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Short-term consequences of slash-and-burn practices on the arbuscular mycorrhizal fungi of a tropical dry forest

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Abstract Rates of land conversion from forest to cultivated land by slash-and-burn practices are higher in tropical dry forest (TDF) than any other Neotropical forest type. This study examined the short-term consequences of the slash-and-burn process on arbuscular mycorrhizal fungi (AMF). We expected that slash-and-burn would reduce mycorrhizal colonization and propagules and change species richness and composition. Soil and root samples were taken from TDF control and pasture plots originated after slash-and-burn at four dates during the year of conversion to examine species composition, spore abundance, and infective propagules. Additionally, spore abundance and viability and viable intraradical colonization were measured twice during the second year after conversion. Forest and pasture plots maintained similar species richness and an overall 84% similarity during the first year after conversion. Infective propagules were reduced in pasture plots during the first year after slash-and-burn, whereas spore abundance and intraradical colonization remained similar in TDF and pasture plots both years of the study. Our results suggest, contrary to the expected, that forest conversion by means of slash-and-burn followed by cultivation resulted in few immediate changes in the AMF communities, likely because of the low heat conductivity of the soil and rapid combustion of plant residues.

Keywords Arbuscular · Fire · Mycorrhiza · Slash-and-burn · Pasture · Tropical dry forest

Introduction

Neotropical forest cover has been drastically reduced by human activities, and among them, dry forests are more threatened than moist and wet forests (Khurana and Singh 2001). The area converted from forest to pasture in Latin America was estimated as 1.35×10^6 ha year^{-1} (Trejo and Dirzo 2000) and approximately 80% of the original tropical dry forest (TDF) cover area is lost (Houghton et al. 1991). TDF on the Pacific coast of Mexico is usually converted by slash-and-burn practices to be used for some years for low-input agriculture, followed by the introduction of grasses for extensive, low-input cattle farming or directly after conversion for cattle farming (Maass 1995; Kauffman et al. 2003). Slash-and-burn is a popular practice because it releases and incorporates nutrients from burnt biomass, clears rapidly and efficiently, and reduces weeds and pests. However, severe water limitation in dry tropical ecosystems exacerbates soil degradation after forest conversion to pastures. It exposes soils to desiccation, high temperatures, and rain erosion, besides consuming soil litter, organic matter, and microbiota (García-Oliva et al. 1999a) that are essential for nutrient cycling (Kauffman et al. 1993). Several studies conducted some years after forest conversion to pastures have documented a decrease in soil microbial activity and nutrient losses associated with the loss of plant cover, severe erosion, and reduction in soil organic matter and

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microbial biomass (Maass et al. 2002). Also, the disruption of soil aggregates and of the processes maintaining long-term soil nutrient and water availabilities contributes to soil deterioration (García-Oliva et al. 1999b).

Few studies have addressed the effects of slash-and-burn practices on arbuscular mycorrhizal fungi (AMF) and mycorrhizal associations (Johnson and Wedin 1997; Allen et al. 1998; Violi et al. 2008), and all of them have documented the consequences many years after land conversion. More studies have investigated the effect of natural or nonintentional fires (Klopatek et al. 1988; Wicklow-Howard 1989; Dhillion et al. 1988; Vilariño and Arines 1991; Rashid et al. 1997), but these differ from slash-and-burn in several ways. There is a large amount of slashed dry biomass lying on the floor and logs burning for long periods on the soil surface may reach temperatures of 500°C for several hours, but elsewhere, fire propagates rapidly and the soil has a large buffering power so temperatures may go down to 100°C at 3 cm depth (Giardina et al. 2000b). The increase in temperature is, therefore, highly irregular depending on the material burning at the soil surface (Kauffman et al. 1992). Dhillion et al. (1988) observed a similar phenomenon in grasslands where fire did not increase temperature substantially beyond the soil surface. Bellgard et al. (1994) suggested as well that moderate fires had no significant impact on the infectivity of AMF or on spore abundance. The impact of disturbance on AM propagules depends on its intensity, severity, and frequency (Abbott and Gazey 1994). Fires are, however, extraordinary events in TDF, so AMF communities are not adapted to resist those conditions as they are in other ecosystems with periodical natural fires. Fire may thus have stronger effects on the AMF of TDF. It is also possible that fire has indirect effects on mycorrhizal fungi by affecting plants and predators (Gibson and Hetrick 1988) and microclimate.

