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ORIGINAL PAPER

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Arbuscular mycorrhizae of the palm *Astrocaryum mexicanum* in disturbed and undisturbed stands of a Mexican tropical forest

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Abstract Tropical forests are dynamic systems with extensive natural disturbance, gaps in the canopy being one of the most important types. Tree and branch fall are often the principal cause of natural disturbance. This research was done on adult individuals of a very abundant palm (*Astrocaryum mexicanum* Liebm, Arecaceae), which is found in the understorey of the forest at Los Tuxtlas, Mexico. Percentages of colonization by arbuscular mycorrhizae were determined for individuals selected randomly from plots located both in gaps and under closed canopy. The highest percentages of total colonization, as well as those of hyphae and vesicles, were recorded for gaps. In forest with closed canopy, arbuscules had the highest percentages of colonization; on these sites the palm has been observed to grow less. The higher production of arbuscules may favour nutrient capture in this microenvironment, which is characterized by strong competition.

Keywords Arbuscular mycorrhizae · Tropical rain forest · Palms · *Astrocaryum mexicanum* · Mexico

Introduction

Tropical rain forest is one of the most diverse plant communities, with various vegetation patches caused principally by natural disturbance (Hartshorn 1978; Brokaw 1985). Most of the natural disturbance in humid forest occurs when trees fall, forming gaps in the canopy that modify microenvironmental conditions (Denslow 1985). At the soil level, there is an increase in temperature, humidity, and decomposition rate (Fetcher et al. 1985), as well as an increase in nutrient concentrations and availability (Vitousek and Denslow 1986), all of which influence the establishment of plant species that grow in those microenvironments (Bazzaz 1984).

Mycorrhizal fungi and plant roots form one of the most important biotic associations, called mycorrhizae, that are found in most ecosystems (Smith and Read 1997). In tropical systems, arbuscular mycorrhizae (AM) are the most important and abundant kind (Janos 1980a); nearly 80% of species examined correspond to this association (Redhead 1968).

Communities of arbuscular mycorrhizal fungi are also modified by disturbance, as microclimatic changes in soil modify spore density and the amount of inoculum (Diem et al. 1981; Cuenca and Lovera 1991) and the efficiency of the association with plants decreases (Creighton et al. 1986).

Fischer et al. (1994) reported that AM play a crucial role in the establishment and growth of seedlings of woody species and that in the adult phase they help increase fertility rate and photosynthetic surface, as well as providing nutrients for the plant, mainly N and P that are not easily available in soil (Marschner and Dell 1994). Thus, AM play an important role in the establishment and survival of plant species (Siqueira et al. 1988).

In Mexico's Los Tuxtlas forest, it has been determined that the greatest diversity in spores of mycorrhizal fungi occurs in closed canopy, while the greatest abundance is observed in pastures during the dry season (Guadarrama and Álvarez-Sánchez 1999). In this forest, it has also been observed that when the mycorrhizal association is present, plants faced with competition experience an increase in biomass and better survival rate as well as greater competitive success (Sánchez-Gallén and Guadarrama 2000).

Astrocaryum mexicanum is a dominant species in the understorey of tropical rain forest in Los Tuxtlas, a site characterized by a density of >1,000 individuals per hectare of this species (Martínez-Ramos and Álvarez-Buylla 1995).

This is a policarpic palm that reaches the reproductive stage at approximately 20–25 years of age; on average it achieves a height of 1–4 m (Piñero et al. 1982). It is a

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plant that has an average life-span of 130 years (Piñero et al. 1984). The species is classified as persistent [species that grow in the understorey and need the light conditions provided during the period of the open gap to grow (Martínez-Ramos 1994)]; it is nevertheless more successful in gaps than under closed canopy (Martínez-Ramos and Álvarez-Buylla 1995). Under the canopy, it can decrease its respiration, photosynthesis, and C fixation rates (Martínez-Ramos and Álvarez-Buylla 1995).

On average, when a gap is opened because a tree or branch has fallen, palms are knocked over but only 4% die. Of those that remain, leaf production increases at an average rate of 1.6–5 leaves per year. It has also been recorded that 40% of reproductive individuals undergo one to three reproductive events over an 8-year period under the canopy, while in gaps 70% had from four to six such events over 6 years (Martínez-Ramos 1985). Of the total energy allocation of this species 50–60% is expended mainly on leaf production (Piñero et al. 1982).

