Mycorrhiza (1996) 6:111–118

ORIGINAL PAPER

Milagros Lovera · Gisela Cuenca

Arbuscular mycorrhizal infection in Cyperaceae and Gramineae from natural, disturbed and restored savannas in La Gran Sabana, Venezuela

Accepted: 10 July 1995

Abstract The mycorrhizae of a tropical savanna growing in oligotrophic and stony soils were compared with those of a disturbed area that had been reclaimed with introduced species and of an area that was disturbed but not revegetated. All were compared with natural regeneration in a savanna that had been disturbed 12 years previously. Arbuscular mycorrhizae (AM) were common in savannas. Cyperaceae species, which were codominant with Graminaea, showed high levels of infection frequency (45%) like the Gramineae (61%). Arbuscules observed in the Cyperaceae indicated functionality. There were few plants in disturbed, nonrevegetated sites, but those present had AM. Observations of roots from soil monoliths showed that AM were present in disturbed areas, but compared with natural, succesional and revegetated savanna had a lower infection frequency (48–59% vs 75%), lower intensity (10–15% vs 25%) and a lower percentage of arbuscules (0.7–0.8% vs 2.3%). The percentage of vesicles was also lower in succesional savanna than in natural savanna (1.6% vs 4.8%). The revegetated site had the highest percentage of vesicles (6.6%). Although a high frequency of mycorrhizal infection has been reestablished in disturbed areas, the intensity and structure of the infection suggests that mycorrhizal function has not been restored to the original levels. We hypothesize that neither plants nor fungi have adapted to the new edaphic conditions.

M. Lovera[1] (✉)
Universidad Simón Bolívar, Departamento de Biología de Organismos, Sartenejas, Caracas, Venezuela

G. Cuenca
Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC), Apartado 21827, Caracas 1020 A, Venezuela

Present address:
[1] Centro de Biofísica y Bioquímica, Instituto Venezolano de Investigaciones Científicas (IVIC), Apartado 21827, Caracas 1020 A, Venezuela
Fax: +58-2-5713164; E-mail: mlovera@cbb.ivic.ve

Key words Arbuscules · Disturbance · Endomycorrhizae · Succession · Tropical savanna

Introduction

In view of the increasing degradation of tropical areas, information about the contribution of mycorrhizae to ecosystem restoration in tropical areas is unfortunately scarce. In tropical soils, phosphorus usually limits plant growth. This is mainly due to the acidity and high content of soluble aluminum in those soils (Sánchez 1976). Thus, mycorrhizae could be very important for tropical communities.

Many studies indicate that obligate mycotrophic plants are common in tropical ecosystems (Janos 1980; Hayman 1982). Such species cannot survive to reproductive maturity if uninfected at the fertility levels encountered in their natural habits (Janos 1980). However, nonmycotrophic plants seem to predominate in disturbed soils. Presumably, arbuscular mycorrhizal fungi (AMF) are mainly distributed in the upper layers of soils and their highest density is encountered in the rhizosphere (Schwab and Reeves 1981; Bellgard 1993). When soil is disturbed and removed, AMF propagules are lost (Hetrick 1984).

Janos (1980) proposed that facultatively mycotrophic plants facilitate succession toward a mycotrophic community by providing an inoculum source that enhances the establishment of obligately mycotrophic plants. This hypothesis was modified by Allen and Allen (1990), who suggested that mycorrhizal status and succession can vary depending on the moisture and nutrient condition of the environment.

Previously, in savannas of La Gran Sabana region, we found that disturbance reduced mycorrhizal propagule density (Cuenca and Lovera 1992). We also showed that the colonizing species are mainly mycotrophic.

The aims of this present work were (1) to determine the mycorrhizal status of a tropical savanna growing in

old acidic nutrient-poor soils, and (2) to describe the change in quantity and quality of the AM infection in areas that had been disturbed and in some cases restored. We also assessed the natural revegetation process in a savanna that was disturbed 12 years ago but not revegetated.

Materials and methods

Site description

The savannas studied are located in the Canaima National Park in the southeast of Venezuela, a part of La Gran Sabana region which extends from 4°30″N to 6°45″N and from 60 34″W to 62°50″W. La Gran Sabana is a plateau with decreasing altitude from 1440 m in the north to 800 m in the south. The work was conducted along the road that joins Km 88 Town in the North with Brazil in the South. For more details about the site, see Cuenca and Lovera (1992). Between Km 88 Town and Santa Elena de Uairén, in the sites disturbed by road building, soil organic layers were removed by bulldozers. In a program to recover the disturbed areas, they were revegetated by introducing grasses and legumes.