How strong the effect of clear-cutting combined with fire and how many propagules are burnt or damaged in the process of slash-and-burn are still unanswered questions in discussions about the effects of land conversion in the tropics on AMF. This study examined the short-term consequences of the slash-and-burn process in TDF through measurements of species richness and composition and infective propagules of arbuscular mycorrhizal fungi during the first growth season and total and viable spore counts and root colonization in the second year. We expected that slash-and-burn would reduce species richness and infective propagules in the first months after the burning process. We expected also that total and viable mycorrhizal colonization and spore numbers in the second growth season would evidence any reductions in mycorrhizal propagules or changes in AMF species composition in the preceding year.

Materials and methods

Study site

The study was conducted in the Ejido San Mateo, municipality of La Huerta, in the coast of Jalisco, México (19°30′ N, 105°03′ W). The air temperature in the region fluctuates very little during the year with a mean of 24.9°C. Precipitation averages 746 mm (1983–2004), distributed mostly from June to October (García-Oliva et al. 2002). Leaf flush is synchronous among most tree species and occurs after the start of the rainy season (Bullock and Solís-Magallanes 1990). The soils have been described as sandy-loams and sandy-clay-loams entisols, commonly with rocks in the superficial horizons and rhyolite parent material (Cotler et al. 2002). The dominant vegetation of the region is tropical dry forest with about 1,120 species of vascular plants (Lott 1993). The study site, previous to slash-and-burn, included 104 woody species (>1 cm diameter at breast height), 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 approximately 118 Mg ha^{-1} (Kauffman et al. 2003).

Treatment plots

The experimental plots were located on a 30% slope with a W aspect, 200 m above sea level. Two 33×100 m treatment parallel plots with undisturbed TDF were slashed at the beginning of February by local farmers, following traditional clearing methods as described by Kauffman et al. (2003). In an adjacent, undisturbed TDF, two plots of similar size were established as control sites. Vegetation was slashed in February, burnt in April, and transformation of the TDF was completed when three pasture grasses (*Pennisetum ciliare* (L.) Link., *Panicum maximum* Jacq., and *Andropogon gayanus* Kunth) were seeded along with two local maize (*Zea mays* L.) varieties within the next 15 days. Following maize harvest at the end of October and early November, cattle were allowed into the pasture.

Sampling

Samples were taken in February (middle of the dry season, just before slashing the vegetation), May (end of the dry season, 1 month after burning the slashed vegetation), September (middle of the rainy season), and November (end of the rainy season) the same year of conversion and in May and October the following year. Nine points were located every 10 m along the long edge of the rectangular plot along the slope. Every 10 m, a random number between 1 and 33 was drawn to establish the sampling point within the width of the plot. Soil and root samples (300 g) were taken with a shovel to a 15-cm depth. The three top, middle, and bottom samples of each plot were bulked and processed separately, but their values were averaged to obtain a single plot value.

Sample processing

Spores were extracted from 50 g samples by wet sieving (Gerdemann and Nicolson 1963) and centrifugation in a sucrose gradient. Spores were counted under the stereomicroscope and the different morphospecies were identified using original species descriptions summarized in Schenck and Pérez (1990) and presented online at http://www.lrz-muenchen.de/~schuessler/amphylo/amphylo_species.html. Isolate descriptions of reference cultures and vouchers for many species are presented online at http://invam.caf.wvu.edu/index.html. Sørensen's similarity index based on presence/absence of species (Magurran 1988) was used to compare forest with pasture.

