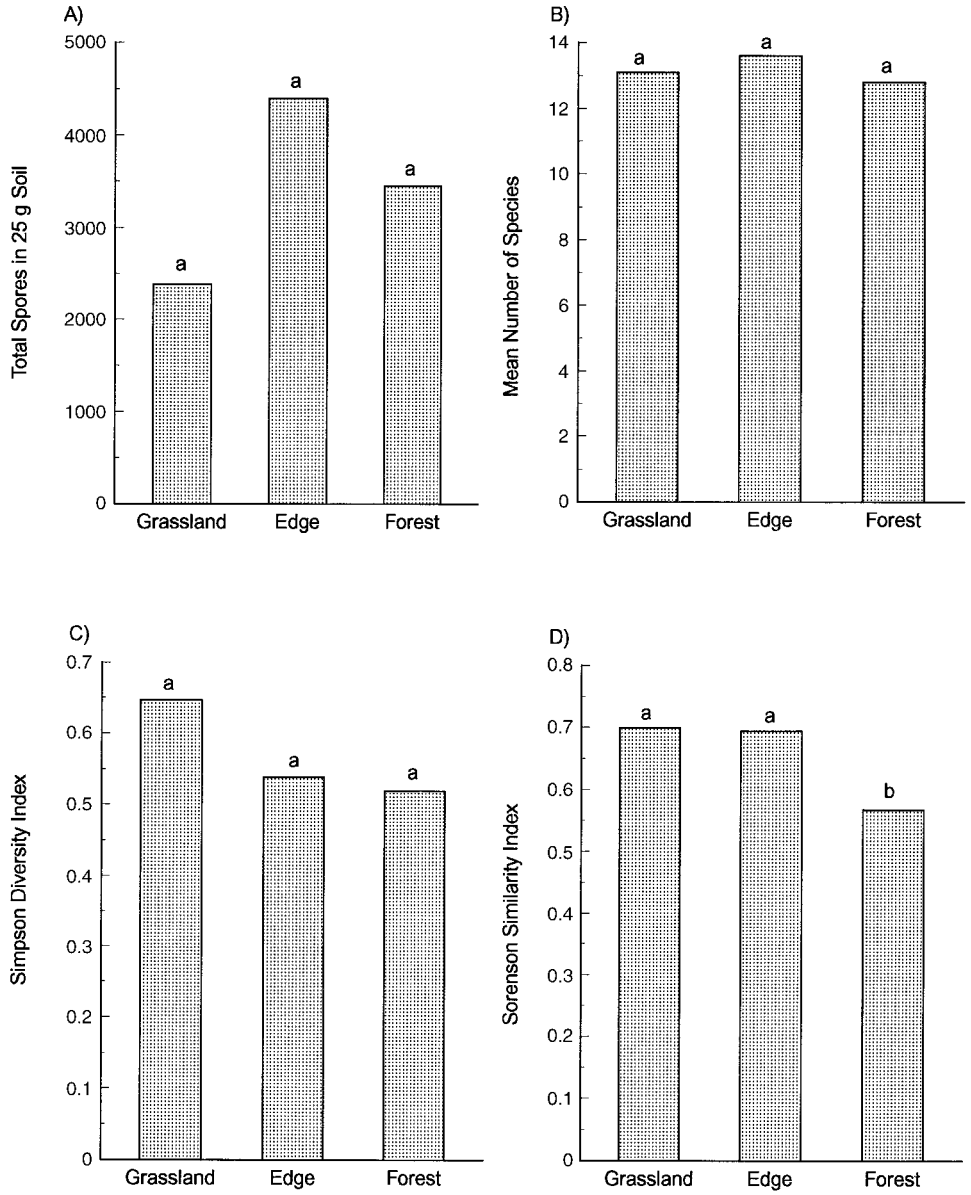

FIG. 3. Comparison of the three vegetation types (grass, edge, and forest) according to mean total spore counts per unit soil mass (A), number of arbuscular mycorrhizal (AM) fungal species (B), Simpson diversity index of the AM fungal spore communities (C), and Sorenson similarity index comparing transects within each vegetation type (D). Within each graph, bars with different letters indicate that means are significantly different ($P < 0.05$).

