Tropical and Subtropical Agroecosystems, 16 (2013) : 399 - 406.

RUDERAL PLANTS: TEMPORARY HOSTS OF ARBUSCULAR MYCORRHIZAL FUNGI IN TRADITIONAL AGRICULTURAL SYSTEMS?

[PLANTAS RUDERALES: ¿HOSPEDEROS TEMPORALES DE HONGOS MICORRÍZICOS EN SISTEMAS AGRÍCOLAS TRADICONALES?]

José Ramos-Zapata[1*], Denis Marrufo-Zapata[1], Patricia Guadarrama-Chávez[2], Uriel Solís-Rodríguez[1] and Luis Salinas-Peba[1]

[1]Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, km 15.5 de la Carretera Mérida-Xmatkuil AP 4-116, Itzimná Mérida, Yucatán, México.
E-mail: aramos@uady.mx
[2]Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, Sisal, Yucatán 97356, México.
**Corresponding author*

SUMMARY

Ruderal plants may serve as temporary hosts of arbuscular mycorrhizal fungi (AMF), by maintaining the availability of active propagules in the soil, which in turn favors rapid colonization of roots of cultivated species during the agricultural cycle. The goals of this study were to: 1) estimate the richness of ruderal plant species in an agricultural plot and determine their mycorrhizal status, 2) quantify the number of live AMF spores in soil samples, and 3) estimate the infection potential and number of active propagules in soil samples from the agricultural site. The agricultural site used was located in Yucatan, Mexico, and consisted of a monoculture of corn subjected to low-impact agricultural practices during the last five years. A total of 20 species of ruderal plants were found at the experimental site, belonging to 11 families. All the sampled species exhibited associations with AMF, and colonization percentages ranged from 11.7±0.07 to 79.6±0.01 among species. The rhizosphere presented an average of 565±324 spores in 50 g of dry soil, of which 58.76% of the spores were alive. The inoculum potential of the soil was 50.4±0.05%, while the number of infective propagules was 193.37 (both in 50 mL of soil). Results from this study show that the presence of ruderal species in agricultural sites may promote the maintenance of AMF communities by acting as temporary hosts of these fungal species. In doing so, ruderal species can favor a higher production of infective AMF propagules and thus stronger mycorrhizal interactions with cultivated species.

Key words: Slash and burn; low-impact agriculture; corn; rhizosphere; infective propagules.

RESUMEN

Las arvenses pueden actuar como hospederos temporales de los hongos micorrizógenos arbusculares (HMA), manteniendo la disponibilidad de propágulos activos en el suelo influyendo en la rápida colonización de las raíces del cultivo subsiguiente. Los objetivos de este trabajo fueron: 1) estimar la riqueza de arvenses presentes y su estatus micorrícico, 2) cuantificar las esporas vivas de HMA y 3) estimar el potencial infectivo y el número de propágulos infectivos del suelo en un cultivo de maíz con diez años de manejo de bajo impacto en el estado de Yucatán, México. Se identificaron 20 especies de arvenses, pertenecientes a 11 familias, todas las especies se encontraron asociadas a HMA, los porcentajes de colonización se estimaron entre 11.7±0.07 a 79.6±0.01. La rizósfera presentó en promedio 565±324 esporas en 50g de suelo seco, el 58.76% estaban vivas, el valor del potencial de inóculo del suelo fue 50.4±0.05% y el número de propágulos infectivos fue 193.37, ambos en 50mL de suelo. Aunque el tipo de manejo agrícola puede reducir la disponibilidad y actividad de los HMA, el arribo de arvenses contribuye a su permanencia al actuar como hospederas temporales, estimulando la producción de propágulos de los HMA.

Palabras clave: Roza-tumba-quema; agricultura de bajo impacto; maíz; rizósfera; propágulos infectivos.

