

## MYCORRHIZAL DYNAMICS AND DEPENDENCE OF *Desmoncus orthacanthos* Martius (ARECACEAE), A NATIVE PALM OF THE YUCATAN PENINSULA, MEXICO

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### Summary

Field observations were carried out to determine the seasonal patterns and recovery from disturbance by arbuscular mycorrhizal (AM) associations in *Desmoncus orthacanthos* Martius, eight years following shifting agriculture and in a mature forest. In addition, a greenhouse experiment was performed to determine the relative mycorrhizal dependency (RMD) of this species. Four growth stages were selected, and roots and rhizosphere soil of five individuals from each stage were monitored during one year. A seasonal pattern, but no difference in abandoned agriculture and mature forest were found in AM fungal activity. Soil moisture, spores per gram of soil, and percentage of root colonization were not correlated during this year. Root colonization was highest at both sites during the wet season, but was equally high during one dry season observation in the abandoned milpa. Spore density was highest during the dry season. The RMD ranged from 7.8 to 54.9%, with greater biomass of mycorrhizal than non-mycorrhizal plants using P solutions that mimicked field soil concentrations. This suggests that this slow-growing palm is highly dependent on mycorrhizal fungi in local soils and maintains relatively high AM activity even during the dry season. Culture of this slow-growing, understory palm for the rattan industry requires that soils be managed for high levels of AM fungi. The study showed that the standard local practice of shifting agriculture enables sufficient recovery of soil inoculum for growth of *D. orthacanthos*.

## DINÁMICA DE LA ASOCIACIÓN MICORRÍZICA Y DEPENDENCIA MICORRÍZICA EN *Desmoncus orthacanthos* MARTIUS (ARECACEAE) PALMERA NATIVA DE LA PENÍNSULA DE YUCATÁN, MÉXICO

### Resumen

Se realizaron observaciones en una parcela (milpa) abandonada de ocho años de edad y en una selva madura para determinar la dinámica estacional y la recuperación de una perturbación en la asociación micorrízica arbuscular (MA) presente en *Desmoncus orthacanthos* Martius. En una prueba de invernadero se evaluó la dependencia micorrízica relativa (RMD) de esta especie. En el campo se seleccionaron cuatro etapas de crecimiento en esta palmera y se monitoreó durante un año las raíces y el suelo rizosférico de cinco individuos de cada etapa de crecimiento. Se detectó una dinámica estacional, pero no diferencia en la actividad de la asociación comparando la milpa abandonada y la selva madura. No se encontró correlación, durante el período de estudio, entre la humedad del suelo, densidad de esporas por gramo de suelo y colonización de raíces. El porcentaje de colonización fue mayor en ambos sitios durante la etapa de lluvias, este porcentaje fue igual de elevado en una temporada de secas en la milpa abandonada. La densidad de esporas fue mayor en la temporada de secas. Los valores calculados de RMD se encuentran entre 7.8 y 54.9%, con una mayor biomasa en las plantas micorrizadas comparadas con las no-micorrizadas usando concentraciones de fósforo similares a las presentes en el suelo de los sitios de estudio. Los resultados sugieren que esta especie es dependiente de la asociación micorrízica en las condiciones evaluadas y mantiene una actividad de AM relativamente alta incluso durante la temporada de secas. Los resultados sugieren que las prácticas agrícolas empleadas en la zona de estudio permiten la recuperación del potencial de inóculo del suelo para el crecimiento de *D. orthacanthos*.

## DINÂMICA DA ASSOCIAÇÃO MICORRÍZICA E DEPENDÊNCIA MICORRÍZICA EM *Desmoncus orthacanthos* MARTIUS (ARECACEAE) PALMEIRA NATIVA DA PENÍNSULA DE YUCATÁN, MÉXICO (em inglês) 364

### Resumo

Realizaram-se observações em um lote (milpa) abandonado de oito anos de idade e em uma selva madura para determinar a dinâmica estacional e a recuperação de uma perturbação na associação micorrízica arbuscular (MA) presente em *Desmoncus orthacanthos* Martius. Em uma prova em invernadeiro se avaliou a dependência micorrízica relativa (RMD) desta espécie. No campo se selecionaram quatro etapas de crescimento nesta palmeira e se monitorou durante um ano as raízes e o solo rizosférico de cinco indivíduos de cada etapa de crescimento. Detectou-se uma dinâmica estacional, mas não difere na atividade da associação comparando a milpa abandonada e a selva madura. Não se encontrou correlação, durante o período de estudo, entre a umidade do solo, densidade de esporas por grama de solo e colonização de raízes. A porcentagem de colonização foi maior em ambos locais durante a etapa de chuvas, esta porcentagem foi igual de elevada em uma temporada de secas na milpa abandonada. A densidade de esporas foi maior na temporada de secas. Os valores calculados de RMD se encontram entre 7.8 e 54.9%, com uma maior biomassa nas plantas micorrizadas comparadas com as não-micorrizadas usando concentrações de fósforo similares às presentes no solo dos locais de estudo. Os resultados sugerem que esta espécie é dependente da associação micorrízica nas condições avaliadas e mantém uma atividade de AM relativamente alta inclusive

