



Research Paper

Native communities of arbuscular mycorrhizal fungi associated with *Capsicum annuum* L. respond to soil properties and agronomic management under field conditions[☆]



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ABSTRACT

We examined the effects of agronomic management (low, moderate, and high inputs) and soil properties on arbuscular mycorrhizal fungi (AMF) community structure collected from the rhizosphere of *Capsicum annuum* cultivated in six agroecosystems in Mexico. Chemical and physical soil parameters differed among agroecosystems. Native communities of AMF-morphospecies differed between agroecosystems depending on intensity of agronomic practice. In total 33 AMF-morphospecies were identified (11 genera, and seven families). Soil P availability and pH negatively affected the distribution and abundance of the AMF species. High input management resulted in significant modifications in the composition and structure of the AMF communities. Agroecosystems with high or moderate input management showed 35% less AMF-morphospecies when compared to low input management systems. The most diverse AMF community was observed from agroecosystems with either moderate or low input management. *Funneliformis geosporum*, *Claroideoglossum claroideum* and *C. luteum* were the predominant species observed in this study. High similarity (> 75%) in the structure of AMF communities among agroecosystems was found, which suggest that the observed differences between AMF communities from agroecosystems with high input management compared to that from low and moderate input management, may be due to changes in species composition.

1. Introduction

Arbuscular mycorrhizal fungi (AMF) are essential for the functioning and sustainability of agroecosystems (Parniske, 2008; Verbruggen and Kiers, 2010; Gianinazzi et al., 2010). Most crops form symbiotic associations with AMF, and have been reported to improve crop nutrition and health (Brundrett, 2009; Kivlin et al., 2011; Alarcón et al., 2012). The abundance and species composition of AMF may be a key factor in determining crop growth, performance, and yield (Klironomos, 2003; Oehl et al., 2010; Verbruggen and Kiers, 2010;

Koch et al., 2011; Verbruggen et al., 2012).

Environmental conditions including soil characteristics and agronomic management practices, affect the abundance, diversity, and traits of AMF within the soil system (Hoeksema et al., 2010; Oehl et al., 2010; Jansa et al., 2014). Soil phosphorus availability is a critical factor for AMF in terms of both root and soil colonization, for instance, high soil phosphorus availability reduces AMF effectiveness and diversity (Oehl et al., 2010; Bainard et al., 2014). While, soil organic matter seems to promote AMF activity in terms of root and soil colonization (Cardona et al., 2008; Vays and Vays, 2012; Alguacil et al., 2014). Other physical

Abbreviations: SM, San Martinito; JCI and JCII, Juárez Coronaco I and II; SMZ, Santa María Zacatepec; SMCI and SMCI, San Mateo Capultitlán I and II