INTRODUCTION

Slash and burn agriculture is one of the most common forms of traditional agriculture used to cultivate corn in tropical regions (Palerm, 1981). In Yucatan, Mexico, this agricultural practice is very common despite the high degree of stoniness in the soil, low rainfall, and low water retention capacity of the soil (Duch, 1991; Arias, 1995). Slash and burn agriculture consists of cutting down and burning the vegetation at the onset of the rainy season, followed by a cultivation period of 2 to 3 years, after which the site remains unused (i.e. fallow) for a 15 to 20-year period during which the vegetation recovers its original structure and species composition, to then be used in another cycle (Duch, 1991). Pool and Hernández (1987), mentioned that in the state of Yucatan, Mexico, this agricultural practice has been modified by reducing the fallow period, leading to a limited regeneration of the vegetation as well as greater soil erosion. Another problem currently associated with slash and burn agriculture is the indiscriminate use of fertilizers to compensate for low nutrient availability in the soil, as well as the use of herbicides for weed control. Although both types of chemical inputs can have negative impacts on soil microbial communities, the effects on biodiversity and functionality (*v.g.* plant protection, P uptake) have been largely neglected (Arias, 1992; Ramos-Zapata *et al.*, 2012).

Ruderal plant species are an undesired component of conventional agricultural practices because they compete for resources (water, nutrients or space) with cultivated species (Hart, 1985; Caamal and Castillo, 2011). During the fallow period, ruderal species proliferate and colonize the abandoned agricultural site, given high nutrient availability. In doing so, ruderal plants play a relevant ecological role by maintaining microclimatic conditions in the soil and contributing to nutrient and mineral recycling (Altieri and Whitcomb, 1979; Gliessman, 1990). Ruderal species also contribute to the pathogen and pest control in cultivated species (Altieri and Whitcomb, 1979) and they are hosts of several groups of symbiotic microorganisms (Baumgartner *et al.*, 2005). For example, ruderal plants are hosts of many species of arbuscular mycorrhizal fungi (AMF) (Baumgartner, 2005; Hausmann and Hawkes, 2009). Previous studies have suggested that ruderal plants favor an increase in diversity and abundance of AMF in the soil of cultivated sites (Vatovec *et al.* 2005; Ramos-Zapata *et al.*, 2012).

In spite of their potentially beneficial effects through increased AMF abundance, ruderal plant species are usually removed manually or with the use of herbicides which may have negative effects on soil biota, including AMF. These negative impacts include the reduction of AMF species richness, diversity and inoculum potential (Kurle and Pfleger, 1994); other agricultural practices such as fertilization or continuo monocultures can also affect the composition and diversity of AMF (Sieverding, 1990; Jansa *et al.*, 2002; Oehl *et al.*, 2003). The use of low-impact agriculture (i.e. not mechanized), cover crops, crop rotation and fallow periods, as well as tolerance for ruderal species (up to certain levels of abundance), are practices which mitigate the negative impacts of conventional agriculture on AMF. Indeed, tolerating the abundance of ruderal species up to a given threshold may favor the maintenance of AMF communities when the crop species is not planted. In this way, the presence of ruderal species favors the early colonization of crop species by AMF. Accordingly, here we test the hypothesis that ruderal plant species may act as potential hosts of AMF and the present study has the following goals: 1) to estimate the richness of ruderal plant species in an agricultural plot and determine their mycorrhizal status, 2) to quantify live AMF spores at this agricultural site, and 3) to estimate the infection potential and number of infective propagules present in the soil of the agricultural study site.

MATERIALS AND METHODS

Site description

The study was conducted at the Campus de Ciencias Biológicas y Agropecuarias (CCBA) of the Universidad Autónoma de Yucatán (20°52’ 3.86’’ N; 89°37’20.05’’ W). The study site is of karstic geological origin, with a high abundance of exposed rocks. The soil type is leptosol with intermediate texture, brown in color (Bautista-Zúñiga *et al.*, 2003). The climate is warm subhumid with rains during the summer and winter. The mean annual precipitation is 900 mm and the mean annual temperature is 27.5 °C (García, 1973). The dominant vegetation type corresponds to a deciduous tropical forest (Flores and Espejel, 1994) with varying levels of disturbance.

The experimental plot has an area of 1 ha, and is surrounded by secondary vegetation derived from a deciduous tropical forest. Starting in 2006, *Zea may* L. have been periodically grown as a monoculture, following traditional fallow periods but without burning or using fertilizers. The soil has a pH of 7.7, a carbon content of 5.3 mg per 100g of soil, while nitrogen and total phosphorus are 1.25 g/kg and 685.8 mg/kg, respectively.