The climate is equatorial and annual rainfall is approximately 2200 mm, well distributed throughout the year except for two relatively dry months (January and February). Temperature changes are small throughout the year with a mean temperature of 20.6 °C. The vegetation is savanna mixed with patches of forest. The savanna is dominated by a mix of Gramineae and Cyperaceae; it is usually burned by the people of the zone.

Sampling Sites

Four sites were selected to perform this study: a natural savanna, a recently disturbed savanna, a disturbed savanna that had been revegetated with introduced species and a savanna that had been disturbed 12 years previously and had not been revegetated. A 20×25 m plot was established at each site.

Selected plots had a similar slope ($<20°$) and the following characteristics:

Natural savanna (NS): This was an open savanna without woody elements. The most common plant families were Gramineae and Cyperaceae (Fig. 1a).

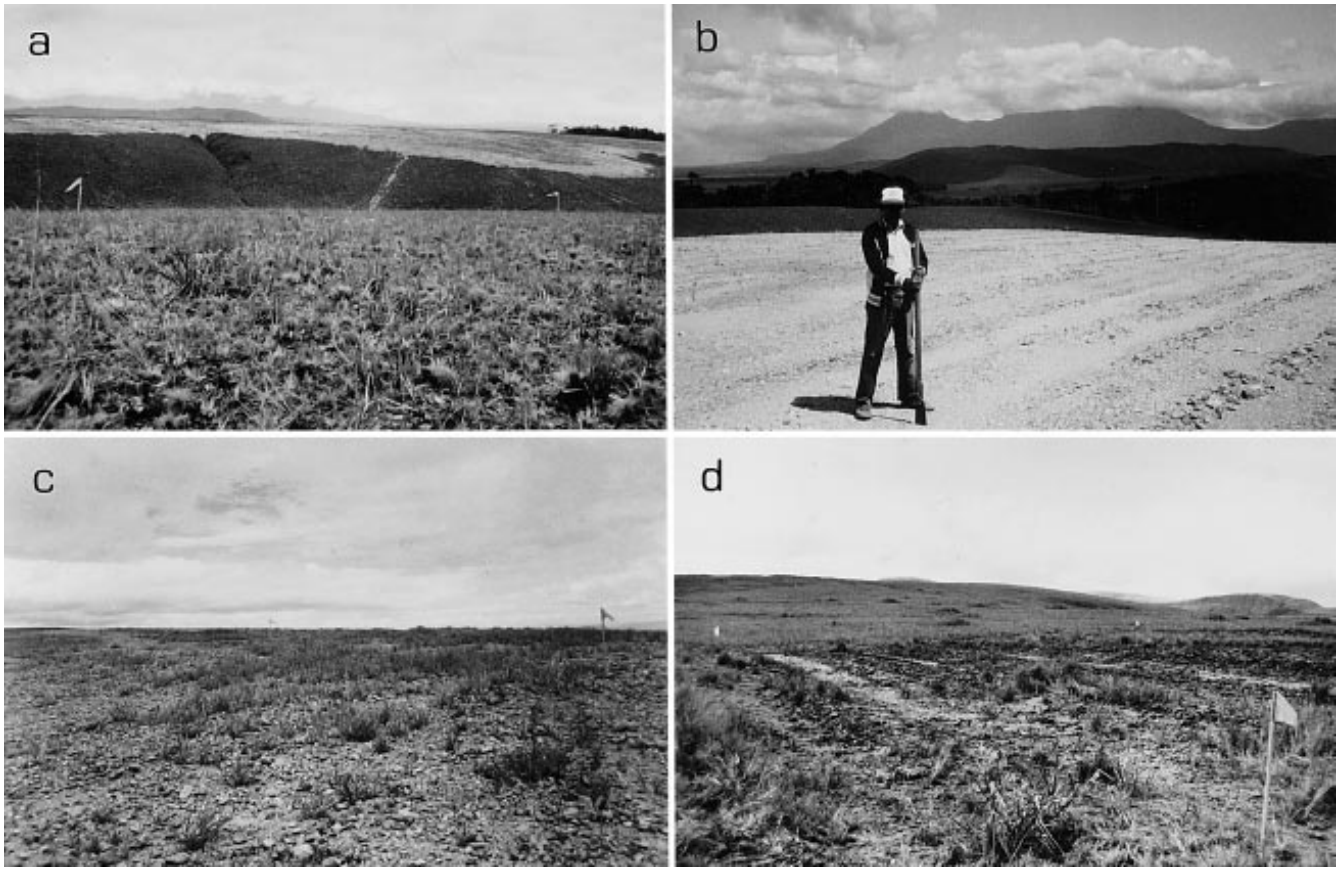
Disturbed savanna (DS): In this plot the soil organic layer had been recently removed to a depth of 1 m. This area was neither sowed nor fertilized (Fig. 1b).