Other soil nutrients

Phosphorus levels were uniformly low, ranging from 1.5 to 3.5 μg/g and were not significantly affected by either vegetation type or transect (Table 1). For the exchangeable base cations, Na concentration was significantly higher in grassland plots, while K was significantly lower in grassland plots. Ca and Mg tended to be higher in grassland plots, but were not significantly affected by vegetation type. All of the base cations except Na were also significantly different among transects. There were significant vegetation × transect interactions for K and Ca. Transects 3 and 5 contained significantly less Ca than the other three transects.

Of the remaining six nutrients examined, Fe, Cu, Pb, and Ni had significantly higher concentrations in grassland plots compared to forest and, in most cases, edge plots (Table 1). Zinc tended to have higher concentrations in grassland plots, but was not significantly affected by vegetation type. Concentrations of three micronutrients (Zn, Cu, and Ni) were also significantly affected by transect. Neither vegetation type or transect had a significant effect on soil pH, which had an overall

TABLE 3. Spore counts (in 25 g dry soil) of the spore types observed in soils of forest, grassland, and edge in a Costa Rican dry province. Data are means ± 1 SE.

Spore type	Vegetation		
	Grass	Edge	Forest
Acaulospora appendicula Spain, Sieverding, and Schenck	0.6 ± 0.4	0.4 ± 0.4	0
A. denticulata Sieverding and Toro	0.6 ± 0.4	0	0
A. elegans Trappe and Gerdemann	0.2 ± 0.2	0	0.3 ± 0.3
†*A. foveata* Trappe and Janos	2 ± 0.7	6 ± 4	4 ± 2
†*A scrobiculata* Trappe	9 ± 2	10 ± 4	6 ± 2
†*A. spinosa* Walker and Trappe	1 ± 0.7	2 ± 0.8	2 ± 0.8
†*Acaulospora* no. 1 (similar to *A. rugosa*)	4 ± 3	5 ± 1	3 ± 1
Acaulospora no. 2 (similar to *A. rehmii*)	1 ± 1	0	0.3 ± 0.3
†*Acaulospora* no. 3 (''lumpy-yellow'')	53 ± 21	33 ± 15	31 ± 12
†*Acaulospora* no. 4 (''pear-shaped'')	4 ± 1	5 ± 2	9 ± 4
Entrophospora infrequens (Hall) Ames and Schneider	0	0	2 ± 2
Entrophospora no. 1	0	0	2 ± 1
Gigaspora gigantea (Nicolson and Gerdemann) Gerdemannand Trappe	0.3 ± 0.3	0.2 ± 0.2	1 ± 0.6
†*Glomus aggregatum* Schenck and Smith emend. Koske	232 ± 68	191 ± 80	217 ± 45
†*G. clavispora* (Trappe) Almeida and Schenck	13 ± 11	9 ± 5	18 ± 7
†*G. etunicatum* Becker and Gerdemann	37 ± 8	45 ± 29	19 ± 7
G. globiferum Koske and Walker	4 ± 4	0	0
†*G. leptotichum* Schenck and Smith	7 ± 4	0.8 ± 0.5	0.7 ± 0.6
†*G. microcarpum* Tulasne and Tulasne	70 ± 36	2 ± 2	0.7 ± 0.4
G. monosporum Gerdemann and Trappe	0.4 ± 0.3	0	0.5 ± 0.4
G. mosseae (Nicolson & Gerdemann) Gerdemann and Trappe	0.2 ± 0.1	0.6 ± 0.4	0.1 ± 0.1
†*Glomus* no. 1 (similar to *G. ambisporum*)	338 ± 179	129 ± 41	172 ± 37
†*Glomus* no. 2 (similar to *G. occultum*)	1561 ± 873	3943 ± 2851	2938 ± 1243
†*Glomus* no. 3 (with *Sclerocystis* like sporocarps)	33 ± 19	4 ± 1	4 ± 2
†*Glomus* no. 4 (with peridium)	1 ± 0.8	7 ± 6	2 ± 1
Scutellospora calospora (Nicolson and Gerdemann)	0	2 ± 1	1 ± 0.6
S. heterogama (Nicolson and Gerdemann) Walker and Sanders	0.8 ± 0.3	0.2 ± 0.2	1 ± 0.5
S. nigra (Redhead) Walker and Sanders	0	0.2 ± 0.2	0
Total spores counted	2385 ± 1075	4697 ± 2963	3441 ± 1263

† Spore type occurred in >30% of the samples.

mean value of 6.1. Transect one, which had significantly higher Ca concentrations, had the highest pH values (mean = 6.4), although differences among transects were not significant ($P = 0.07$).