Species richness and mycorrhizal status of ruderal plants

During the fallow period in June 2011, we characterized the community of ruderal species present in the experimental plot. Specimen sampling was conducted by randomly placing 15 quadrats of 0.5 x 0.5-m, throughout the plot. We collected all ruderal species present inside each quadrat, and identified them using specific keys and herbarium specimens. Once all plants were identified, we collected the fine roots (<2 mm in diameter) of three specimens per species.

Roots were labeled and transported to the laboratory where AMF presence and percentage of mycorrhizal colonization were determined. Roots were washed with tap water and dyed with trypane blue following Phillips and Hayman (1970), modified by Hernández-Cuevas *et al.* (2008). Subsequently, we prepared permanent samples with polyvinyl alcohol, lactic acid and glycerin (PVLG) and estimated the percent of total AMF colonization for each fungal structure (hyphae, vesicles, spores, arbuscules and coils) in each sample using the intersection method by McGonigle *et al.*, (1990).

AMF propagules

Within each of the 15 sampling quadrats, we collected 1-kg soil sample from the first 15 cm of soil. The soil samples from five randomly chosen quadrats, were mixed, and finally three compound samples were drawn from this mixture. From each compound sample, a 100 g sub-sample were placed in the oven at 80°C for 24 h, in order to estimate the soil dry weight, and 50 g from these compound samples were used to isolate and quantify AMF spores, using the humid sieving method by Gerdemann and Nicolson (1963), modified by Hernández-Cuevas *et al.* (2008). Spores were observed under an optic microscope (40-100X), separating and counting live spores (i.e. with lipid content and no signs of damage), and dead spores (damaged wall, lacking lipid content), for each soil sample.

The infection potential of the soil samples was evaluated with a bioessay conducted in the greenhouse using 300-mL pots for each compound soil sample (three compound samples, five replicates per sample, n= 15). Pots were filled with 200 mL of soil that was previously steam sterilized, a layer of 50 mL of soil to be subsequently sampled (not mixed), and finally a layer of steam sterilized soil in order to avoid contamination. A single sorghum plant (*Sorgum vulgare* L.) was transplanted to each pot, with plants being previously germinated with a sterile substrate. Pots were randomly distributed and rotated weekly. Plants were watered every second day during a six-week period, after which they were harvested and roots were collected to evaluate the presence of AMF structures and to determine the total percentage of AMF colonization following McGonigle *et al.* (1990).

The number of AMF infective propagules was estimated with a bioessay in the greenhouse, using the technique of the most probable number of infective propagules (MPN) (Porter, 1979) which consists of a series of dilutions (4^{-0} to 4^{-7}) using steam sterilized soil samples, with five replicates per dilution. Each dilution was placed in pots, as described previously using the same methodology, and after six weeks each seedling was harvested and the roots were collected to evaluate the presence of AMF structures following McGonigle *et al.* (1990); the MPN of infective propagules was calculated as described in Ramos-Zapata *et al.* (2011).

Data analyses

Ruderal species richness (S) was calculated based on the specimens collected in each of the sampled quadrats. Spore density was quantified considering both live and dead spores. The number of infective propagules in 50 mL of soil per compound sample (3 replicates) was analyzed by means of a likelihood test (Ramos-Zapata *et al.*, 2011).

RESULTS AND DISCUSSION

A total of 20 ruderal plant species were identified during the fallow period of the study plot. These species belonged to 11 plant families, of which Euphorbiaceae and Poaceae had the highest number of species (three species each) (Table 1). The species reported for both of these families are common in agricultural systems (Villaseñor and Espinosa, 1998), in particular those in the Yucatan Peninsula (Caamal *et al.*, 2001; Castillo-Caamal *et al.*, 2010). However, our finding is comparatively lower in relation to the findings by Cocom *et al*. (2008) who reported up to 40 ruderal species during the fallow period of an agricultural site from the same area of Yucatan Peninsula. This difference in results may be related to the life history traits of the species found, in particular the competitive ability for light, water and nutrients (Holm *et al.*, 1979; Gupta *et al.*, 2008). In addition, the continuous application of herbicies may select for specific ruderal species which are more resistant and therefore become dominant in agricultural sites

(Caamal *et al.*, 2001). Therefore, by restricting the use of herbicides, the number of ruderal species present in agricultural sites will likely increase.