At Los Tuxtlas forest, three gaps >40 m^2/ha are created every year, of which 75% are opened by the fall of branches between 13.9 and 55.5 cm in diameter. There are 1.6 gaps of 100 m^2 produced per hectare created mainly by tree fall effects (Martínez-Ramos 1985). According to Hartshorn (1978) in a tropical rain forest, 6% of the soil surface is cover by gaps which are 6 years old or less.

The aim of this study was to determine changes in AM colonization of the palm *A. mexicanum*, which is found in both gaps and under closed canopy stands.

Materials and methods

Study site

The study was carried out at the Los Tuxtlas Tropical Biology Station, Universidad Nacional Autónoma de México. The station is located in Veracruz between 94°42′ and 95°27′ W and 18°10′ and 18°45′ N at an altitude of 15–530 m above sea level (Lot-Helgueras 1976). The soil is classified as an andisol, which has been replaced by alfisol in some sites; soils have a clayish-crumbly texture and accumulated organic matter in the upper layers (1.64–11.1%); porosity is medium, pH is between 4.1 and 6.1, and cationic exchange capacity changes for the A horizon from 18.8 to 46.9 mEq/100 g (Flores-Delgadillo et al. 1999).

The climate is warm and humid with a total annual precipitation of 4,700 mm. The lowest values are from March to May, when the dry season occurs (100 mm average per month); the rainy season is from June to February (486 mm on average per month). The region is affected by tropical hurricanes and strong cold northerly winds "nortes") from September to February. The mean annual temperature is 24°C, with a maximum in June (27.1°C) and a minimum in January (21.1°C).

The vegetation is tropical rain forest (Miranda and Hernández 1963). In the study site there are 940 species belonging to 129 Angiosperm families (Ibarra-Manríquez and Sinaca 1995). The most important species in the understorey is *Astrocaryum mexicanum* Liebm., whereas *Nectandra ambigens* (Blake) C.K. Allen, *Pseudolmedia oxyphyllaria* Donn. Sm., *Brosimum alicastrum* Sw., *Ficus yoponensis* Desv. and *Guarea glabra* Vahl. are frequent in the canopy (Bongers et al. 1988). A low density characterizes this forest (2,976 individuals with >1.0 cm DBH per hectare) (Bongers et al. 1988).

Arbuscular mycorrhizal colonization

Plots were randomly chosen, three under closed canopy (forest) and three in open canopy areas (gaps), 118.8, 235 and 250.14 m^2, respectively, and featuring adult individuals of *A. mexicanum*; the forest sites selected were in close proximity to the gaps. A brief description of each plot is shown in Table 1; the data are mean values of half-hourly measurements taken over a period of 5 h during 1 day in February 1999.

For each location, two groups containing three adult *A. mexicanum* individuals each were selected randomly. From each individual, fine roots were removed; three of the six were selected randomly for root collection in July (rainy season) and November (strong winds season) of 1996 and March (dry season) of 1997. The other three constituted a second group analysed in September (rainy season) of 1996, January (strong winds season) of 1997, and May (dry season) of 1997.

Each root sample was taken to the laboratory and cut into 1-cm-long fragments. They were then stained using the technique developed by Phillips and Hayman (1970); later, five mixtures that contained 15 root fragments each were prepared according to Schenck and Pérez (1990). For quantification of colonization levels, we employed the method of McGonigle et al. (1990), which consists of noting the presence and absence of each of the fungal structures (intraradical hyphae, arbuscules, and vesicles). In order to evaluate colonization percentages, totals of each structure were counted and divided among the total number of fields, thus providing the percentage for each structure as well as total colonization per sample. Average colonization was recorded for each microenvironment (closed forest and gap).

A two-way ANOVA with repeated measures was performed, as two samplings were done for each season, to determine significant differences between colonization percentages per structure and total for seasons and microenvironments. Later, a means analysis was done with the Tukey test (Zar 1999).

Because data take the form of percentages, transformation to give the natural logarithm was performed for arbuscules, vesicles, and total colonization; for hyphae, arc-sin transformation was used.