durante a temporada de seca. Os resultados também sugerem que as práticas agrícolas empregadas na zona de estudo permitem a recuperação do potencial de inóculo do solo para o crescimento de *D. orthacanthos*.

Keywords / Arbuscular Mycorrhiza / Dependency / Seasonal Patterns / Understory Palms /

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## Introduction

The role of the arbuscular mycorrhizal (AM) association in improving the growth of individual plants has been extensively investigated. This association offers the host plant protection against soil pathogens (Azcón-Aguilar and Barea, 1996), improved water uptake and resistance to water stress (Ruiz-Lozano et al., 1995; Augé, 2001; Querejeta et al., 2003), and increased nutrient uptake (especially P and N; Marschner and Dell, 1994; Siqueira and Saggin-Junior, 2001). The mycorrhizal association is important for nutrient cycling since roots with external hyphae can explore and capture nutrients from a larger volume of soil compared to non-mycorrhizal roots (Attiwill and Adams, 1993; Bhatia et al., 1996).

Mature tropical ecosystems are characterized by continual, year-long nutrient cycling for the incorporation of mineral resources into biomass (Pankow et al., 1991; Johnson and Wedin, 1997). In tropical forests where competition for light, nutrients and water may be high, the AM association can influence the ability of plants to acquire nutrients and increase plant growth and fitness (Zobel et al., 1997; Allen et al., 2003). In spite of the importance of the mycorrhizal association in tropical ecosystems, there is relatively little basic information on the role of this association in such a diverse and complex system (Janos, 1980a; Huante et al., 1993), as well as a lack of knowledge of the mycorrhizal fungal life cycle and their capacity to track changes in edaphic and microclimatic conditions (Brundrett, 2002).

In tropical systems, studies of seasonal root colonization or density of spores in soil (e.g. Johnson and Wedin, 1997; Guadarrama and Álvarez-Sánchez, 1999; Picone, 2000) are scarce, and even fewer studies have evaluated these for the long term (Allen et al., 1998, 2003). It is important to evaluate temporal and disturbance dynamics of the mycorrhizal association since the seasonality of host plants and their response to the symbiosis are related to their strategy for nutrient uptake and competition (Bethlenfalvay, 1992). Nevertheless, these dynamics are poorly understood, and it is difficult to make predictions about the importance and response of plants to mycorrhizae (Bethlenfalvay, 1992; Sanders and Fitter, 1992).

The purpose of this study was to determine the seasonal patterns and recovery from disturbance by arbuscular mycorrhizal (AM) associations in *Desmoncus orthacanthos* Martius in the southern part of the Yucatan Peninsula (Mexico). This species grows in the understory of seasonal tropical forest in mature as well as secondary forest. It is harvested by local people to produce handcrafts, so it has commercial value and could be included in reforestation efforts. AM fungi have been observed in the roots of this species (Carrillo et al., 2002), but their function has not been examined. As part of a program to understand the ecology and horticulture of this species (Orellana et al., 1999b), a study was initiated to observe the dynamics of AM root colonization and

spore production of *D. orthacanthos* in mature and secondary forest, and to test its dependency on AM in greenhouse conditions.

## Methods

### Species of study

*Desmoncus orthacanthos* is a Neotropical, scandent Arecaceae that is broadly used for the production of furniture and handicrafts by farmers in regions that were originally covered with evergreen and semi-evergreen tropical forests from southern Mexico to Brazil and Bolivia (Henderson et al., 1995). People who use this palm species prefer to harvest mature individuals with stems more than 30m in length. *D. orthacanthos* can dominate the canopy in some secondary forests, and is recognized by the production of infructescences composed of red berries that mature from July to September, and are probably dispersed by birds. Juveniles are frequently found at low densities in mature forests; but by contrast, their densities are higher in disturbed areas such as abandoned croplands, even though predation and sapling mortality may be intense. Biological and ecological studies of this species are scarce (Orellana et al., 1999b; Siebert, 2000). Carrillo et al. (2002) found AM associations in roots of individuals occurring in both disturbed and undisturbed areas. Their roots were described as Magnolioid type, as originally classified by Baylis (1975).