Plant species belonging to Commelinaceae, Portulacaceae and Zygophyllaceae families have been previously reported as non-mycorrhizal (Gerdemann, 1968; Trappe, 1987). However, in this study we found that several ruderal species belonging to these families had their roots colonized by AMF, so these plants may act as temporal hosts of AMF species. Our results emphasize the importance of conducting exhaustive studies which screen for the presence of mychorrhizae in roots of ruderal species belonging to families previously thought to be non-mycorrhizal, in order to reduce the use of herbicides to promote the presence of potentially mycorrhizal ruderal plants in different agriculture sites and management conditions.

Moreover, according to Baumgartner *et al.* (2005), ruderal plant species exhibit a variable mycorrhizal status depending on their abundance at an agricultural site. Indeed, although we found that all the ruderal species sampled established mycorrhizal interactions, colonization levels varied considerably (range from 11.7±0.07 in *Euphorbia ocymoidea* to 79.6±0.01 in *Andropogon virginicus*). The species *Sanvitalia procumbens*, *Sida acuta* and *Bidens pilosa* exhibited high levels of colonization (greater than 40%), which contrasts with results previously reported by Ramos-Zapata *et al.* (2012) for the same species (less than 15%) in an agricultural system with corn. Nonetheless, the comparatively lower numbers reported by this latter work may have resulted from a shorter fallow period at such agricultural site, which could have restricted the establishment of mycorrhizal interactions.

Table 1. List of ruderal species present in a traditional agricultural system with maize (Yucatan, Mexico). The agricultural system was sampled during the fallow period; values given are mean percent (± SE) of overall AMF colonization (AMF), as well as mean colonization for each fungal structure separately (H: hyphae, V: vesicles, S: spores, C: arbusculate and hyphal coils).

Family	Species	AMF	H	V	S	C
Acanthaceae	*Justicia* sp.	36.02 (±3.3)	32.52 (±2.9)	5.78 (±1.2)	1.14 (±0.7)	1.49 (±0.6)
	Ruellia nudiflora	47.56 (±4.1)	41.99 (±3.5)	20.33 (±9.2)	6.20 (±4.2)	2.77 (±0.5)
Asteraceae	*Bidens pilosa* L.	79.67 (±0.9)	71.67 (±1.8)	30.67 (±5.7)	11.33 (±4.4)	
	Sanvitalia procumbens	67.77 (±10.6)	64.79 (±11.2)	7.61 (±4.7)	3.12 (±1.02)	
Commelinaceae	*Commelina elegans*	35.33 (±9.9)	31.33 (±10.6)	12.44 (±7.8)	5.78 (±4.5)	1.33 (±1.1)
Euphorbiaceae	*Acalypha alopecuroides*	47.11 (±3)	32.19 (±1.1)	24.12 (±10.1)	9.23 (±3.3)	1.63 (±0.8)
	Euphorbia heterophylla	42.02 (±9.6)	38.35 (±9.2)	17.00 (±5.9)	6.48 (±2.5)	
	Euphorbia ocymoidea	31.49 (±6)	20.59 (±7.2)	12.68 (±0.3)	6.42 (±1.6)	
Leguminosae	*Desmanthus virgatus*	41.44 (±6.4)	39.11 (±6)	15.67 (±5.8)	3.67 (±2.7)	
Malvaceae	*Abutilon hirtum* (Lam.)	11.73 (±4.4)	11.40 (±4.3)	3.12 (±1.2)		
	Corchorus siliquosus L.	30.28 (±6)	25.68 (±5.6)	7.60 (±1.6)		
	Sida acuta Burm	49.87 (±2.2)	42.79 (±2.9)	23.87 (±8.2)	6.07 (±1.3)	
Passifloraceae	*Passiflora obovata*	64.40 (±10.3)	58.06 (±8.6)	16.21 (±12)	5.51 (±4.3)	0.67 (±0.5)
Poaceae	*Andropogon virginicus*	52.18 (±1.9)	48.46 (±1.8)	10.16 (±0.5)	3.39 (±0.3)	0.35 (±0.3)
	Cynodon dactylon (L.)	60.09 (±1.6)	46.52 (±6.4)	24.16 (±4.6)	8.08 (±2.2)	0.42 (±0.3)
	Urochloa fusca (Sw.)	69.33 (±12.4)	47.00 (±7)	46.67 (±17.7)	20.67 (±7.8)	
Portulacaceae	*Portulaca oleracea* L.	54.77 (±3.7)	50.59 (±5.4)	17.76 (±3.8)	4.43 (±1.4)	0.33 (±0.3)
	Portulaca pilosa L.	22.14 (±12.6)	15.19 (±7.2)	11.52 (±8.5)	3.57 (±3.6)	
Rubiaceae	*Moringa yucatanensis*	50.06 (±6.7)	42.56 (±10.3)	7.40 (±3)	2.94 (±1.9)	1.13 (±0.5)
Zigophyllaceae	*Kallstroemia maxima*	46.64 (±1.2)	28.01 (±6.4)	25.64 (±1.7)	8.51 (±1.8)	