Table 1 Microclimate description for the plots at Los Tuxtlas Forest. Mean values of data collected at half-hourly intervals for 5 h are presented

	Gap 1	Gap 2	Gap 3	Closed canopy 1	Closed canopy 2	Closed canopy 3
Temperature (°C)	20.7	21.8	22.3	19.8	21	22
Soil temperature (°C)	18.2	20.6	20.8	17	18.8	19.4
Humidity (%)	82.4	83.2	81.8	90.7	97.4	93.2
Light under the canopy (lux)	33.8	6	18.8	8.4	2.8	4
Light above the canopy (lux)	30.8	10.1	31.2	15.7	3.2	7.9
Size (m^2)	118.85	234	250.14			

Results

Total colonization of AM

The highest percentages of total colonization were observed on palms in gaps during the rainy season, reaching a maximum of 80% in August during the second rainy season sampling. This was followed by the strong wind season (nortes), while the lowest percentages were recorded in the dry season. In forest sites, the highest colonization percentage (69%) also occurred during the second rainy season (Fig. 1a).

The ANOVA had significant *P* values for sampling period, microenvironment, and the interaction (Table 2).

According to the Tukey test, the dry and strong winds seasons were comparable and both notably different from the rainy season (Fig. 2a). For the interaction between season and microenvironment, two groups were distinguished: the first for a forest microenvironment combined with the dry and strong winds seasons, and the second consisting of gaps in all seasons (Fig. 2b). Forest stands in the rainy season yielded total colonization percentages similar to those of gaps.

Colonization percentages per structure

The hyphae in the roots formed coils, showing *Paris*-type colonization (Fig. 3).

Hyphae

Colonization percentages for hyphae are shown in Fig. 1b; the highest value was recorded in April, during the dry season. In gaps, this increase in colonization was observed starting with the second strong winds sampling (January 1997), while in forest sites, the highest percentages of hyphae were measured during the rainy and dry seasons. According to ANOVA, there were significant differences between microenvironments and seasons (Table 2).

According to the Tukey test, it was apparent that the strong wind season was different from both the rainy and dry seasons (Fig. 2c).

Arbuscules

Unlike all other structures analysed, the highest colonization percentages for arbuscules were recorded in forest sites, the maximum value appearing during the rainy season (August); the highest percentages in gaps appeared during the same season (Fig. 4a). Although they were present in every sample, a substantial decrease in the presence of arbuscules was observed as the strong winds season drew near.

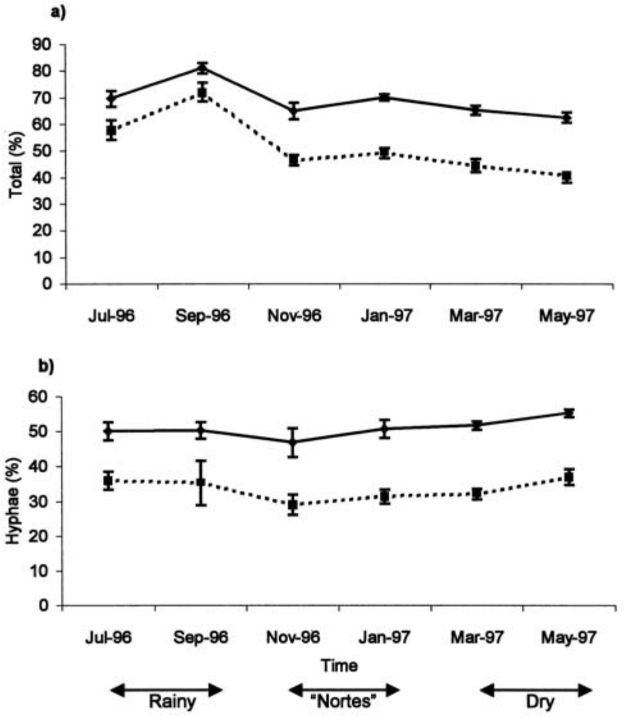

Fig. 1 Mean percentage (%) of **a** total colonization and **b** hyphae (±SE) in closed forest (*interrupted line*) and gaps (*continuous line*). *Jul-96* July 1996, *Sep-96* September 1996, *Nov-96* November 1996, *Jan-97* January 1997, *Mar-97* March 1997, *May-97* May 1997

Table 2 Results of ANOVA analysis (*F*-values) for total, hyphae, arbuscules and vesicles colonization. *S* Season, *M* microenvironment

	Hyphae	Arbuscules	Vesicles	Total
S	3.34*	43.00***	2.89	18.74***
M	100.59***	15.03***	29.81***	60.07***
S×M	1.53	0.52	0.99	3.70*

<p>*P<0.05, ***P<0.001</p>

ANOVA showed significant differences between both seasons and microenvironments (Table 2). Furthermore, the Tukey test showed differences between each season and the next (Fig. 2d).