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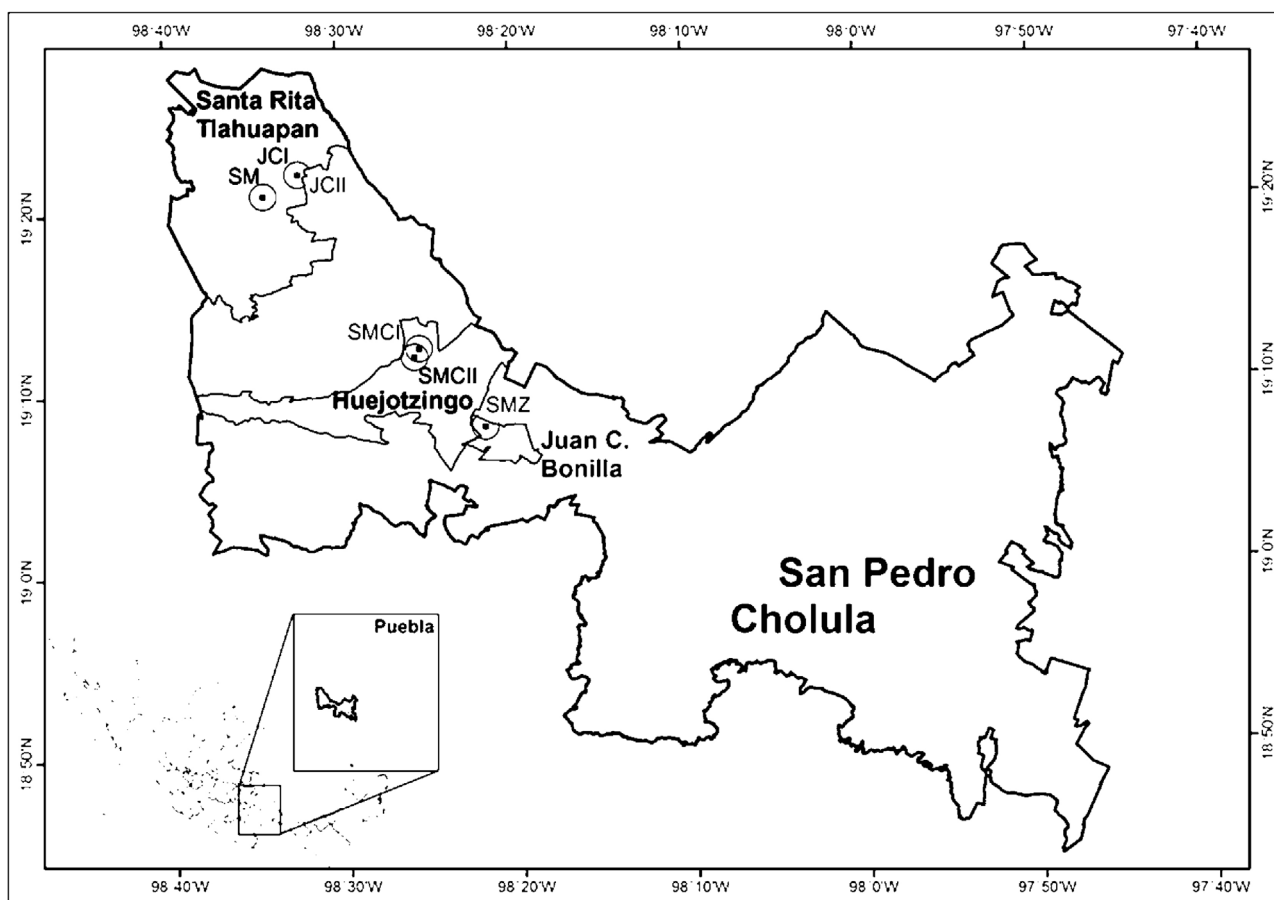


Fig. 1. Location of the “poblano” pepper agroecosystems in Puebla State (Mexico). Abbreviations: SM = San Martinito; JCI and JCII = Juárez Coronaco I and II; SMZ = Santa María Zacatepec; SMCI and SMCII = San Mateo Capultitlán I and II.

or chemical soil characteristics including soil texture, moisture, and pH may affect AMF abundance, diversity, and species composition (Hijri et al., 2006; Kivlin et al., 2011; Bainard et al., 2014; Jansa et al., 2014).

High input agricultural practices, employing agrochemicals and intensive tillage have been reported to reduce AMF species richness in coffee, avocado, and maize production systems (Trejo et al., 2011; Arias et al., 2012; González-Cortes et al., 2012; Alguacil et al., 2014). In addition, the crop species also seems to affect the composition and diversity of the of native AMF communities, either by favoring some Glomeraceae species (Oehl et al., 2010; Verbruggen et al., 2012), or by suppressing other AMF species with specific ecological niches (González-Cortes et al., 2012; Öpik and Moora, 2012; Verbruggen et al., 2012).

Pepper (*Capsicum annuum* L.) is an important part of the diet many parts of the world (Piñeiro et al., 2008). Pepper plants are originated from Mexico, which is center for the domestication of several plant species (Piñeiro et al., 2008; Contreras et al., 2011; Castellón-Martínez et al., 2012). The “poblano” pepper is economically one of the most important varieties, both in terms of cultivated land and human consumption (Rodríguez et al., 2007), and is also of considerable nutritional and cultural importance in Mexico (Rodríguez et al., 2007; Contreras et al., 2011; Morán-Bañuelos et al., 2008).