### Study area

Field observations and sampling were carried out at the ejido (communal farmland) of Noh-Bec, located in the central-southern portion of Quintana Roo State, Mexico, between 19°02'30" to 19°12'30"N and 88°13' 30"W to 88°27'30"W. The climate is warm sub-humid with the rainy season from May through October. Annual mean temperature varies from 24 to 26°C, and precipitation is 1200-1500mm ([Figure 1](#)). Soils in this area originated from calcareous materials, and rendzins, vertisols, luvisols and gleysols dominate. The original vegetation is evergreen to semi evergreen tropical forest with 20-30m canopy heights. Plants were sampled in mature forest and abandoned cropland, where soil chemical parameters are different ([Table I](#)). The populations of *D. orthacanthos* present in the two sites had different plant structure in terms of age distribution and size.

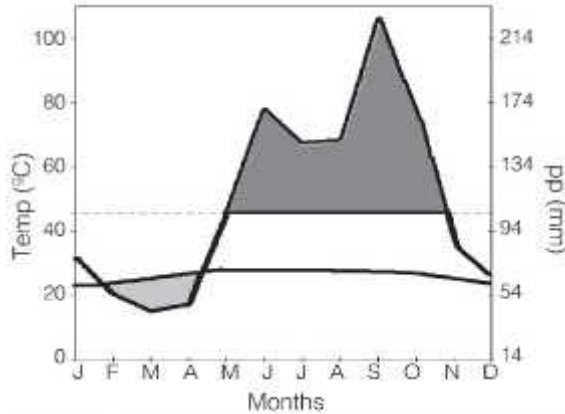


Figure 1. Ombrothermic diagram of long term mean monthly temperature and monthly precipitation at study area. Data from the nearest observatory (modified from Orellana *et al.*, 1999a).

TABLE I  
CHEMICAL CHARACTERISTICS OF SOILS FROM  
FOREST AND ABANDONED *MILPA*

Soil parameters	Mature forest	Abandoned <i>milpa</i>
Extractable phosphorous (mg·kg <sup>-1</sup> soil)	18.8	13.5
Total nitrogen (cmol·kg <sup>-1</sup> soil)	67.8	16.9
Organic matter (%)	5.2	3.3
pH	7.3	7.1

Mature forest. The mature forest site is located at 19°07'28''N and 88°20'25''W. It is a semi-evergreen mature forest that, according to some elder inhabitants, was not disturbed for 80 years or more. The tree canopy was 20-30m tall, dominated by *Pouteria unilocularis* (Engel) Eyma, *Alseis yucatanensis* Standl., *Metopium brownei* (Jacq.) Urban, with the understory palms *Cryosophila stauracantha* (Heynh.) R. Evans and *Sabal mauritiiformis* (H. Wendl. Ex- H. Karst.) Griseb. and H. Wendl.

Abandoned milpa (cornfield). The abandoned milpa site is located at 19°05'54''N and 88°13'30''W. This area was covered with early secondary vegetation; originally it was used for traditional maize slash and burn agriculture to grow corn for 2 years (8-10 years before present field work was initiated). The dominant tree species were *Cecropia peltata* L., *Bursera simaruba* (L.) Sarg., *Guazuma ulmifolia* Lam. and *Guettarda combsii* Urb., with a canopy of 10-15m.

#### Field methods

In March 2001, 5 individuals of *D. orthacanthos* from 4 previously defined growth stages were selected and labelled in each site. Growth stages were determined assuming a relationship between height and development stage (Orellana *et al.*, 1999b). Individuals 35-50cm in height were considered juveniles (J); individuals 50-120cm were considered saplings (S); those with height >120cm and without signs of reproduction were considered immature adults (A); and those >120cm with visible

signs of reproductive structures (inflorescence or fruit) were considered mature adults (M). Every 3 to 4 months both sites (mature forest and abandoned milpa) were sampled and survival of individuals was recorded; in case an individual died it was replaced by the nearest palm at the same growth stage. Roots and rhizosphere soil were collected from labelled individuals to a depth of 20cm, selecting roots  $\leq 2$ mm in diameter. Roots were rinsed and fixed in a 70:29:1 (volumetric) water: ethanol:glycerine solution. At least 250ml of rhizosphere soil were collected from every individual and air dried. Soil moisture was determined gravimetrically.