Our finding that mycorrhizal colonization was widespread among all ruderal species present at the studied agricultural plot differs from previous studies (*v.g.* Janos, 1980; Pringle *et al.*, 2009). Indeed, several authors (v.g. Grime *et al.* 1987, Francis and Read 1994, Smith and Read, 2008) have suggested that high dispersal ability, high growth rates, early reproduction, and high tolerance to a wide range of abiotic conditions represent life history traits which may preclude a strong dependency on interactions with AMF. Nonetheless, it has been shown that different genotypes of the ruderal species *Ruellia nudiflora* vary in their response to mycorrhizal interaction, influencing plant survival as well as establishment (Ramos-Zapata *et al.*, 2010). Therefore, interactions among ruderal plants and AMF, and the benefits obtained by the former will depend on factors such as plant and AMF genotype as well as environmental conditions and the availability of AMF propagules as has been proposed (Annapurna *et al.* 1996, Smith and Read, 2008).

All of the ruderal species sampled presented AMF hyphae and vesicles in their roots, and some species presented spores and coils (both arbusculate and hyphal) (Table 1). The presence of coils in roots examined suggests a colonization of *Paris* type, in spite of being the *Arum* type the most common for plants with high growth rates such as ruderal species (Smith and Smith, 1997). Our results support the idea that the type of colonization depends not only on plant life-history traits, but also on identity of AMF and their availability, based on which a continuum between both types of colonization may be found as has been suggested before (v.g. Cavagnaro *et al.* 2001, Dikson, 2004). Any way, it is clear from our results that the majorities of ruderal species at least in tropical agrosystems establish a colonization of *Paris* type (but see Ramos-Zapata *et al.*, 2010), and this may be advantageous in environment which exhibit strong fluctuations in resource availability as is the case of the studied plots.

The mean number of AMF spores found was 565±324 in 50 g of dry soil, of which 58.76% were alive (332±199 spores). Spore density varies among cultivation cycles depending on the availability of potential hosts, based on which it is important to conserve a stock of ruderal species associated with a given crop, especially when the cultivated species is planted in monoculture (Feldmann and Boyle, 1999). On the other hand, the soil inoculum potential (50.4±0.05%) and the number of infective propagules (193.37 [47.33 lower limit, 637.64 upper limt]) calculated in this study in 50mL of soil, reveals that during the fallow period (when the main crop is absent) the community of AMF remains active. Levels of AMF soil inoculum may respond to the type of agricultural management scheme (Brundrett *et al.*, 1996; Ramos-Zapata *et al.*, 2012) influencing the presence of AMF both into the roots of ruderal species as well as in the rhizosphere soil. The high density of live spores of AMF and the presence of infective propagules found in our study may respond to the presence of ruderal species which act as AMF host during periods when the crop species is not planted (Baumgartner *et al*., 2005). Therefore, we hypothesize that ruderal plants maintain the production of spores and propagules throughout long periods of time, and in doing so guarantee the maintenance of a stock of AMF to colonize crops (Jordan *et al.*, 2000; Zangaro *et al.*, 2000).