Despite the origin and global importance of pepper plants, there is limited information on the native AMF communities associated with this crop. Most AMF studies with pepper plants have focused on plant growth responses (Sensoy et al., 2007; Kaya et al., 2009; Kim et al., 2010; Douds et al., 2012), with limited attention given to the AMF communities at field conditions. Twenty AMF species, dominated by members of Glomeraceae family, have been reported to form associations with *C. annuum* and *C. frutescens* (Cardona et al., 2008; Castillo

et al., 2010; Boonlue et al., 2012; Chen et al., 2012; Vays and Vays 2012). However, information about how native communities of AMF associated with pepper plants respond to soil characteristics and to agronomic management practices is limited. The main objective of this study was to examine how native communities of AMF associated with “poblano” pepper respond to the intensity of agronomic management practices and soil properties under field conditions. Here, we tested the hypothesis that the intensity (low, moderate or high) of agronomic management significantly affects AMF communities associated with “poblano” pepper under field conditions.

2. Materials and methods

2.1. Study site

Root and soil samples were collected from six “poblano” pepper agroecosystems located within three municipalities in San Pedro Cholula and Puebla, Mexico (Fig. 1). These selected areas represent zones with a high “poblano” pepper production from small local farm. The climate of the region is temperate subhumid, with a rainy summer-autumn period and a dry winter-spring period. This region is dominated by agricultural lands, with small pockets of remnant pine-oak forest (INEGI, 1997).

The six “poblano” pepper agroecosystems included in the study were divided in three groups according to agronomic management: a) San Martinito (SM) with low input management; b) Santa María Zacatepec (SMZ), Juárez Coronaco I and II (JCI and JCII) with moderate input management; and c) San Mateo Capultitlán I and II (SMCI and SMCII) with high input management (Table 1).

Table 1
Description of the six sampled “poblano pepper” (*Capsicum annuum*) agroecosystems in Puebla State (Mexico).

Municipality	Agroecosystems	Location	Altitude (masl)	Agroonomic management practice
Santa Rita Tlahuapa	San Martinito (SM)	19°21.03' N 98°33.98' W	2548	Low agronomic inputs, fertilized (Urea and 18 N–46P) once or twice per crop cycle, manual weed control, one application of insecticides and/or fungicide, and two applications of organic amendments.
	Juárez Coronaco I (JCI)	19°22.24' N 98°31.97' W	2441	Moderate agronomic inputs with three applications of fertilizers (Urea and 18 N–46 P, and Triple 17), manual weed control, three applications of insecticides, nematicides, and fungicides, and one application of organic amendments.
	Juárez Coronaco II (JCII)	19°22.23' N 98°32.08' W	2458	
Juan C. Bonilla	Santa María Zacatepec (SMZ)	19°07.93' N 98°21.34' W	2233	
Huejotzingo	San Mateo Capultitlán I (SMCI)	19°12.29' N 98°25.52' W	2287	High agronomic inputs with four to five applications of fertilizers (Urea and 18 N–46P, and Triple 17), manual and chemical weed control, three applications of insecticides, nematicides, fungicides, and herbicides, and one application of organic amendments.
	San Mateo Capultitlán II (SMCII)	19°12.02' N 98°25.69' W	2289	

2.2. Soil collection and physical and chemical properties

At the fruit setting growth stage, the soil was sampled from five “poblano” pepper plants from each agroecosystems, yielding 30 soil samples in total. From each plant, four subsamples were collected at 20 cm depth. These four subsamples were then mixed to obtain one composite sample per plant (Robles et al., 2008). Each composite sample was divided in two subsamples, one for the analysis of AMF communities and the other for physical and chemical analysis of the soil. Subsamples for the analysis of AMF communities were stored at ~5 °C. Subsamples for soil physical and chemical properties were air-dried, homogenized, and passed through a 2-mm sieve. Soil pH (soil:water, 2.5:1 w/v), texture, electrical conductivity (EC), soil organic matter (SOM; Walkley-Black), available phosphorus (Bray and Kurtz), and inorganic nitrogen (microKjeldahl) were determined (SEMARNAT, 2002).

2.3. Abundance and taxonomic identification of spores of AMF

Spores of AMF were extracted from soil by wet-sieving and decanting (Gerdeman and Nicolson, 1963) following a step-gradient of sucrose (20 and 60%) centrifugation (Sieverding, 1983). Spores were microscopically separated in accordance to their morphological features (form, size, color, presence/absence of hyphae), and mounted on glass slides in polyvinyl alcohol-lactic acid-glycerol. Only intact and healthy spores were counted and examined using a Nomarski differential contrast interference microscopy (Nikon Optiphot II Plus). Taxonomic identification of AMF morphospecies was performed by comparing and contrasting species descriptions provided by the International Collection of Vesicular and Arbuscular Mycorrhizal Fungi (INVAM) (<http://invam.wve.edu/>) and the home page of Dr. Janusz Blaszowski (<http://www.zor.zut.edu.pl/Glomeromycota/>). Identification of AMF species was based on the classification of Redecker et al. (2013).