Mycorrhizal spore populations

Large spore populations were observed in most soil samples, however, variance was high. Spore counts ranged from 117 to 15 531 spores in 25 g dry soil. Average spore counts tended to be highest in the edge plots and lowest in the grassland plots, although the vegetation effect on total spore count was not significant (Table 2, Fig. 3A). There were significant transect and transect × vegetation interaction effects on total spore count (Table 2). Spore counts in transects three and five were an order of magnitude greater than those from the other transects and resulted from exceptionally high populations of *Glomus* no. 2. This extremely small spore type (16 to 23 μm in diameter) accounted for 81% and 76% of the spores recovered from transects three and five, compared with ≤30% of the spores recovered from the other transects.

Across all sites, a total of 28 spore types, or morphospecies (sensu Morton et al. 1992, hereafter referred to as ''species''), were observed (Table 3). Numbers were assigned to four *Acaulospora* species, four *Glomus* species, and one *Entrophospora* species because insufficient high-quality specimens were available to make a positive identification, or because the spores' characteristics did not correspond to previously described species (Schenck and Pérez 1990). Statistical analyses were only conducted for the fifteen species that occurred in >30% of the samples. Variance in relative spore densities for 12 of these 15 species could be accounted for by transect, and a transect × vegetation interaction accounted for a significant amount of the variance for five species. Variance of only one species, *Glomus microcarpum,* could be accounted for by vegetation alone (Table 2).

Species richness ranged from 10 to 18 species (per 25-g soil sample) and was not influenced by either vegetation type or transect (Table 2, Fig. 3B). The Simpson diversity index was not influenced by vegetation type, although it was influenced by transect (Table 2, Fig. 3C). The overdominance of *Glomus* no. 2 in transects three and five corresponded with significantly lower diversity indices in these transects compared to the other three transects. The across-transect analysis of Sorenson's index indicated that vegetation type accounted for a significant amount of the variance in community similarity (F-ratio = 10.02, $P = 0.0002$, $N = 50$). Arbuscular mycorrhizal (AM) fungal com-

TABLE 4. Spearman rank correlations between soil chemical properties and characteristics of arbuscular mycorrhizal (AM) fungal communities in a Costa Rican dry province.

Variable	Rank correlation with: pH	N	C	C:N
Total spore count	−0.07	0.76***	0.75***	−0.63***
Species richness	−0.46*	0.22	0.16	−0.28
Simpson diversity index	0.2	−0.68***	−0.66***	0.58**
Spore type				
Acaulospora foveata	0.04	0.24	0.25	−0.28
A. scrobiculata	−0.41*	−0.06	−0.06	0.07
A. spinosa	−0.11	0.34	0.3	−0.45*
Acaulospora no. 1	−0.48*	−0.19	−0.23	0.13
Acaulospora no. 3	0.1	−0.39*	−0.35	0.42*
Acaulospora no. 4	0.11	−0.19	−0.21	0.12
Glomus aggregatum	−0.32	0.72***	0.70***	−0.63***
G. clavispora	0.05	0.68***	0.64***	−0.64***
G. etunicatum	−0.34	0.06	0.06	−0.11
G. leptotichum	0.06	−0.39*	−0.3	0.32
G. microcarpum	−0.53**	−0.28	−0.24	0.34
Glomus no. 1	−0.17	0.60**	0.52**	−0.66***
Glomus no. 2	0.01	0.68***	0.70***	−0.54**
Glomus no. 3	−0.34	0.44*	0.39*	−0.46*
Glomus no. 4	−0.04	0.04	−0.03	−0.11

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$ (significance level of correlations).

munities in grassland and edge plots had higher intertransect similarity than communities in forest plots (Fig. 3D).