Despite the benefits of AMF in agroecosystems, for example by modifying the abundance of ruderal species (Jordan *et al.*, 2000) or suppressing aggressive weeds in agricultural systems (Vatovec *et al.*, 2005; Jordan and Huerd, 2008; Rinaudo *et al.*, 2010), much work remains to be conducted in order to understand the interactions among AMF and ruderal species in tropical agricultural systems; here with our results, we are able to suggest that the presence of ruderal species acting as temporal host of AMF may play an essential role mantaining active the AMF community until the fallow period ends and the principal crop is planted and in consequence provoking a rapid colonization of its roots.

CONCLUSIONS

Traditional agricultural systems with maize involve low-impact practices that promote the abundance and richness of ruderal plant species that are potentially colonized by AMF, at least during the fallow period of the cultivation cycle. In doing so, ruderal species that establish mycorrhizal interactions may act as temporary hosts of AMF species and contribute to the long-term establishment and stability of communities of these symbiotic microorganisms which may have positive effects on crop yield in agricultural systems.

REFERENCES

Altieri, M.A., Whitcomb, W.H. 1979. The potential use of weeds in the manipulation of beneficial insects. HortScience. 14:12-18.

Annapura, K., Tilak, K.V.B.R., Mukerji, K.G. 1996. Arbuscular mycorrhizal symbiosis recognitions and specificity. In: Mukerji, K.G. (ed.). Concepts in mycorrhizal research. Kluwer Academic Publishers. Dordrecht, The Netherlands. pp 77-90.

Arias, R.L. 1992. El proyecto dinámica de la milpa en Yaxcaba, Yucatán. In: Zizumbo, D., Rasmussen, Ch., Arias, L. M., Terán, S. (eds.). La modernización de la milpa en Yucatán: Utopía o Realidad. Centro de Investigación Científica de Yucatán. Mérida. Yucatán. México. pp. 195-201.

Arias, R.L. 1995. La producción milpera actual en Yaxcaba, Yucatán. In: Hernández, E., Bello, E., Levi, S. (comps.). La Milpa en Yucatán, un sistema de producción agrícola tradicional. Colegio de Postgraduados. México. pp. 171:200.

Baumgartner, K., Smith, R.F., Bettiga, L. 2005. Weed control and cover crop management affect mycorrhizal colonization of grapevine roots and arbuscular mycorrhizal fungal spore populations in a California vineyard. Mycorrhiza. 15:111–119.

Bautista–Zúñiga, F., Jiménez–Osornio, J., Navarro–Alberto, J. 2003. Microrelieve y color del suelo como propiedades de diagnóstico en leptosoles cársticos. Terra. 21:1–11.

Brundrett, M.C., Bougher, N., Bernie, D., Grove, T., Malajczuk, N. 1996. Working with micorrhizas in forestry and agriculture. Monografía ACIAR 32, Canberra Australia.

Caamal, J.A., Jiménez J., Torres-Barragán, A., Anaya, A. 2001. The use of allelopathic legume cover and mulch species for weed control in cropping systems. Agronomy Journal. 93(1):27-36.

Caamal, J.A., Castillo, J.B. 2011. Muestreo de arvenses In: Bautista, F., Palacio, J.L., Delfín, H. (eds.). Técnicas de muestreo para manejadores de recursos naturales. Universidad Nacional Autónoma de México. México, D. F. pp. 537-561

Castillo-Caamal, J.B., Caamal-Maldonado, J.A., Jimenéz-Osornio, J.J., Bautista-Zúñiga, F., Amaya-Castro, M.J., Rodríguez-Carrillo, R. 2010. Evaluación de tres leguminosas como coberturas asociadas con maíz en el trópico subhúmedo. Agronomía Mesoamericana. 21:39-50.

Cavagnaro, T.R., Gao, L.-L., Smith, F.A., Smith, S.E. 2001. Morphology of arbuscular mycorrhizas is influenced by fungal identity. New Phytologist. 151:469–475

Cocom, R., Avilés, L., Garrido, J., Ortiz, J. J. 2008. Plantas silvestres asociadas al cultivo de maíz en Yucatán. Universidad Autónoma de Yucatán. Fundación Produce Yucatán A. C. México.