Revegetated savanna (RS): This plot was established in an area disturbed in the same manner and at the same time as DS, but in this case, the plot had been planted with *Brachiaria decumbens* (7 kg/ha), *Brachiaria humidicola* (3 kg/ha) and *Calopogonium* sp. (1 kg/ha). Seeds were mixed with fertilizers (200 kg/ha of NPK in the proportions 12:24:12) at the time of sowing, and 800 kg/ha of lime was also added. Four months later, a second dose of fertilizers was applied at the same rate (Fig. 1c).

Old disturbed savanna (OS): This plot had been disturbed 12 years previously and the soil organic layer removed to a depth of 1 m. It had not been replanted or fertilized (Fig. 1d).

All samples (soil and plants) were collected during the rainy season in May and June, 1989.

Fig. 1a–d The study sites in La Gran Sabana. **a** Natural savanna (NS) in the first plane; behind it can be seen a disturbed and revegetated area. **b** Disturbed savanna (DS) 1 year after disturbance. **c** Recovered savanna (RS); note the stoniness of the soil. **d** Old disturbed savanna (OS) 12 years after disturbance



Vegetation description

Twenty 0.5 × 0.5 m quadrats placed at random were used to estimate coverage, frequency and density values. In addition, the importance value index was obtained for each species encountered (Kershaw 1973) at each studied site.

Fine root biomass and length

Fine roots (< 3 mm in diameter) were quantified by taking monoliths from the soil profile following the method of Bohm (1979), and adapted by Herrera (1985) to assess the importance of AM in natural ecosystems. In each plot (except in DS) five 15 × 15 × 10 cm randomly distributed soil monoliths were extracted. To extract the roots, all the soil from each monolith was screened through 2-mm and 0.5-mm sieves with the help of a jet of water. The two fractions obtained were dried at 60 °C to constant weight and all roots extracted by hand using tweezers. A mix of the finest root fragments and organic matter remained. To quantify the roots within this fraction, three aliquots were examined under the stereomicroscope to select roots. From the weight of these finest roots the weight for the entire finest root fraction was estimated by extrapolation. Root biomans was quantified for two root diameter categories (1–3 mm and < 1). Root length of fine roots (diameter < 1 mm) was estimated by the method of Newman (1966).

Arbuscular-mycorrhizal infection

Fine roots of five individuals from the most abundant plant species were extracted. Composite samples of five individuals were collected from the plant species with lesser frequency values (< 5 in NS, < 0.25 in RS and < 0.15 in OS). To assess AM infection only fine roots < 1 mm were stained (Phillips and Hayman 1970).

Mycorrhizal infection was assessed using the method of Trouvelot et al. (1986) with some modifications. This method allows simultaneous evaluation of percentage infection (%F), the intensity of this infection (%M) and the proportion of arbuscules (%A) and vesicles (%V) present.

In our study, it was difficult to evaluate the mycorrhizal infection of the whole fragment because roots were heavily pigmented and colonized by non-mycorrhizal fungi that also stained with trypan blue. Therefore, the infection was quantified in four microscope fields, unsing 50 2-cm-long root segments. Percentage infection of soil monoliths was also assessed on a sample of 50 2-cm root segments.

In these samples, the proportion of arbuscules and vesicles present was calculated as the mean abundance of each structure by:

$$\%A = \frac{75\,nA + 30\,n\underline{A} + 5\,n\underline{\underline{A}}}{N}$$

where nA is the number of microscope fields with 51–100% arbuscules in the infected area (class A), n$\underline{A}$ is the number of microscope fields with 11–50% of arbuscules in the infected area (class $\underline{A}$) and n$\underline{\underline{A}}$ is the number of microscope fields with 1–10% of arbuscules in the infected area (class $\underline{\underline{A}}$).

Soil analyses

Soils from the selected plots were sampled to a depth of 0–15 cm. Soil texture was assessed by the Bouyoucos method and bulk density according to Herrera (1979). Soil pH, organic matter (Walkey-Black) and total N (microKjeldahl) were measured according to Jackson (1976). Extractable P was assessed by extracting 5 g of soil in 25 ml of weak acid (1:1 0.05 M HCl and 0.025 M H_2SO_4) according to Nelson et al. (1953). Total phosphorus was digested with a binary mix ($H_2SO_4 - HClO_4$). In both extracts, phosphorus was measured by the method of Murphy and Riley (1962). Exchangeable Ca, K and Mg were measured by atomic absorption spectrophotometry. Soil acidity and exchangeable Al were determined according to Thomas (1982).