#### Laboratory methods

Root samples were bleached in 10% KOH and H<sub>2</sub>O<sub>2</sub> and stained with trypan blue (Phillips and Hayman, 1970). From each sample, 10 fragments of 1cm were randomly selected, and mycorrhizal root colonization was determined by microscope observations (40 $\times$ ). For each sample, 75 microscopic fields (1mm diameter) were examined and counted as colonized when hyphae, vesicles or arbuscules were observed (McGonigle et al., 1990). Colonization % was calculated as the ratio of the number of colonized sections and total number of fragments analyzed.

AM fungal spore density in rhizosphere soil was estimated by a modified detergent-sucrose flotation method (Allen et al., 1979): soils were air-dried and sieved to  $< 2$ mm; from each soil sample 1g was centrifuged in water and then suspended in detergent-sucrose solution (720mg/ml sucrose, 10mg/ml sodium hexametaphosphate). Spores contained in the suspension were collected and filtered over a 45 $\mu$ m pore paper. Only whole spores were counted and spore density was expressed as a number of spores per gram of dry soil.

#### Mycorrhizal dependency of *D. orthacanthos*

Seeds of *D. orthacanthos* were collected in both forest and abandoned milpa, and were germinated in humid chambers using sterilized vermiculite as substrate. After 10 days of germination, one seedling was transplanted per pot, and each pot was filled with 350ml of sterilized vermiculite. In the mycorrhizal treatment 100ml of soil from the forest (36 propagules: colonized roots, spores and extraradical hyphae of arbuscular mycorrhizal fungi per 100ml soil) was applied. Non-mycorrhizal treatments were inoculated with 100ml of pasteurized forest soil to eliminate mycorrhizal propagules. To recover the natural soil microbiota in the non-mycorrhizal treatment, 100ml of soil filtrate using Whatman 42 filter paper was applied according to Azcón-Aguilar and Barea (1996).

Pots were randomly distributed in a greenhouse. Six treatments were applied: three levels of P concentration (4, 12 and 24ppm) available for plants in the substrate, and two mycorrhizal levels (mycorrhizal and non-mycorrhizal). Each treatment had six replicates. Every 15 days 100ml of Hoagland's nutrient solution was applied to the pots, using KH<sub>2</sub>PO<sub>4</sub> (1M) to adjust the P level required. Relative mycorrhizal dependency of *D. orthacanthos* was calculated according to Plenchette et al. (1983) as  $RMD = [(mean\ dry\ weight\ of\ mycorrhizal\ plants - mean\ dry\ weight\ of\ non-mycorrhizal\ plants) / mean\ dry\ weight\ of\ non-mycorrhizal\ plants] \times 100$ .

#### Statistical analyses

All field data were square-root transformed to ensure equality of variance and normality. One-way analysis of variance for repeated measurements (ANOVA-RM) was used (Kleinbaum et al., 1998) to compare root colonization and spore density in different sampling dates; one-way ANOVA was used to compare the same parameters between growth stages for each observation date; and Student's t-tests were used to compare differences among stages and between sites. In addition, Pearson's correlation test was used to evaluate relationships between root colonization, spore density and soil moisture.

## Results

### Survival

Except for juveniles, which had 60% and 80% survivals in mature forest and abandoned milpa, *D. orthacanthos* had a survival of 100% in all stages of growth, one year of observation. The decreased survival of juveniles may have been from leaf and stem predation observed in the field.

### AM structures

AM fungal structures were found in all root observations. The most common structures observed were intraradical hyphae inside the cortical tissue, but hyphal coils, vesicles and internal spores were also observed, and in few cases small arbuscules. The AM colonization was originally recognized as Paris type. Only % total colonization is reported, as structures other than internal hyphae were sparse (<5% of observations).

### Patterns of root colonization

Roots of *D. orthacanthos* had AM fungal colonization at all sampling dates. The values ranged from 5 to 33% for individuals in the mature forest, while colonized individuals from the abandoned milpa varied from 6 to 34%. Higher values of root colonization were observed in September for all stages in the mature forest ([Figure 2a](#)). In the abandoned milpa the highest values of root colonization were observed in March 2001 and also in September for all stages ([Figure 2b](#)). Overall AM root colonization in mature forest ( $F=19.8$ ,  $p<0.001$ ) and in abandoned milpa ( $F=14.3$ ,  $p<0.001$ ) showed seasonal dynamics for all growth stages, except for saplings in both sites and juveniles in abandoned milpa.