Spore populations of five of the nine *Glomus* species were positively correlated with soil N and C and negatively correlated with soil C:N ratio, Ca, and Mg (Table 4). Spore populations of the *Acaulospora* species generally exhibited fewer significant correlations with soil properties. Except for a negative correlation with Ca and pH, species richness was not correlated with any of the soil properties we measured. Because of the overabundance of *Glomus* no. 2 in some plots, the relationship between total spore counts and soil properties paralleled that of *Glomus* no. 2 and soil properties, while the relationship between the Simpson diversity index and soil properties was the inverse (Table 4). Reanalysis of a modified data set that excluded *Glomus* no. 2 showed essentially the same relationships.

DISCUSSION

Soil organic matter and nutrient dynamics during grass invasion

Our results indicate a shift in the quantity and quality of SOM during the transition from dry forest to jaraguá grassland. The short-term (17-day) N mineralization we observed for soils from the intact forest plots are comparable to rates reported for humid Costa Rican forests (Vitousek and Denslow 1986). In contrast, short-term N mineralization from the grassland soils was 75% lower than values for the forest soils. Other studies (Binkley and Hart 1989, Wedin and Pastor 1993) have shown that short-term laboratory measures of N mineralization are well correlated with actual N availability (i.e., annual in situ net N mineralization). We assume, therefore, that the differences we observed in short-term N mineralization reflect real differences in N availability among our three vegetation types.

Over the course of the 1-yr incubations, the significant differences between vegetation types in relative N mineralization, considered either as cumulative N mineralized or as daily rates, disappeared (Fig. 2). In contrast to the small labile pool of SOM dominating short-term mineralization dynamics, most SOM in these soils is relatively recalcitrant. Volcanic soils, such as the Tropepts at our site, generally have higher SOM levels than other tropical soils and lose SOM more slowly following disturbance (Henrot and Robertson 1994). After incubation for 1 yr at 30°C, >90% of the N in the soils of all vegetation types had not been mineralized and was still organically bound. Conversion to grassland did not appear to have affected the quality of this larger recalcitrant SOM pool, at least in terms of N turnover rates.

The high N mineralization rates found in these dry-forest soils are consistent with the conclusion of other studies that lowland tropical forests are characterized by high rates of N mineralization, relatively high concentrations of available mineral N, and high concentrations of N in plant litter, i.e., a low N use efficiency (Vitousek 1984, Matson et al. 1987). The significantly lower C:N ratios of the forest soils compared to the grassland soils are also consistent with a pattern of high litter inputs of N, rapid decomposition, and high N availability. Vitousek (1984) concluded that ''it seems unlikely that production could be N limited in such forest (lowland tropical forests) as long as the soil–plant N cycle remains intact.''

In contrast to the low N use efficiency that characterizes most tropical forest woody species, perennial C_4 grasses, particularly fire-adapted grasses such as ja-

TABLE 4. Continued.

Rank correlation with:					
P	K	Ca	Mg	Zn	Cu
−0.32	−0.05	−0.74***	−0.62**	−0.62**	−0.50**
−0.11	−0.04	−0.42*	−0.34	0.06	−0.19
0.28	−0.16	0.51**	0.58**	0.81***	0.52**
0.31	0.32	−0.27	−0.31	−0.27	−0.39*
0.13	0.01	−0.32	−0.13	0.14	−0.11
−0.23	0.14	−0.24	−0.08	−0.2	0.04
−0.02	−0.28	−0.19	0.09	0.44*	0.11
−0.03	−0.02	0.48**	0.49**	0.58**	0.57**
−0.19	0.32	0.29	0.27	0.31	0.40*
−0.23	−0.09	−0.80***	−0.69***	−0.55**	−0.57**
−0.21	0.27	−0.66***	−0.65***	−0.68***	−0.61**
−0.19	−0.24	−0.33	−0.17	0.13	0.17
0.2	−0.14	0.42*	0.38	0.14	0.24
0.25	−0.69***	−0.1	0.05	0.60**	0.22
−0.44*	−0.05	−0.66***	−0.64***	−0.52**	−0.41*
−0.2	−0.07	−0.68***	−0.57**	−0.58**	−0.49**
−0.48*	−0.13	−0.54**	−0.59**	−0.25	−0.22
−0.29	0.18	0.25	0.22	0.23	0.27