2.4. Ecological analyses and statistics

The AMF community structure was examined by determining AMF-spores abundance, species richness, species composition, and isolation frequency. The Pielou evenness index, Simpson dominance-diversity index, and the Shannon-Wiener diversity index were also estimated. The Sorensen coefficient was utilized to examine the similarity of the AMF communities among the “poblano” pepper agroecosystems in terms of beta-diversity (Magurran, 1988; Dandan and Ziwey, 2007).

The Hutchinson modified Student *t*-test was used to compare AMF diversity measurements among “poblano” pepper agroecosystems. Data

from soil properties and number of spores were subjected to one-way analyses of variance (ANOVA) in order to examine possible differences among “poblano” pepper agroecosystems ($n = 5$). Post hoc treatment means comparisons were performed using Tukey ($P \leq 0.01$). Correlations among soil physical and chemical properties, and AMF species abundance and distribution, were tested using canonical correspondence analyses. All statistical analyses were performed with the program STATISTICA version 9.0. Variance homogeneity and normal distribution were tested prior ANOVA, and transformed when necessary. Data for number of AMF spores (g^{-1} dry soil) was \log_{10} transformed, but presented in original units.

3. Results

3.1. Effects of agronomic management on the composition and structure of the AMF community

The species composition of the AMF-community from the agroecosystems with low and moderate input management differed from those with high input management (Table 2; Fig. 2). *Scutellospora* species were not found at the high input management agroecosystems SMCI and SMCII. *Ambispora colombiana*, *Glomus* aff. *microcarpum*, *Glomus* sp. 2, and *Glomus* sp. 3, were exclusively observed at these two agroecosystems (Table 2). By comparing the AMF community composition, by means of the Sorensen's coefficient, a high similarity between the agroecosystems with low and moderate input management (SM, SMZ, and JCI) was observed. In contrast, the two agroecosystems with high input management (SMCI and SMCII) were joined in different group (Fig. 2).

In total, in this study, 33 AMF morphospecies were identified belonging to 11 genera and seven families (Table 2). Glomeraceae family presented the highest number of morphospecies (39% of the total), followed by the Acaulosporaceae and Gigasporaceae families (25% and 12%, respectively). Overall, management type did not affect AMF species richness. SMCI and SMCII (high inputs) had 24 species, as well as the SMZ, JCI and JCII (moderate inputs), while SM (low inputs) had 23 species. However, at individual scale, the agroecosystems SMCI and JCII, with high and moderate input management respectively, showed 35% less AMF morphospecies when compared to the agroecosystems with low input management (SM). Regardless the agronomic management, ten of the 33 AMF morphospecies were frequently recorded in all sampling agroecosystems. In contrast, only five morphospecies (*A. splendida*, *E. infrequens*, *P. coralloidea*, *P.* aff. *franciscana*, and *G. minutum*) were recorded at one of the moderate input management agroecosystems (JCI). *Acaulospora colombiana* was only observed in the agroecosystems SMCII (high input management), and *A. bireti-*

Table 2
Arbuscular mycorrhizal fungi (AMF) morphospecies recorded in the rhizosphere of “poblano pepper” collected from six agroecosystems in Puebla State (Mexico).