Spore and intraradical mycelium viability were measured from samples obtained in May and October of the second year after conversion with similar field procedures. Vital staining based on dehydrogenase succinate activity with nitrotetrazolium blue (NBT) was used to determine viable intraradical colonization as described in Schaffer and Peterson (1993) and tetrazolium chloride (TTC) was used to test spore viability as in Meier and Charvat (1993). TTC was found to work better for spore viability than tetrazolium bromide (Aguilar-Fernández 1993) and was used in a 5 mg TTC mL^{-1} (0.5%) solution, pH 8.4. Spores from 50 g samples were extracted as explained above and were surface-disinfected for 20 min in a streptomycin sulfate (2%) and chloramine T (0.02%) solution. Spores were placed in Petri plates with 5 mL of TTC solution and incubated in darkness at 28°C for 7 days. Spores were then examined for pink/red stains indicating viability by crushing the spore and evaluating color change in the spore contents. Roots were stained with NBT to determine viable mycorrhizal structures, following the method of Schaffer and Peterson (1993), the same day they were collected from the field. Total, arbuscular, and vesicular colonization, distinguishing between viable and nonviable structures, were measured on 150 intersections from roots mounted on slides under the microscope (McGonigle et al. 1990).

Infective AMF propagules were determined by the most probable number (MPN) method (Porter 1979) using soil of the composite samples taken from nine points in the plots. MPN assays were run from samples taken in February, May, September, and November of the conversion year from control plots established in intact mature forest and slash-and-burn plots. Samples taken in February, before slash, were taken only from the treatment plots as representative of conditions previous to slash-and-burn, as both control and treatment plots were initially part of a mature forest site. Samples from May to November were taken from two control and two treatment plots. Autoclaved soil from outside the plots was used to make the dilutions in a tenfold series to 10^{-7} with four replicates of each dilution. Onion (*Allium cepa* L.) plants were used as hosts. The bioassay was maintained for 6 weeks in the greenhouse after which roots were harvested, washed, and stained (Phillips and Hayman 1970). The presence of mycorrhizal structures was examined under the microscope.

Statistical analyses

To determine the effects of slash-and-burn on the total number of spores and to describe and compare its dynamics in TDF and pasture the first year of study, a repeated-measures analysis of variance was used with fixed factors and a split-plot design. The plots were the subjects, time was the within-subject factor, and treatment was the between-subject factor. 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 to decide rejection or acceptance of the differences with time and the time by treatment interactions. Data were transformed to log $(X+1)$ to meet normality and homoscedasticity assumptions. Values are presented in their original scale of measurement.

Data from the second year of study (i.e., mycorrhizal colonization [total, viable and nonviable], the proportion of arbuscules and vesicles, and spore numbers) were analyzed with a logistic regression model (Alvarez-Santiago et al. 1996) with the statistical package GLIM v. 3.1. We used a Poisson distribution for spore numbers and a binomial distribution for colonization data. We compared the change in deviance (Δ) with χ^2 values to determine significance of treatment effects (forest vs pasture), date (May vs October), and their interaction.

Results

Total species richness (forest+pasture) was 18 species (Table 1). Species richness and composition of AM were similar between forest and pasture during the year of forest conversion to pasture (Table 2). The accumulated number of species at the end of the first year was 15 in the forest and 16 in the pasture. Thirteen species were common to both, two were present only in the forest and three only in pasture. The Sørensen index showed that similarity was above 80% at the end of the dry season (May) and the beginning of the rainy season (July) but diminished

Table 1 AMF morphospecies present at each sampling date and the total for all dates in forest (F) and pasture (P) sites during the first year after forest conversion