Results

In NS, more than 40% is bare soil. The plant coverage consists mainly of Gramineae and Cyperaceae, and both families are present in approximately the same proportion. Plant species with the highest importance value indices are two grasses (*Paspalum carinatum* and *Trachypogon plumosus*) and two Cyperaceae (*Bulbostylis paradoxa* and *Rhynchospora brasiliensis*) (Table 1).

In DS, the plant coverage is still only 0.1% 1 year after disturbance. In RS, plant coverage was restored partially but it is still lower than in NS. RS is dominated by *Brachiaria decumbens* (Table 1). *Brachiaria decumbens* individuals showed phosphorus deficiency symptoms. The sowed legume *Calopogonium* sp. appeared rarely and did not show deficiency symptoms but was always without nodules for N^2 fixation.

Ten plant species were present in RS. Of these species, three were sown and the others were indigenous. Many of the indigenous plant species are typical of NS (Huber 1986). The fern *Pityrogramma calomelanos,* the Cyperaceae *Bulbostylis capillaris* and some Compositae species are colonizing species rarely seen in NS. OS had a plant coverage of only 13% with *Trachypogon plumo-*

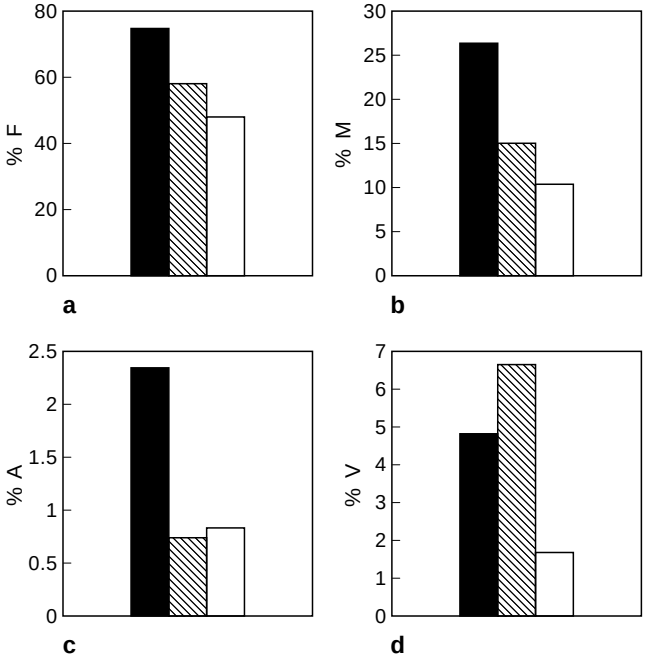


Fig. 2a–d AM infection characteristics of the intact soils. **a** Frequency of AM infection (% *F*); **b** percentage intensity of AM infection (% *M*); **c** percentage arbuscules (% *A*); **d** percentage vesicles (% *V*). Experimental plots: ■ NS, ▨ RS, □ OS

Table 1 Species composition of the sites studied in La Gran Sabana (– importance value index not measured)

Species	Family	Importance value index
Natural savanna		
Paspalum cf. *cartinatum**	Gramineae	152.4
Bulbostylis paradoxa Kth.*	Cyperaceae	138.3
Trachypogon plumosus (H&B ex Willd) Ness	Gramineae	136.8
Rhynchospora cf. *brasiliensis*	Cyperaceae	134.5
Sclerya cyperina Kth.*	Cyperaceae	102.9
Axonopus pruinosus Henr.	Gramineae	102.4
Lagenocarpus cf. *guianensis*	Cyperaceae	99.5
Raddiella esembeckii (Stend) Cald. & Soder.	Gramineae	42.7
Panicum micranthum H.B.K.	Gramineae	37.6
Rhynchospora barbata (Vahl.) Boeck	Cyperaceae	37.0
Echinolaena inflexa (Poir) Chase	Gramineae	10.5
Hypolytrum pulchrum (Rudge) Pfeiffer*	Cyperaceae	5.2
Sisyrinchium alatum Hook	Iridaceae	5.2
Revegetated savanna		
Brachiaria decumbens (Stapf) Prain	Gramineae	139.1
Brachiaria humidicola (Rendle) Schweickerdt	Gramineae	48.4
Calopogonium sp.	Leguminosae	21.1
Rhynchospora barbata (Vahl.) Boeck	Cyperaceae	20.5
Sclerya cyperina Kth.*	Cyperaceae	11.0
Bulbostylis cf. *capillaris*	Cyperaceae	10.8
Paspalum cf. *carinatum**	Gramineae	6.1
Panicum micranthum H.B.K.	Gramineae	5.3
Pityrogramma calomelanos Link	Pteridophyta	5.2
Unidentified	Compositae	5.1
Old disturbed savanna		
Bulbostylis paradoxa Kth.*	Cyperaceae	61.8
Trachypogon plumosus (H&B ex Willd) Ness	Gramineae	50.3
Paspalum cf. *carinatum**	Gramineae	18.3
Sclerya cyperina Kth.*	Cyperaceae	11.7
Hypolytrum pulchrum (Rudge) Pfeiffer*	Cyperaceae	11.6
Bulbostylis cf. *capillaris**	Cyperaceae	11.0
Panicum micranthum H.B.K.	Gramineae	10.8
Axonopus pruinosus Henr.	Gramineae	6.4
Raddiella esembeckii (Stend) Calder. & Soer.	Gramineae	6.0
Palicourea rigida H.B.K.	Rubiaceae	5.6
Disturbed savanna		
Bulbostylis cf. *conifera*	Cyperaceae	–
Lagenocarpus sp.	Cyperaceae	–
Unidentified	Solanaceae	–