raguá, generally have high N use efficiencies. These grasses have high belowground productivities and high C:N ratios in both aboveground and belowground senesced tissues, thus creating the potential for significant N immobilization during decomposition (Daubenmire 1972, Bilbao and Medina 1990, Medina and Silva 1990, Wedin 1995). Just as the plant–soil feedback proposed by Vitousek (1984) makes N limitation unlikely in intact tropical forests, the feedback of litter quality on N cycling promotes N limitation in tropical grasslands (Medina and Silva 1990, Wedin 1995).

Although our samples were collected at a single point in time, the sampling design essentially creates five chronosequences, the forest plots representing the oldest and original vegetation type, edges representing intermediate, and grassland plots representing the youngest vegetation type derived from the forest. Given this design, differences between forest and grassland plots may be interpreted as changes that occurred during grass invasion. The 17% decrease in total soil C (i.e., SOM) from forest plots to grassland plots appears to have occurred early during grass invasion and is accounted for by SOM losses in the edge plots. However, neither soil C:N ratios nor short-term relative N mineralization rates differed between intact forest plots and edge plots, indicating that a significant shift in SOM quality and N cycling did not occur until after dense jaraguá stands had invaded the relatively open edge environments.

The edge plots also account for most of the N loss that occurred across the forest-to-grassland transition. Thus, although annual burning in the grasslands volatilizes roughly 90% of the N in grass litter (Crutzen and Andreae 1990) and certainly reinforces the low N availability of the jaraguá grassland, most of the N losses from the system occurred prior to the full establishment of the grassland. Because tropical forests are characterized by high rates of N mineralization and high litter N concentrations, fire in intact forests inevitably leads to large N losses both through volatilization during burning and through leaching and volatilization from large pools of soil mineral N that build up in the absence of plant uptake (Matson et al. 1987).

Although N availability was lower in grassland plots than in forest plots, availabilities of most nutrients were higher or the same (Table 1). Unlike N, a relatively high proportion of the base cation and micronutrient content of plant tissues is returned to the soil via ash following burning (Raison 1979). The exception in our case may be K, which is often volatilized above 500°C (Raison 1979). The role of fire may explain why we found lower K availability in grassland plots while Reiners et al. (1994) observed higher K concentrations following anthropogenic conversion of humid Costa Rican forest to active pastures. Alternatively, measures of K concentrations are strongly affected by soil moisture status and our single dry-period sampling may not adequately reflect annual K availability (Luebs et al. 1956). The generally low concentrations of P we observed across all the sites corroborate other analyses of Costa Rican soils (Vitousek and Denslow 1987) and are below the suggested critical concentration for P-deficiency (Mengel and Kirkby 1982).

It is unclear why transects 3 and 5 differed from the other three transects. Total soil C and N were significantly higher, soil Ca and C:N ratio were significantly lower, and spore densities of *Glomus* no. 2 were an order of magnitude greater, in transects 3 and 5 than in the other three transects. These patterns may reflect vegetation differences (e.g., abundance of leguminous

trees), or alternatively, soil texture, parent material, or disturbance history may have differed in these areas. Transect proximity cannot account for these patterns because transects 3 and 5 were relatively far apart (nearly 3 km). In contrast, transect 4 was only 100 m from transect 5, yet it was more similar to transects 1 and 2 which were ≈7 km away (Fig. 1).