Dickson, S. 2004. The Arum–Paris continuum of mycorrhizal symbiosis. New Phytologist. 163:187–200

Duch, G.J. 1991. Condicionamiento ambiental y modernización de la milpa en el estado de Yucatán. In: Zizumbo, D., Rasmussen, Ch., Arias, L.M., Terán, S. (eds.). La modernización de la milpa en Yucatán: Utopía o Realidad. Centro de Investigación Científica de Yucatán. Mérida. Yucatán. México. pp. 227-246.

Feldmann, F., Boyle, C. 1999. Weed-mediated stability of arbuscular mycorrhizal effectiveness in maiz monocultures. Journal of Applied Botany 73:1-5.

Flores, J.S., Espejel, I. 1994.Tipos de vegetación de la península de Yucatán. Fascículo 3. Etnoflora Yucatanense. Facultad de Medicina Veterinaria y Zootecnia. Universidad Autónoma de Yucatán. México.

García, E. 1973. Modificaciones al sistema de clasificación climática de Köppen. Universidad Nacional Autónoma de México, México.

Gerdemann, J.W. 1968. Vesicular-arbuscular mycorrhiza and plant growth. Annual Review of Phytopathlogy. 6: 397-418.

Gerdemann, J.W., Nicolson, T. 1963. Spores mycorrhizal endogone species extracted from soil by wet sleving and decanting. Transactions of the British Mycological Society. 42:235-244.

Gliessman, S. R. 1990. Agroecology. Researching the Ecological Basis for Sustainable Agriculture. Springer-Verlag. New York.

Grime, J.P, Mackey, J.M.L,, Sillier, S.H., Read, D.J. 1987. Floristic diversity in a model system using experimental microcosm. Nature. 328: 420–422.

Gupta, A., Joshi, S.P., Manahas, R.K., 2008. Multivariate analysis of diversity and composition of weeds communities of wheat fields in Doon valley India. Tropical Ecology. 49:103-112.

Hart, R.D. 1985. Conceptos básicos sobre agroecosistemas. Centro Agronómico Tropical de Investigación y Enseñanza (CATIE). Turrialba, Costa Rica.

Hausmann, N.T., Hawkes, C.V. 2009. Plant neighborhood control of arbuscular mycorrhizal community composition. New Phytologist. 183:1188–1200.

Hernández–Cuevas, L., Guadarrama–Chávez, P., Sánchez–Gallén, I., Ramos–Zapata, J. 2008. Micorriza arbuscular: colonización intrarradical y extracción de esporas. In: Álvarez–Sánchez, J., Monroy–Ata, A. (comps.). Técnicas de Estudio de las Asociaciones Micorrízicas y sus Implicaciones en la Restauración. Facultad de Ciencias. Universidad Nacional Autónoma de México. México. D.F. pp. 1–15.

Holm, L., Pancho, J., Herberger, J., Plucknett., D. 1979. A Geographical Atlas of World Weeds. John Wiley & Sons. Nueva York.

Janos, D.P. 1980. Vesicular arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology. 61:151-162.

Jansa, J., Mozafar, A., Anken, T., Ruh, R., Sanders, I. R., Frossard, E. 2002. Diversity and structure of AMF communities as affected by tillage in a temperate soil. Mycorrhiza. 12:225–234.

Jordan, N., Huerd, S. 2008. Effects of soil fungi on weed communities in a cornsoybean rotation. Renewable Agriculture and Food Systems. 23:108–117.

Jordan, N.R., Zhang, J., Huerd, S. 2000. Arbuscular-mycorrhizal fungi: potential roles in weed management. Weed Research. 40:397–410.

Kurle, J.E., Pfleger, F.L. 1994. The effects of cultural practices and pesticides on VAM fungi. In: Pfleger, F. L., Linderman, R. G. (eds.). Mycorrhizae and Plant Health. APS Press, St. Paul, Minnesota. pp. 101-131.

McGonigle, T.P., Miller, M.H., Evans, D.G., Fairchild, G.L., Swan, J.A. 1990. A method which gives and objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. New Phytologist. 115:495-501.