* Flowering plants at the moment of sampling

sus and *Bulbostylis paradoxa* being the most important species (Table 1).

Fine roots represented most (85%) of total root biomass. NS contained the highest root biomass (in both diameter categories) and root length of all plots, and RS showed higher values for these variables than OS (Table 2).

AM infection for each plot is shown in Fig. 2. Frequency (%F) was higher in NS than in DS, and there were differences between OS and RS (Fig. 2a). The intensity of infection (%M) was higher in NS than in disturbed areas (Fig. 2b). The same results were obtained for percentage arbuscules, the functional structures of arbuscular mycorrhizae (Fig. 2c). The highest value for percentage vesicles was found in RS and the lowest in OS (Fig. 2d).

Colonization of plant species in NS and DS showed several interesting patterns (Table 3). All plants sam-

Table 2 Root biomass and root length (<1 mm) at the studied sites in La Gran Sabana

Parameter	Natural savanna	Disturbed savanna	
	NS	RS	OS
Root biomass (g/m^2) (1–3 mm)	36.1	4.6	2.6
Root biomass (g/m^2) (<1 mm)	222.8	82.6	66.5
Root length (km/m^2) (<1 mm)	8.4	3.9	3.1
Length (km/m^2) of AM-infected roots (<1 mm)	6.3	2.5	1.5

Table 3 Arbuscular-mycorrhizal (AM) infection in plant species from the study sites. Values are the mean of five individuals, except those marked cs, which come from composite samples. Each * indicates an individual or a cs without arbuscules

Species	Family	AM infection	
		%F	%M
Natural savanna			
Paspalum cf. *carinatum*	Gramineae	74.0	17.0
Trachypogon plumosus	Gramineae	75.4	15.3
Bulbostylis paradoxa	Cyperaceae	74.9	17.0
Rhynchospora brasiliensis	Cyperaceae	45.1	5.6 **
Axonopus pruinosus	Gramineae	70.1	16.7
Lagenocarpus guianensis	Cyperaceae	35.1	4.5 ***
Sclerya cyperina	Cyperaceae	59.0 cs	13.8 cs
Raddiella esembeckii	Gramineae	71.0 cs	17.0 cs
Panicum micranthum	Gramineae	63.0 cs	6.6 cs*
Rhynchospora barbata	Cyperaceae	59.8 cs	8.3 cs
Echinolaena inflexa	Gramineae	55.5 cs	5.0 cs*
Hypolytrum pulchrum	Cyperaceae	55.0 cs	16.0 cs*
Revegetated savanna			
Brachiaria decumbens	Gramineae	74.2	23.8
Brachiaria humidicola	Gramineae	72.2	24.0
Rhynchospora barbata	Cyperaceae	62.1	22.0
Calopogonium sp.	Leguminosae	84.2 cs	24.4 cs
Sclerya cyperina	Cyperaceae	32.7 cs	3.3 cs
Bulbostylis cf. *capillaris*	Cyperaceae	10.5 cs	1.0 cs
Paspalum cf. *carinatum*	Gramineae	28.5 cs	23.7 cs
Panicum micranthum	Gramineae	26.1 cs	14.2 cs
Old disturbed savanna			
Trachypogon plumosus	Gramineae	51.8	6.3
Bulbostylis paradoxa	Cyperaceae	40.0	5.1 *
Paspalum cf. *carinatum*	Gramineae	64.4	10.5 *
Sclerya cyperina	Cyperaceae	46.6	5.5 **
Hypolytrum pulchrum	Cyperaceae	35.2	2.3 ***
Bulbostylis cf. *capillaris*	Cyperaceae	32.8	2.8 ***
Panicum micranthum	Gramineae	56.3	6.0 **
Axonopus pruinosus	Gramineae	64.0	13.7
Raddiella esembeckii	Gramineae	62.6	12.7 *
Palicourea rigida	Rubiaceae	36.0 cs	5.8 cs
Disturbed savanna			
Bulbostylis cf. *conifera*	Cyperaceae	36.6	14.2
Lagenocarpus sp.	Cyperaceae	1.0	0.01 ***
Unidentified	Solanaceae	44.9 cs	9.9 cs