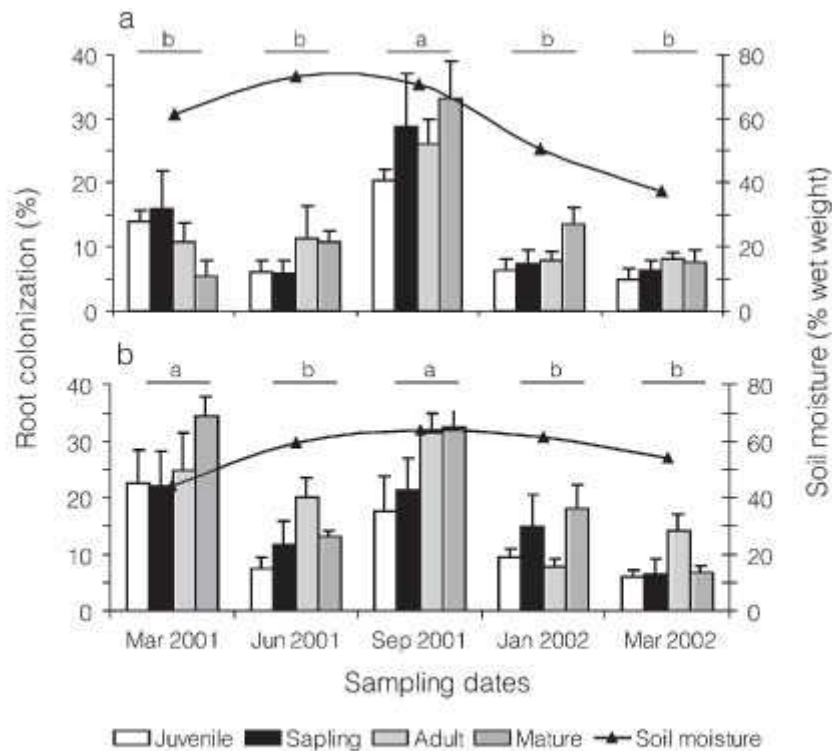


Figure 2. Average  $\pm$ SE of root colonization in *D. orthacanthos* from mature forest (a) and abandoned milpa (b). Bars marked with different letters are significantly different ( $p < 0.05$ ).  $n = 5$ .

In general there were no significant differences in % root colonization among growth stages within a sample date at either the mature forest or abandoned milpa. One exception occurred in abandoned milpa in June 2001, when juveniles (J) had significantly lower % colonization than immature adults (A) ( $F = 3.36$ ,  $p < 0.05$ ). There were no significant differences among stages in any sample dates in spore density at either site ( $p > 0.05$  in all cases).

Root colonization was significantly different between the two field sites ( $t = 2.97$ ,  $p < 0.02$ ) on one date only (March 2001), and only at the mature adult stage. Mature adults from the abandoned milpa had higher root colonization (34.4%) than mature adults from the mature forest (5.4%; [Figure 2a, b](#)).

#### Spore density

Spores of AM fungi were observed in rhizosphere soils on all dates and growth stages. The density of spores from mature forest was higher in both March 2001 and 2002 than at the other sampling dates. In the abandoned milpa, this tendency toward higher spore density in March was only observed in samples from juveniles (J) and mature palms (M; [Figure 3a, b](#)). Spore density of AM fungi from the rhizosphere of individuals in the mature forest showed seasonal variation ( $F = 16.9$ ,  $p < 0.0001$ ; [Figure 3a](#)). Seasonality was also observed when different growth stages were analyzed separately. Spore density patterns in the abandoned milpa showed the same dynamics as those observed in mature forest, with significant differences in spore density among sampling dates ( $F = 12.2$ ,  $p < 0.0001$ ). Separate analyses for different stages showed no



significant differences between sample dates for saplings (S) in the abandoned milpa, but there was seasonal variation in spore density for all other growth stages.