Mycorrhizal dynamics during grass invasion

Our results do not support Janos' (1980*b*) hypothesis that disturbance of tropical forest leads to decreased populations of mycorrhizal fungi and that grass invasion combined with annual burning maintains depauperate populations of mycorrhizal fungi. Mycorrhizal fungi in wet forests, such as those studied by Janos, may be more vulnerable to disturbance than those in dry forests because of fundamentally different means of propagation. Janos (1992) suggested that hyphal growth from both living and senescing roots is the primary source of AM fungal inoculum in aseasonal wet tropical forests and reported typical spore populations of <125 spores per 25 g dry soil. In contrast, we found unusually high populations of mycorrhizal fungal spores in both seasonally dry forest and grassland sites (averaging >3400 and 2300 spores per 25 g soil, respectively). Plant senescence, either natural or induced, is known to trigger sporulation of AM fungi (Sutton and Barron 1972). Consequently, seasonal forests, such as the dry deciduous forests at Lomas Barbudal, may be expected to have larger spore populations than aseasonal wet forests. Jasper et al. (1992) suggested that mycorrhizae in ecosystems that naturally produce large spore populations may be more resilient to disturbance than ecosystems that do not typically form large spore populations.

The drastic reduction in vascular plant species that occurred after grass invasion was not accompanied by a reduction in AM fungal species. Alpha diversity, measured by the number of spore types (species richness) and the Simpson diversity index, did not differ significantly between the jaraguá grasslands and the adjacent forests. These findings corroborate a recent study that reports spore density and species richness of AM fungi actually increased over a 15-yr period following conversion of natural tropical forest into *Terminalia* plantations in Côte d'Ivoire (Wilson et al. 1992).

Communities of AM fungi in dry tropical forests may be surprisingly resilient to fires and grass invasion. Another African C_4 grass, *Sorghum sudanense* (Piper) Stapf., is recommended as a ''universal host'' for culturing AM fungi (Ferguson and Woodhead 1982) so it is likely that jaraguá grass is a suitable host for most, if not all, of the forest AM fungi. Given that these fungi depend upon living plants for all of their C requirements, the invading grasslands at Lomas Barbudal would be expected to maintain high populations of AM fungi if the rate at which C is carried belowground is comparable in jaraguá grassland and intact forest. Recent studies at La Selva Biological Station in Costa Rica support this hypothesis (Fischer et al. 1994, Asbjornsen and Montagnini 1994). In both studies, bioassays indicate that densities of AM fungal inoculum in abandoned pasture lands (dominated by grasses) were as high or higher than inoculum densities in intact forests.

Deforestation and grass invasion at Lomas Barbudal reduced beta diversity of AM fungi. Across the five transects, communities of AM fungi in grassland plots were significantly more similar to one another than those in forest plots, suggesting that grass invasion is causing the composition of AM fungal communities to converge. The loss of forest AM fungi may lag behind that of forest plants. Janzen (1986) suggested that many tropical species are ''living dead,'' legacies of past forests with little potential for long-term survival in their now drastically altered ecosystems. Because the jaraguá grasslands in our study were relatively young (≤15 yr old; G. W. Frankie, *personal communication*), many of the spore types we observed in the grasslands could be eventually eliminated if their fitness is reduced when jaraguá grass is their host. Future studies are necessary to monitor changes in AM fungal diversity over time and assess the functional significance of landscape level (beta) diversity of AM fungal communities.

Methodological considerations

Analysis of spore populations is currently the only method to assess the species composition of AM fungal communities, but interpretation of these results remains conditional. Spores do not perform a mutualistic function. Furthermore, isolates of AM fungi vary greatly in spore production; some isolates produce copious spores, while others rarely or never sporulate. Thus, while interspecific comparisons of spore populations are generally not useful, intraspecific comparisons (across treatments) may be meaningful. Such a comparison in our system revealed that spore populations of only one species (*Glomus microcarpum*) were significantly affected by vegetation type.

Conclusions

With regard to SOM, soil nutrients, and the AM fungal community, invading tropical grasslands may be as sustainable as the native forests they replace. Grass invasion may actually be a greater threat to native forest biodiversity than conversion to cropland because these grasslands appear to be alternative stable states. Positive feedbacks between the alien grassland vegetation and both fire and nutrient cycling reinforce this alternative state (D'antonio and Vitousek 1992, Wedin 1995). These results suggest that persistence and regeneration of forest species in the jaraguá grasslands may not be constrained by the lack of mycorrhizal symbionts.

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