Table 4 Physical characteristics of soils (0–15 cm depth) from the study sites

		Natural savanna	Disturbed savanna		
		NS	RS	OS	DS
Soil texture		Sandy-loam	Sandy-loam	Loam	Sandy-loam
Granulometry	<2 mm	17.6	22.5	26.0	25.6
	2–5.6 mm	14.7	16.1	20.6	14.2
	>5.6 mm	65.2	61.4	53.4	60.3
Stoniness (%)		79.9	77.5	74.1	74.3
Bulk density (g/cm^3)		1.6	1.7	1.6	1.8

pled were mycorrhizal, with the highest infection found in *Calopogonium* sp. and the lowest in the two indigenous Cyperaceae: *Lagenocarpus* sp. (DS) and *Bulbostylis capillaris* (RS). These two species were considered nonmycorrhizal because they did not have arbuscules. While the majority of samples taken had arbuscules, species of the Cyperaceae frequently lacked arbuscules. However, *Bulbostylis paradoxa* and *Rhynchospora barbata* were notably exceptions. These species had higher percentage infection than many grasses (Table 3) with both arbuscule and hyphal coils (Fig. 3).

Soils from La Gran Sabana are oligotrophic. The texture and stoniness of the soils appeared to unchanged by removing the organic layer (Table 4). All soils were stony (74%). Bulk density values were higher for DS, indicating that this soil became more com-