Month	May		July		September		November		Total	
Site	F	P	F	P	F	P	F	P	F	P
Diversisporales										
Acaulosporaceae										
Acaulospora dilatata J.B. Morton	x		x	x	x	x	x	x	x	x
Acaulospora scrobiculata Trappe	x	x	x	x	x	x	x	x	x	x
Acaulospora sp.1	x		x	x	x	x	x	x	x	x
Acaulospora sp.2							x		x	
Gigasporaceae										
Gigaspora aff. *albida* N.C. Schenck & G. S. Sm.						x				x
Gigaspora decipiens I.R. Hall & L.K. Abbott					x	x			x	x
Gigaspora ramisporophora Spain, Sieverd. & N.C. Schenck	x	x	x		x		x		x	x
Gigaspora sp.2								x		x
Scutellospora aff. *calospora* (T. H. Nicolson & Gerd.) C. Walker & F.E. Sanders	x	x		x		x	x		x	x
Scutellospora persica (Koske & C. Walker) C. Walker & F.E. Sanders								x		x
Scutellospora sp.1			x						x	
Glomerales										
Glomeraceae										
Glomus aff. *diaphanum* J.B. Morton & C. Walker	x	x			x		x		x	x
Glomus aff. *fasciculatum* (Thaxt.) Gerd. & Trappe, emend. C.Walker & R. Koske	x	x	x	x	x	x	x	x	x	x
Glomus clavisporum (Trappe) R.T. Almeida & N.C. Schenck							x	x	x	x
Glomus monosporum Gerd. & Trappe		x	x	x		x		x	x	x
Glomus sinuosum R.T. Almeida & N.C. Schenck	x	x	x	x	x	x	x	x	x	x
Glomus sp.1	x	x	x	x	x	x	x	x	x	x
Glomus sp.2			x	x					x	x

x the species is present

progressively in September and November (Table 2). Similarity on a whole-season basis was 84% during the first year after conversion.

Total spore production did not differ between forest and pasture both years of study ($P>0.1$; Fig. 1a; data for the first year not shown). The percentage of viable spores was extremely low both in forest (4%) and pasture (3%). The number of viable spores was higher in the dry than in the wet season month ($\Delta=8.21$; $P<0.01$; Fig. 1a), but it did not differ between forest and pasture ($\Delta=0.08$, $P>0.05$). Both spore numbers and viability measurements suggested that only few new spores were produced in the entire sampling period.

Percent mycorrhizal colonization was slightly, but significantly ($\Delta=5.15$, $P<0.025$), higher in the pasture (44%) than in the forest (37%) and did not change between sampling dates (Fig. 1b). Percent viable colonization did not differ between sites or dates ($P>0.1$; Fig. 1b), but nonviable colonization was higher in the pasture than in the forest ($\Delta=11.14$, $P<0.001$).

Arbuscular colonization represented a very low percentage, not higher than 2%, and viable arbuscular colonization was higher in October (wet) than in May (dry; $\Delta=7.26$, $P<0.01$). Nonviable arbuscular colonization ranged from 0% to 0.2%. Viable vesicular colonization did not differ between sites or dates and varied between 2% and 3%.

Table 2 Total number of AMF species, with unique and shared species, and similarity index found for each sampling date and for the entire period sampled in forest and pasture sites the first months after conversion (February–April of the same year)

	May		July		September		November		Total	
	F	P	F	P	F	P	F	P	F	P
Total number of species	9	8	10	9	9	10	11	10	15	16
Unique species	2	1	2	1	2	3	4	3	2	3
Shared species	7		8		7		7		13	
Similarity index	0.82		0.84		0.73		0.66		0.84	

F forest, *P* pasture

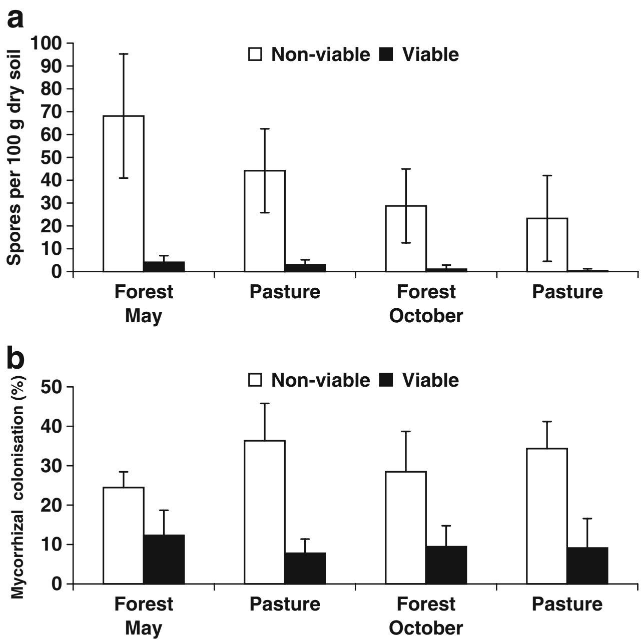

Fig. 1 Nonviable and viable spores (**a**) and intraradical colonization percentages (**b**) in the dry (May) and wet (October) seasons, the second year after forest conversion. Total colonization includes intraradical hyphae, arbuscules, coils, and vesicles. Data are presented as the mean±SD

Nonviable vesicular colonization was higher in the pasture (14%) than in the forest (9%; $\Delta=11.64$, $P<0.001$).