Muthukumar, T., Prakash, S. 2009. Arbuscular mycorrhizal morphology in crops and associated weeds in tropical agro-ecosystems. Mycoscience. 50:233–239.

Oehl, F., Sieverding, E., Ineichen, K., Mader, P., Boller, T., Wiemken, A. 2003. Impact of land use intensity on the species diversity of arbuscular mycorrhizal fungi in agroecosystems of central Europe. Applied and Environmental Microbiology. 69:2816–2824.

Palerm, A. 1981. The agricultural basis of urban civilizations in Mesoamerica. In: Graham, J. (ed.). Ancient Mesoamerica. Selected Readings. Peek Publications, USA. Pp. 101-116.

Phillips, J., Hayman, D. 1970. Improved procedures for clearing roots and staining parasitic and vesicular–arbuscular mycorrhizal fungi for assessment of infection. Transactions of the British Mycological Society. 55:158–161.

Pool, N.L., Hernandez-Xolocotzi, E. 1987. Corn producction intensification under flash and burn agricultura in Yaxcaba, Yucatán, México. Terra. 5:149-162.

Porter, W. 1979. The Most Probable Number method for enumerating infective propagules of vesicular arbuscular mycorrhizal fungi in soil. Australian Journal of Soil Research. 17:515-519.

Pringle, A., Bever, J.D., Gardes, M., Parrent, J.L., Rilling, M.C. 2009. Mycorrhizal Symbioses and Plant Invasions. Annual Review of Ecology and Systematics. 40:699–715.

Ramos-Zapata, J., Campos, M.J., Parra-Tabla, V., Abdala-Roberts, L., Navarro, J. 2010. Genetic variation in the response of the weed *Ruellia nudiflora* (Acanthaceae) associated to arbuscural mycorrhizal fungi. Mycorrhiza. 20:275-280.

Ramos-Zapata, J.A., Guadarrama, P., Navarro-Alberto, J., Orellana, R. 2011.Arbuscular mycorrhizal propagules in soils from a tropical forest and an abandoned cornfield in Quintana Roo, Mexico: visual comparison of most-probable-number estimates. Mycorrhiza. 21:139-144.

Ramos-Zapata, J., Marrufo-Zapata, D., Guadarrama, P., Carrillo-Sánchez, L., Hernández-Cuevas, L., Caamal-Maldonado, A. 2012. Impact of weed control on arbuscular mycorrhizal fungi in a tropical agroecosystem: a long-term experiment. Mycorrhiza. DOI 10.1007/s00572-012-0443-1

Rinaudo, V., Barberi, P., Giovannetti, M., van der Heijden, M.G.A. 2010. Mycorrhizal fungi suppress aggressive agricultural weeds. Plant and Soil. 333:7-20.

Sieverding, E. 1990. Ecology of VAM fungi in tropical agrosystems. Agriculture, Ecosystems and Environment. 29:369–390.

Smith, F.A., Smith, S.E. 1997. Structural diversity in (vesicular)-arbuscular mycorrhizal symbioses. New Phytologist. 137:373-388.

Smith, S.E., Read, D.J. 2008. Mycorrhizal symbiosis. Academic Press. London.

Trappe, J.M. 1987. Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an evolutionary standpoint. In: Safir, G.R. (ed). Ecophysiology of VA Mycorrhizal Plants. CRC Press, Boca Raton. Florida. pp 5-25.

Vatovec, C., Jordan, N., Huerd, S. 2005. Responsiveness of certain agronomic weed species to arbuscular mycorrhizal fungi. Renewable Agriculture and Food Systems. 20:181–189.

Villaseñor, R.J.L., Espinosa, F.J.G. 1998. Catálogo de malezas de México. Universidad Nacional Autónoma de México. Consejo Nacional Consultivo Fitosanitario. Fondo de Cultura Económica. México, D.F.

Zangaro, W., Bononi, V.L.R., Truffen, S.B. 2000. Mycorrhizal dependency, inoculum potential and habitat preference of native woody species in South Brazil. Journal of Tropical Ecology. 16:603-622.

Submitted July 19, 2012– Accepted October 14, 2012
Revised received September 18, 2013