Vesicles

There were two colonization peaks for vesicles in gaps, in the rainy and high wind seasons (September and January, Fig. 4b), while in the forest, only one peak was observed during the rainy season (September). The ANOVA showed significant differences only between microenvironments (Table 2).

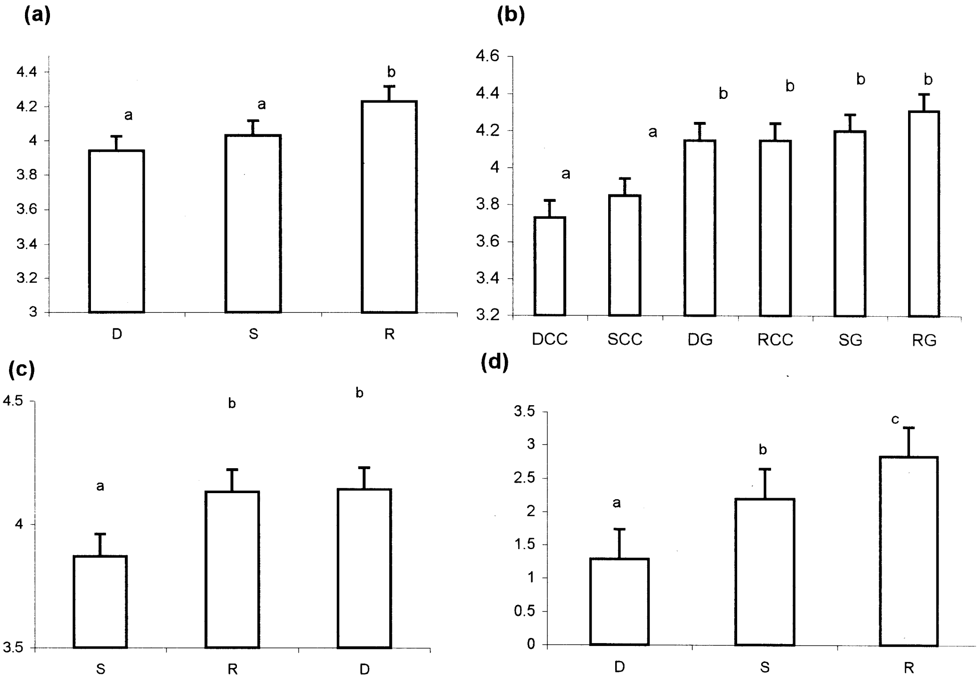

Fig. 2a–d Mean percentages of colonization (+SE) for each season [dry (*D*), strong winds (*S*), rainy (*R*)] and microenvironment [closed canopy (*CC*), gap (*G*)]. *Different letters* show significant differences according to Tukey' test ($P<0.05$). **a** Total, **b** season×microenvironment, **c** hyphae, **d** arbuscules

Fig. 3 Paris-type colonization on *Astrocaryum mexicanum* roots

Discussion

Just as natural disturbance affects the dynamics of forest plant cover, it influences microorganisms found in soil, including the inoculum potential of mycorrhizal fungae (Allen and Allen 1990). Janos (1980a) reports that after disturbance of great intensity, the first species to appear are those that do not interact with fungi (non-mycotrophic); later, the species that establish may or may not be plants with mycorrhizae. Finally, the species that establish permanently are those that need mycorrhizae in order to survive. What, then, occurs with *Astrocaryum mexicanum*, a tolerant species that thrives despite the creation of canopy gaps? It is useful to analyse why an increase in colonization percentages occurred.

It was noted that the highest colonization percentages for *A. mexicanum* were recorded during the rainy season (September 1996); this could be due to the fact that a greater abundance of spores occurs in the dry season (Guadarrama and Álvarez-Sánchez 1999), leading to the possibility that during the rainy season, germination begins and colonization of new roots follows (Gavito and Varela 1993).