The MPN of infective propagules showed a clear reduction in May and September, 1 and 3 months after slash-and-burn in pasture plots compared to forest (Table 3). The differences disappeared in November when the rains and the growing season had ceased.

Discussion

We found some minor differences in species richness and species composition between the forest and the pasture sites the first year after land conversion. Many species, especially in the genera *Glomus* and *Acaulospora*, could not be identified to the species level and it is likely that they represent new species. However, most species were not evident in the trap cultures, and in some cases, we were unable to establish the genus from field samples. TDF and pasture plots maintained an overall similar species richness and composition during the first months after the fire, suggesting a minor immediate impact on spores. There was, however, some indication for changes in pasture plots 6 months after the slash-and-burn process. Similarity dropped to 66% and three species were detected only in pasture plots. Unfortunately, these measurements could not be followed for a longer time to confirm species divergence because the establishment of the introduced plants in converted plots would have been confused with the effects of the slash-and-burn process. The hypothesis of immediate change due to fire on AMF species richness and composition was, in general, not supported by the data.

There is evidence indicating that species richness decreases and species composition changes in pastures 10 years after conversion at the same location (Álvarez-Santiago 2002). It was also observed that spore counts in pasture were dominated by five species and that spore density was three times greater in pasture when compared to primary forest. This was suggested to be a consequence of the introduction of grass (Allen et al. 1998) that likely selects some AMF species and promotes their proliferation through its large production of fine and short-living roots. Gavito et al. (2008) found 18 morphospecies in 26-year-old pastures, compared to 29 in primary forests, and only ten of these morphospecies were shared. These results for the Chamela region and those reported by Guadarrama et al. (2007) in the region of Nizanda, Oaxaca, Mexico, suggest that AMF species composition in this region continues to change decades after the conversion process.

There was also little change in spore production and viability and in intraradical colonization a year after land transformation. Moreover, the new pastures showed very

Table 3 MPN quantification of mycorrhizal infective propagules in samples taken in February (middle of the dry season, just before slashing the vegetation), May (end of the dry season, 1 month after slash-and-burn), September (middle of the rainy season), and November (end of the rainy season) from two mature forest plots (F1 and F2) and in slash-and-burn plots converted to pastures (P1 and P2)

	February ↓	May	September	November
F1	nm	209	30	5.2
F2	nm	26	88	3.6
Mean (95%CI)	nm	117 (49–267)	59 (21–114)	4.4 (1.6–8.9)
P1	165	1.6	3.7	1.8
P2	41	2.3	0.5	1.3
Mean (95%CI)	103 (38–210)	1.9 (0.8–4.4)	2.1 (0.8–4.2)	1.6 (0.6–3.2)