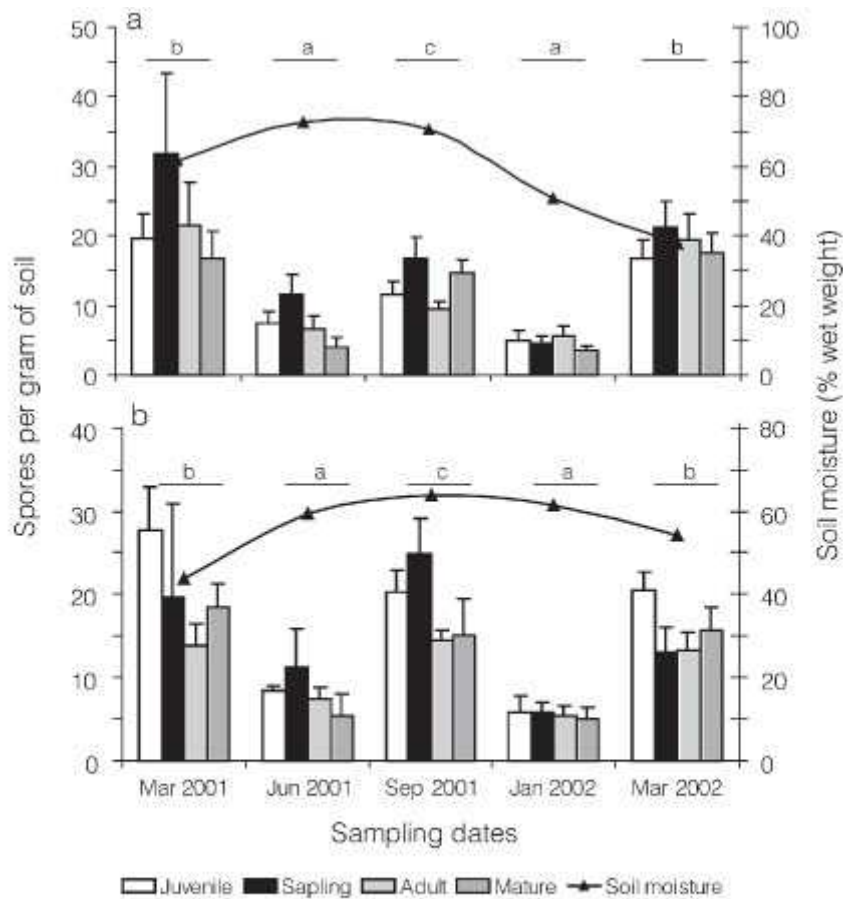


Figure 3. Average  $\pm$ SE of spores per gram of soil from rhizosphere of *D. orthacanthos* from mature forest (a) and abandoned milpa (b). Bars marked with different letters are significantly different ( $p < 0.05$ ).  $n = 5$ .

Spore density was higher in juvenile palms in abandoned milpa than mature forest in September ( $t = 2.84$ ,  $p < 0.05$ ), but not on any other date. Immature adult palms also showed differences in September ( $t = 2.97$ ,  $p < 0.02$ ) but not on other dates (Figure 3a, b).

#### Correlation between root colonization, spores and soil moisture

Using Pearson's correlation test, there is no significant correlation ( $p > 0.05$  in all cases) between the values of either spore density or % colonization and soil moisture, and between root colonization and spore density. Both AM fungal activity and soil moisture showed seasonal dynamics, but these did not track each other closely. Fungal activity was maintained during the dry season, often with no significant reduction compared to the rainy season.

#### Mycorrhizal dependency of *D. orthacanthos*

A positive effect of AM inoculation on the production of dry weight (DW) for the *D. orthacanthos* seedlings was observed. The highest DW in the seedlings was found in the treatment with 4ppm of P. The treatment with AM inoculation also showed higher values than the non-inoculated treatment (Table II). The relative mycorrhizal dependency was greatest for the plants that received the lowest level of P, but there was a positive biomass response to all three levels of added P (Figure 4).

TABLE II  
AVERAGE  $\pm$ SE OF TOTAL DRY WEIGHT OF *D. orthacanthos* GROWING AT THREE AVAILABLE P LEVELS

	Dry weight (g)		
	4ppm P	12ppm P	24ppm P
Mycorrhizal plants	1.24 $\pm$ 0.14	0.55 $\pm$ 0.12	0.51 $\pm$ 0.12
Non-mycorrhizal plants	0.73 $\pm$ 0.18	0.44 $\pm$ 0.11	0.47 $\pm$ 0.12

(n= 6)

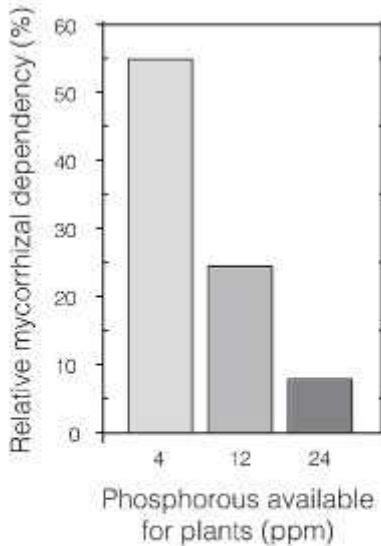


Figure 4. Relative mycorrhizal dependency of *D. orthacanthos* calculated according to Plenchette *et al.* (1983). n= 6.