Several conditions in both of the microenvironments affect palm development (light, nutrients, moisture, etc.), the principal limiting factor being light. Its presence favours the development of this species of palm

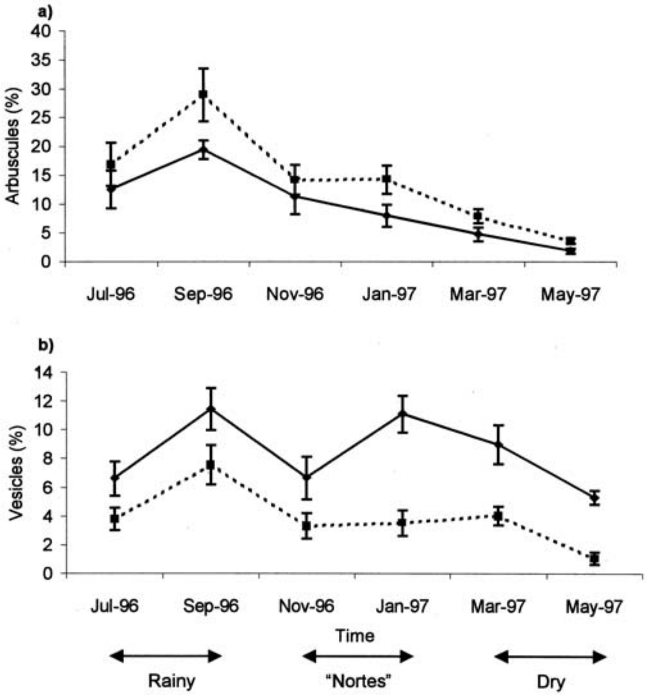

Fig. 4 Mean percentage (%) of colonization for **a** arbuscules and **b** vesicles (±SE) in closed forest (*interrupted line*) and gaps (*continuous line*)

(Martínez-Ramos 1994); the amount of colonization of hosts is likewise influenced.

Light increases height as well as the number of leaves and fruits; it also stimulates fine root production in forest (personal observation), which occurs as a response to disturbance in the first few centimetres of topsoil. For forest in general, it has been observed that fine root production is higher in the first 20 cm of soil (Sánchez-Gallén and Álvarez-Sánchez 1995), permitting the plants to offer a greater colonization surface for the fungus. It is important to note that *A. mexicanum* is characterized by few fine roots, as the diameters are usually >0.5 mm and lack root hairs like those of most palms (Tomlison 1990); they can be considered to be of the magnolioid variety and therefore susceptible to high degrees of mycorrhizal colonization in both forest microenvironments (Baylis 1975).

Nutrient availability is another factor that influences the amount of colonization by mycorrhizal fungi (Johnson et al. 1992). In Los Tuxtlas, the availability of P is extremely low (Flores-Delgadillo et al. 1999). These authors determined that P retention in Los Tuxtlas forest ranges from 5 to 96%; mycorrhizae there play an important role in the forest system by favouring the absorption of this nutrient.

Hyphal colonization percentages were high both in forest (40% on average) and gaps (50%); as the dry season drew near, the highest percentages were recorded. In the dry season, as arbuscules decrease, hyphae may become active nutrient interchange sites, although not with the same efficiency as arbuscules (Harrison 1997).

Unlike all other types of mycorrhizal colonization, arbuscular colonization reached its highest levels in forest. Arbuscules may play a more important role in forest under closed canopy than in gaps, as apparently competition for light and nutrients is greater in the former setting (Lewis and Tanner 2000); in this microenvironment, the palm is faced with more limiting resources than in gaps, where individuals of this species develop better (Martínez-Ramos and Álvarez-Buylla 1995). Thus, arbuscular colonization would increase nutrient absorption, lessening the competition.

Vesicles indicated higher levels of colonization in gaps than in closed canopy forest. As mentioned previously, the function of these structures is nutrient storage (Harrison 1997). Because higher percentages were found in gaps, individuals growing in this microenvironment may have the benefit of better nutrient storage than in closed canopy forest sites, as greater nutrient availability has been reported for gaps (Denslow et al. 1998). This in turn generates an increase in the production of carbohydrates, a vital resource for the fungus (Smith and Read 1997).

Another factor that may influence colonization in forest is competition, principally for N and P (Conell 1990). Such competition is not limited to seedling establishment but continues during the adult stage (Allen and Allen 1984,1990). According to Janos (1980b), competition for both light and soil nutrients could explain the increased importance that arbuscules have in these habitats.

Just as changes occur in vegetation when gaps are created (Bazzaz 1984), so there are differences in the mycorrhizosphere of undisturbed and disturbed sites, both in terms of spore composition and colonization (Janos 1980a). In Los Tuxtlas, high species diversity (Ibarra-Manríquez 1985) generates a heterogeneous patchiness; this must also be true for mycorrhizal associations, as both their physiology and the nutritional conditions under which they grow (Habte and Manjunath 1991) require plant species to develop this association, the extent of which depends on their life history (Martínez-Ramos 1994).

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