Mean and 95% confidence intervals (95%CI) are shown

nm not measured, assumed to be similar in the entire plot before conversion started at the end of February similar values to those measured in forest plots, indicating an overall minimum change in AMF propagule dynamics and, therefore, not supporting our prediction of changes expressed in the second year. Apparently, fire did not damage mycorrhizal fungi directly, likely due to quick fire propagation on most of the burnt area and to the low heat conductivity of soil. High temperatures during slash fires are mostly limited to the soil surface where maximum temperatures average above 500°C in the surface 0.5 cm and drop to 100°C at 3 cm depth (Giardina et al. 2000a). The dispersed distribution of spores may have resulted in high temperatures affecting them only in the areas where large wood was combusted. In contrast, other propagules like infected roots occur in the upper soil profile and may be more exposed to heat (Allsopp and Stock 1994). Castellanos et al. (2001) reported that fine root (<1 mm diameter) biomass (live and dead) in the same study plots showed a nearly 30% reduction in the 10 cm profile immediately after burning. The largest decrease was recorded in the top 2 cm of soil where fine root biomass diminished by 41%. This was reflected in the bioassay examining the capacity of all propagules to colonize new host plants. Although MPN results were highly variable, they showed a decrease in infective propagules in pasture plots during the first months after transformation. MPN propagules were highest at the end of the dry season, likely due to decomposition being highly seasonal and drastically reduced during the 7- to 8-month period without rain. New mycorrhizal propagules develop in the rainy season (at the same time, old ones are decomposed) and accumulate during the dry season. Propagules diminished during the rainy season in all plots, likely due to their participation in the establishment of new colonization and to the decomposition of old propagules when water entered the system after several rainless months. The progressive loss of propagules in the rainy season occurred in both forest and pasture plots, so the lower MPN in the pasture plots already in May (before the rain and the new growth season started) and maintained in the rainy season was interpreted as a result of damaged propagules. This reduction, however, seemed not to have a strong effect considering the entire study period and the other variables measured. The extremely low proportion of viable spores and intraradical colonization in both forest and pasture might explain why, despite the clear MPN reduction immediately after burning, the differences became smaller in the subsequent months.

The low viability was probably due to heat desiccation in the dry months and to predator activities, which were evident upon inspection. Low spore production and low spore viability suggest these are not important propagules in our tropical dry forest site, similar to other ecosystems in which colonized root fragments and pre-existing hyphal networks (Jasper et al. 1989; McGee 1989) are the main inoculum source of AM. Studies by Allen et al. (1998) in neighboring forests and pastures of the Chamela region and Guadarrama et al. (2008) in Oaxaca, Mexico have reported similarly low spore numbers with many damaged or desiccated spores. They concluded that these propagules may have a low contribution to the colonization potential of soils in tropical dry forests. Spore numbers reported for tropical dry forests are also one or two orders of magnitude lower than those reported for Neotropical forests with more than 1,000 mm mean annual rainfall (Johnson and Wedin 1997; Picone 2000; Lovelock and Ewel 2005).

In contrast to spore seasonality, neither total mycorrhizal colonization nor viable colonization differed between the dry (May) and wet (October) months in forest and pasture. This indicates that intraradical colonization remains active during the dry period when plants have shed their leaves and ceased to grow due to low water availability. Allen et al. (1998) had also observed root colonization in the dry period in other tropical forest sites of the Chamela region. Castellanos et al. (2001) have shown that a pool of live fine roots (<1 mm) persists during the dry season at the same study plots and that roots 1.1–5.0 mm in diameter are not sensitive to seasonality in both forest and pasture. The presence of live roots and intraradical colonization reported before and our observation of viable intraradical colonization suggest that plants continue to support the symbiont despite the lack of photosynthesis in the dry season. The source of carbon for root and symbiont activity and the mechanism to avoid root desiccation and decay remain to be determined.

Several authors have reported that disturbed ecosystems show a decrease in the number of AM infective propagules (Reeves et al. 1979; Janos 1980; Jasper et al. 1989) and changes in species diversity (Cuenca and Lovera 1992; Allen et al. 1998) and spore abundance (Dhillion et al. 1988; Wicklow-Howard 1989; Vilariño and Arines 1991). However, other results have shown little or no changes in AM fungi diversity and abundance due to fire and the establishment of new conditions (Bentivenga and Hetrick 1991, 1992; Bellgard et al. 1994; Johnson and Wedin 1997; Rashid et al. 1997). Apparently, a single fire followed by cultivation in our study resulted in some small immediate changes in AMF communities and propagules. However, in this ecosystem which does not experience natural periodical fires, forest conversion to cultivated land seems to establish a set of new conditions that originates a slow, but steady, transformation whose strongest effects can be measured several years later (Allen et al. 1998; Alvarez-Santiago 2002; Gavito et al. 2008). The prolonged effects of conversion and management, through changes in plant species composition, soil quality, and microclimate, seem to play a more important role than the slash-and-burn process in defining the AMF communities established after forest conversion to pasture, as reported in other studies and discussed above.

We conclude that, likely because of the low heat conductivity of the soil and the rapid combustion of most plant residues, the direct and immediate damage by fire on AMF was minor.

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