## Discussion

Many reports indicate that the development of a mycorrhizal association plays an important role in improving establishment of seedlings in a competitive system, such as a tropical forest (Gange *et al.*, 1993; Francis and Read, 1994; Lovera and Cuenca, 1996; Pedersen and Sylvia, 1996; Zobel *et al.*, 1997). The reduced survivorship of juveniles in both the mature forest (60%) and the abandoned milpa (80%) indicate that this is the limiting stage for successful establishment of the species (e.g. Escalante *et al.*, 2004). The values of root colonization by AM fungi in juveniles were not different in the abandoned milpa and mature forest, nor was colonization different in general among the four growth stages, indicating that mycorrhizal inoculum was not the major limiting factor for establishment (unpublished data).

In another study that examined mycorrhizal inoculum following slash and burning in Quintana Roo, the percentage of colonization was comparable to mature forest within a year, and the AM spore species composition recovered within 4 years after the fire (Allen et al., 2003). Leaf and stem predation, most likely by insects (Siebert, 2000; J. Ramos-Zapata, personal communication) was probably the cause of mortality of the juvenile stage. Thus, there is no direct relationship between % colonization and survival of juveniles at the abandoned milpa and forest sites. In fact, later growth stages had no higher colonization than juveniles, either. Instead, it is more useful to understand the seasonal dynamics of AM as an important factor for the establishment and growth of this species.

Mycorrhizal fungi usually track seasonal soil moisture changes quite closely, especially in seasonal climates such as seasonally dry tropical forest (Allen et al., 1998, 2003). The results of this study on *D. orthacanthos* were surprising in that the relationships between both % root colonization and spore density were not significantly correlated with soil moisture, and there were still active roots with relatively high % colonization during the dry season. This may indicate that this species is dependent on mycorrhizae during the entire year; in fact % colonization in the abandoned milpa during the height of the dry season in March 2001 was as high as in the following September, at the middle of the rainy season, as has been found for other palm species in a tropical forest (Núñez-Castillo and Álvarez-Sánchez, 2003). September is also the flowering season for *D. orthacanthos*, a time when other researchers have reported higher than normal % colonization (Corkidi and Rincón, 1997) so high colonization could be an indicator of high effort of growth and development, however there are also contrasting reports (Koide and Dickie, 2002).

The studies that have reported seasonality of the mycorrhizal association generally assume a direct influence of environmental conditions such as temperature and moisture on the fungi (Sigüenza et al., 1996; Mohammad et al., 1998; Nehl et al., 1998). In fact, the percentage of root colonization may decrease during the rainy season if there is a high rate of root production (Allen, 2001). Conversely, during drought there may be high values of root colonization due to a slow rate of root growth (Koide and Mooney, 1987; Cade-Menun et al., 1990). In the present study, soil moisture was related to root production; samples from June 2001 and March 2002 had a high density of fine new roots, even though June is in the rainy season and March is in the dry season; both of these times had reduced % colonization. In fact, multiple factors are likely responsible for the percentage of colonization, including environmental conditions, rate of root vs fungal growth, phenology and physiological status of the plant (De Mars and Boerner, 1995; Allen, 2001; Brundrett, 2002).

The presence of arbuscules is often considered the best indicator of functioning in the AM association (Tester et al., 1987; McGonigle et al., 1990; Corkidi and Rincón, 1997; Gange and Ayres, 1999), but arbuscules were found only in about 1% of the observations. This was also the case for other tree and herb species of seasonal tropical forest (Allen et al., 1998, 2003). Arbuscules are not the only structure for transporting nutrients, and vesicles and intraradical hyphae, which were observed in *D. orthacanthos*, are indicators of current and past colonization (Allen, 1991). Furthermore, arbuscules are ephemeral structures that degrade after 3-7 days (Toth and Miller, 1984; Tester et al., 1987; Mohammad et al., 1998). Anyway in this species Paris colonization type were observed and small arbuscules may be difficult to observe, but it is probable that both Paris and Arum types may be present, as reported by Dickson (2004).

Seasonality of spore production has been observed in wet tropics (Guadarrama and Álvarez-Sánchez, 1999) and seasonal tropics (Allen et al., 1998, 2003). The results from *D. orthacanthos* show a higher density of spores during the dry season (March of both years) than the rainy season, indicating that spore production was inversely related to soil moisture. This inverse relationship has also been observed in other studies on seasonality of spore production (Douds and Millner, 1999; Miller and Bever, 1999). The density of spores was in the same range of values as other studies in tropical and seasonal tropical forest (Johnson and Wedin, 1997; Allen et al., 1998, 2003; Picone, 2000) although higher than wet tropical forest (Guadarrama and Álvarez-Sánchez, 1999).