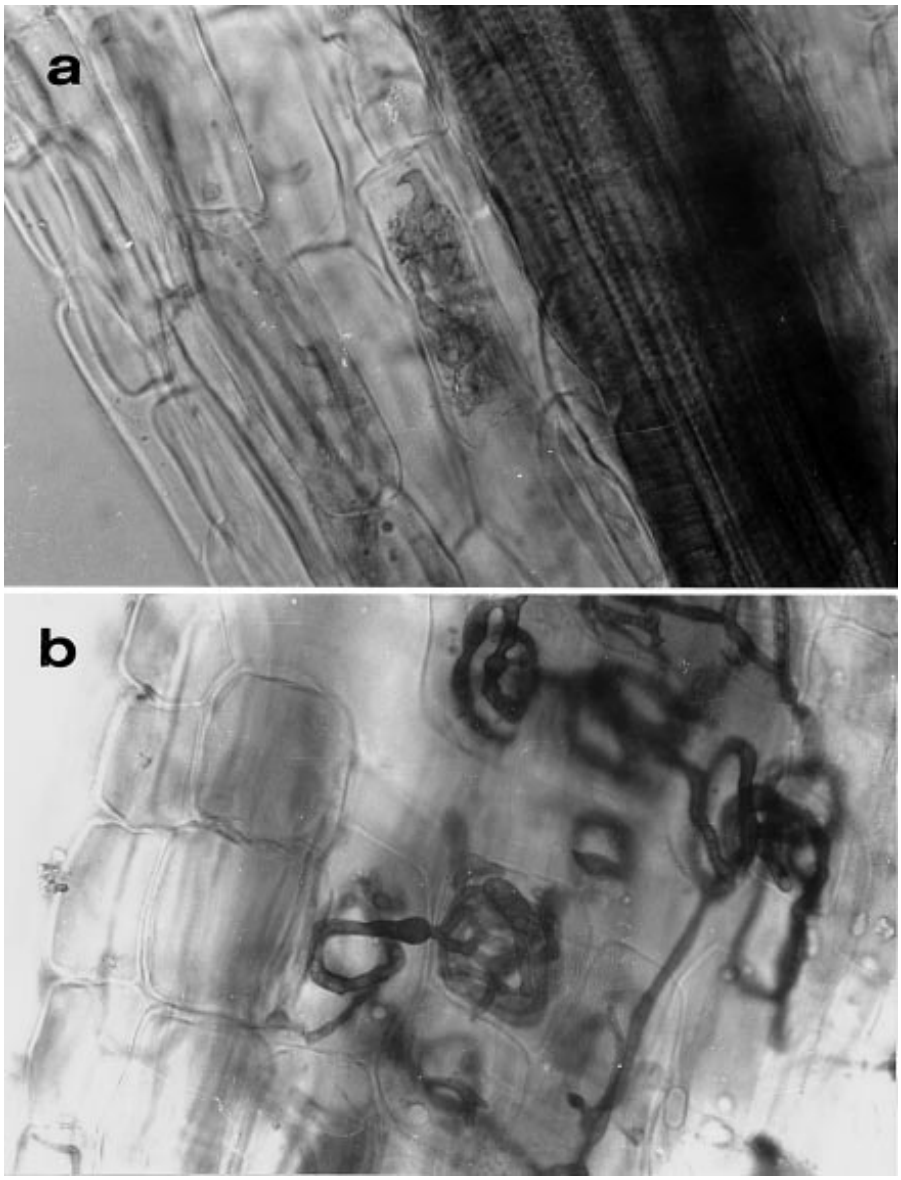


Fig. 3a, b General aspects of mycorrhizal infection in *Rhynchospora barbata* (Cyperaceae). **a** Arbuscule; **b** hyphal coils

Table 5 Chemical analyses of soils (0–15 cm depth) from the studied sites

	pH		OM (%)	C (%)	N (mg/g)	P (μg/g)		K	Ca	Mg	H+Al	Al	H
	H_2O	KCl				Exchangeable	Total	mEq/100 g					
Natural savanna	4.9	3.9	3.97	2.30	2.52	0.00	65.8	0.077	0.089	0.082	1.75	0.50	1.25
Revegetated savanna	5.1	4.2	2.14	1.24	0.91	0.70	115.1	0.157	0.356	0.035	0.23	0.05	0.18
Old disturbed savanna	4.3	4.1	2.80	1.62	1.16	0.00	121.9	0.068	0.122	0.050	0.25	0.04	0.21
Disturbed savanna	4.5	4.4	0.99	0.57	0.39	0.00	18.8	0.017	0.099	0.028	0.09	0.01	0.08

pact after soil disturbance. The soils were strongly acidic (Table 5), with the slightly higher pH of RS due to applied lime. Disturbance also reduced organic matter. The exchange capacity of all soils was dominated by Al^{3+} and H^+ (Table 5); however, the aluminum concentration did not reach toxic levels at any studied site.

Discussion

In an oligotrophic environment such as La Gran Sabana, severe disturbance hinders the establishment of the vegetation. In most ecosystems, fast-growing annual plants are the first to colonize bare areas, and they often facilitate succession towards a stable community.

However, their establishment needs an initial pulse of nutrients, such as can come from slashing and burning the original forest (Grime 1977). In the present case, removal of the soil surface layer caused a much greater disturbance in which not only the vegetation but also soil nutrients were lost.

Mycorrhizae are clearly an important component of these oligotrophic savannas. These results contrast with the hypothesis of Janos (1980) that nonmycotrophic species predominate in disturbed areas. Alternatively, Allen and Allen (1990) pointed out that facultative mycotrophic plants would be more important than nonmycotrophic ones in oligotrophic sites. All plants collected in disturbed areas were infected, despite the low number of propagules present after disturbance (Lovera 1991).

A further important observation was that all Cyperaceae species sampled were mycorrhizal, although this is considered to be a nonmycorrhizal family. In most plants of the Cyperaceae studied, the mycorrhizae were well developed and in most of them arbuscules were observed. In the individuals without arbuscules, we found an abundance of hyphal coils in the root cortex (peletons) for which the functional role is not yet clearly defined. However, because there is ATPase activity in coils (Smith and Gianinazzi-Pearson 1988), some exchange may occur. Allen (1983) obtained results very similar to ours in field samples with arbuscules in shrubby Chenopodiaceae.

Mycorrhizal associations were very common in NS and disturbed sites, but there was less infection (both in intensity and frequency) in disturbed plots than in NS in the monolith samples. Allen and Allen (1980), Stahl et al. (1988) and others have obtained similar results in cases in which the disturbance did not eliminate all propagules. The revegetation improved the total root length and AM infection, and the introduction of *Brachiaria decumbens* could have been a key factor in the recuperation of disturbed areas, because it prevented the loss of AM fungi after disturbance. Clearly, the rate of recovery was higher in RS than in those regions where only natural processes were involved. The higher values for percentage vesicles observed in RS could be related to encouragement of AMF activity produced by the sowing of this plot.

In summary, we conclude that in the nutritionally poor condition of La Gran Sabana soils, the presence of AM is a general trait of the savanna vegetation and it seems to be a key factor in their maintenance. The infection found in Cyperaceae suggests that even plant species that usually do not form mycorrhizae have this symbiosis. Nevertheless, it is necessary to experimentally manipulate the fertility levels and AM in these plant species in order to determine more exactly the degree of mycorrhizal dependency of Cyperaceae. Finally, although AM infection occurred in disturbed areas, the lower percentage of arbuscules indicates that mycorrhizal function had not been restored to the original levels of the natural savanna.