An absence of differences in the mycorrhizal association between a mature forest and abandoned cultivated field could be explained in terms of sufficient time for recovery (successional stage), since the latter was abandoned 8 to 10 years ago, and secondary vegetation has colonized the area. Furthermore, slash and burn agriculture maintains high levels of soil inoculum (Allen et al., 2003). The ability of juveniles to form a mycorrhizal association similar to older stages may be promoted by the high soil inoculum. The AM association likely influences the fitness of this species at all growth stages.

Individuals of *D. orthacanthos* showed mycorrhizal dependency, even at high available P concentration in the solution. The response of tropical plants to mycorrhizae ranges from facultative to obligate, depending on the successional stage, size of seed, and nutrient requirements (Janos, 1980b; Huante et al., 1993; Siqueira et al., 1998; Sharma et al., 2001; Siqueira and Saggin-Junior, 2001; Allen et al., 2003). The RMD value and the presence of magnolioid roots in this species (Baylis, 1975) suggest that, according to Janos (1980a), *D. orthacanthos* may be an obligate mycorrhizal plant in the semi-evergreen tropical forest of Quintana Roo, Mexico.

Gemma et al. (2002) pointed out that the "ecological mycorrhizal dependency" can be evaluated if the experiments to calculate dependency are carried out at the same P substrate concentrations as in the field where the plants grow in normal conditions. The values of 12 and 24ppm correspond to values found in field soils, and promoted a mycorrhizal growth response. Of course, the greenhouse growth conditions did not simulate field conditions, especially as an artificial growth medium was used so that low P conditions could be tested. We are not aware of the occurrence of natural soils in the region with the low P of 4ppm used in our experiment, as these soils tend to have moderate to high P concentrations (Estrada-Medina, 2000; Allen et al., 2003; Ceccon et al., 2003). Poor root colonization often occurs under high levels of soil P (Amijee et al., 1989; Allen, 1991; Wang et al., 1993; Srivastava et al., 1996; Smith and Read, 1997; Douds and Millner, 1999; Olsson et al., 1999) but not in these soils, where moderate to high P levels are normal and high levels of colonization also occur (Allen et al., 2003).

The pot experiment also did not simulate drought stress that may occur in the field during the dry season. Soil moisture was still nearly 40% in these highly organic soils for plants sampled at the dry season. These values of soil moisture are high considering that there had been virtually no rain for 2-3 months at the March sample dates. One hypothesis that could explain high soil moisture during dry periods is the hydraulic lift from areas of higher soil water, such as deeper soil layers, to the soil surface where plants deplete soil moisture. Mycorrhizal fungi are especially important in promoting hydraulic lift, as the surfaces of extramatrical hyphae act as a capillary

conduit (Querejeta et al., 2003). *D. orthacanthos* maintains mycorrhizal colonization during the dry season. This recent discovery of the importance of the extramatrical hyphae in promoting hydraulic lift further explains the importance to plants in maintaining a mycorrhizal association during the dry season. *D. orthacanthos* may be an obligatory mycorrhizal dependent in order to survive and maintain physiological activity during the dry season. Further physiological studies of this species in the field are required.

*D. orthacanthos* produced new fine roots during both the wet and the dry season, and the % AM colonization of *D. orthacanthos* was high during both seasons. The fact that the species always maintained a mycorrhizal association suggests that the fungi are important to its growth during the entire year, and may indicate the obligate nature of the association, even when viability of fungi was not measured in this work. By contrast, fine roots could seldom be found for other native tree species, both mature and saplings, in Quintana Roo during the dry season (Allen et al., 2003), so this palm maintains an active root system when others become dormant. Flower and fruit production of *D. orthacanthos* occur during the wet season, when AM fungi may be important to maintain growth, but AM fungi may be important to reduce drought stress and promote hydraulic lift during the dry season (Querejeta et al., 2003).

Mycorrhizae in tropical palms have received relatively little attention (Fisher and Jayachandran, 1999). An understanding of the mycorrhizal relationships of *D. orthacanthos* can contribute to its conservation and, given its high potential (Orellana et al., 1999b; Siebert 2000; Escalante et al., 2004), enable cultivation for economic purposes. The fact that mycorrhizal colonization was equally high in the abandoned milpa and the mature forest indicates that the indigenous practice of slash and burn agriculture maintains a healthy soil inoculum, and is congruent with initiating a plantation program for a species such as *D. orthacanthos* that has mycorrhizal dependency.

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