Acknowledgements We thank EDELCA (Caroní River Hydroelectric Company) for their logistic support in La Gran Sabana and Mr. Luis Tovar and Mr. Gonzalo Febres for their help in the field work. We are grateful to Dr. Otto Huber, who kindly identified the plant species, and to Dr. Rafael Herrera, who read the manuscript and offered helpful comments. We also thank Laura Martín, Gladys Escalante and Erasmo Meneses for their valuable help with the soil analyses and Berta Sánchez for typing the manuscript.

References

Allen EB, Allen MF (1980) Natural re-establishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. J Appl Ecol 17:139–147

Allen EB, Allen MF (1990) The mediation of competition by mycorrhizae in succesional and patchy environments. In: Grace JB, Tilman GD (eds) Perspectives on plant competition. Harcourt Brace Jovanovich, Academic Press, New York, pp 367–389

Allen MF (1983) Formation of VA-mycorrhizae in *Atriplex gardneri* (Chenopodiaceae): seasonal response in a cold desert. Mycologia 75:773–776

Bellgard SE (1993) The topsoil as the major store of the propagules of vesicular-arbuscular mycorrhizal fungi in southeast Australien sandstone soils. Mycorrhiza 3:19–24

Bohm W (1979) Methods of studying root systems. In: Ecological studies. Springer, Berlin Heidelberg New York

Cuenca G, Lovera M (1992) Vesicular-arbuscular mycorrhizae in disturbed and revegetated sites from La Gran Sabana, Venezuela. Can J Bot 70:73–79

Grime JP (1977) Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Hayman DS (1982) Influence of soils and fertility on activity and survival of vesicular-arbuscular mycorrhizal fungi. Am Phytopathol Soc 72:1119–1125

Herrera R (1979) Nutrient distribution and cycling in an Amazon Caatinga Forest on spodosols in Southern Venezuela. PhD thesis, University of Reading, UK

Herrera RA (1985) Las micorrizas VA como ayuda para la repoblación forestal de Cuba. In: Ciclo lectivo sobre: Técnicas de investigación en micorrizas. Informe Provisional No. 18, International Foundation for Science, Stockholm, Sweden, pp 377–407

Hetrick BAD (1984) Ecology of VA-mycorrhizal fungi In: Powell CL, Bagyaraj DJ (eds) VA-mycorrhiza. CRC Press, Boca Raton, Fla, pp 35–55

Huber O (1986) La vegetación de la Cuenca del Río Caroní. Interciencia 11:301–310

Jackson ML (1976) Análisis químico del suelo, 3rd edn. Edic Omega SA, Barcelona

Janos DP (1980) Mycorrhizae influence tropical succession. Biotropica 12:56–64

Kershaw KA (1973) Quantitative and dynamic plant ecology, 2nd edn. Academic Press, London, pp 308

Lovera M (1991) El papel de las micorrizas VA en la recuperación de zonas perturbadas de La Gran Sabana (Edo. Bolívar, Venezuela). Licenciature thesis, Simón Bolívar University, Caracas

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27:31–36

Nelson WL, Mehlich A, Winters E (1953) The development, evolution and use of a soil test for phosphorus availability. Agronomy 4:153–18

Newman EI (1966) A method of estimating the total length of root in a sample. J Appl Ecol 6:293–300

Phillips JM, Hayman DS (1970) Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans Br Mycol Soc 55:158–161

Sánchez P (1976) Properties and management of soils in the tropics. Wiley, New York

Schwab S, Reeves FB (1981) The role of endomycorrhizae in revegetation practices in the semiarid west. III. Vertical distribution of VA-mycorrhiza inoculum potential. Am J Bot 68:1293–1297

Smith SE, Gianinazzi-Pearson V (1988) Physiological interactions between symbionts in vesicular-arbuscular mycorrhizal plants. Annu Rev Plant Physiol Plant Mol Biol 39:221–244

Stahl PD, Williams SE, Christensen M (1988) Efficacy of native vesicular-arbuscular fungi after severe soil disturbance. New Phytol 110:347–354

Thomas GW (1982) Exchangeable cations. In: Page AL, Miller RH, Keeny DR (eds) Methods of soil analysis. 2. Chemical and microbiological properties. Agronomy Monograph No. 9. American Society of Agronomy, Madison, Wis, pp 159–165

Trouvelot A, Kough JL, Gianinazzi-Pearson V (1986) Measure du taux de mycorrhization VA d'un syeeme radiculair. Recherche de methodes d'estimation ayent une signification fonctionnelle. In: Gianinazzi-Pearson V, Gianinazzi S (eds) Physiological and genetical aspects of mycorrhizae. INRA, Paris, pp 626–630