AMF morphospecies	Agroecosystems					
	Low management		Moderate management		High management	
	SM	JCI	JCII	SMZ	SMCI	SMCII
DIVERSISPORALES						
Acaulosporaceae						
<i>Acaulospora bireticulata</i> Rothwell & Trappe	X					
<i>Acaulospora colombiana</i> (Spain & Schenck) Kaonongbua, Morton & Bever						X
<i>Acaulospora laevis</i> Gerd. & Trappe	X	X		X	X	X
<i>Acaulospora mellea</i> Spain & Schenck	X					X
<i>Acaulospora morrowiae</i> Spain & Schenck	X	X	X	X	X	X
<i>Acaulospora scrobiculata</i> Trappe				X	X	X
<i>Acaulospora spinosa</i> Walker & Trappe	X			X		X
<i>Acaulospora splendida</i> Sieverd., Chaverri & Rojas		X				
Diversisporaceae						
<i>Diversispora aurantia</i> (Błaszk., Blanke, Renker & Buscot) Walker & Schuessler	X	X	X	X	X	X
<i>Diversispora spurca</i> (Pfeiff, Walker & Bloss) Walker & Schuessler	X		X			
Entrophosporaceae						
<i>Entrophospora infrequens</i> (Hall) Ames & Schneider		X				
Gigasporaceae						
<i>Gigaspora candida</i> Bhattacharjee, Mukerji, Tewari & Skoropad	X	X	X	X		X
<i>Gigaspora margarita</i> Becker & Hall	X					X
<i>Scutellospora dipurpurascens</i> Morton & Koske	X	X	X			
<i>Scutellospora pellucida</i> (Nicol. & Schenck) Walker & Sanders	X	X	X	X		
Pacisporaceae						
<i>Pacispora coralloidea</i> Oehl & Sieverd.		X				
<i>Pacispora</i> aff. <i>franciscana</i> Oehl & Sieverd.		X				
GLOMERALES						
Claroideoglomeraceae						
<i>Claroideoglomus claroideum</i> (Schenck & Smith) Walker & Schuessler	X	X	X	X	X	X
<i>Claroideoglomus luteum</i> (Kenn., Stutz & Morton) Walker & Schuessler	X	X	X	X	X	X
<i>Claroideoglomus</i> sp.1	X	X	X	X		X
Glomeraceae						
<i>Funneliformis constrictum</i> Sieverd., Silva & Oehl	X					X
<i>Funneliformis geosporum</i> (Nicolson & Gerd.) Walker & Schuessler	X	X	X	X	X	X
<i>Funneliformis mosseae</i> (Nicol. & Gerd.) Walker & Schuessler	X	X	X	X	X	X
<i>Funneliformis</i> sp. 1	X	X	X	X	X	X
<i>Glomus</i> aff. <i>microcarpum</i> Tulasne & Tulasne					X	X
<i>Glomus minutum</i> Błaszk., Tadych & Madej		X				
<i>Glomus</i> sp. 1	X	X	X	X	X	X
<i>Glomus</i> sp. 2						X
<i>Glomus</i> sp. 3					X	X
<i>Glomus</i> sp. 4	X		X	X		X
<i>Glomus</i> sp. 5	X				X	X
<i>Rhizophagus fasciculatus</i> (Thaxt.) Walker & Schuessler	X	X	X	X	X	X
<i>Sclerocystis sinoua</i> Gerd. & Bakshi	X	X	X	X	X	X
Total number of species	23	20	16	17	15	24
Total number of spores (50 g of dry soil ⁻¹) ^a	67abc	98ab	53bc	30c	111ab	153a

Abbreviations: SM = San Martinito; JCI and JCII = Juárez Coronaco I and II; SMZ = Santa María Zacatepec; SMCI and SMCII = San Mateo Capultitlán I and II.

^a Means with the same letter are not significantly different (Tukey, $\alpha = 0.05$).

culata was only recorded at SM with low input management (Table 2).

The high input management negatively affected the AMF community and seemed to favor the dominance of some the Glomeromycota morphospecies. Eighty percent of the spores at the sites with high input management corresponded to members of Claroideoglomeraceae and Glomeraceae families, but only 65% of them corresponded to agroecosystems with moderate and low input management. In addition, AMF communities were dominated by *Claroideoglomus luteum* and *Funneliformis geosporum* at high input management (29 and 31%, respectively from total spores) (Table 3). In that, high input management seemed to favor a low evenness and diversity of AMF (Table 4). However, the most diverse and even AMF communities were recorded at the SMZ and SM agroecosystems with moderate and low input management, respectively; and were significantly different ($P \leq 0.01$) to agroecosystems with high input management (Table 4).

3.2. Effects of soil properties on the AMF distribution and abundance

In the canonical correspondence analysis, the two axes accounted for 63.4% of the variation in the data, and the relationships among variables were significant ($F = 1.34$ and $p \leq 0.010$). This indicates that the distribution and abundance of AMF species could be the result of the chemical properties of soil. *Funneliformis geosporum*, *Acaulospora colombiana*, *A. laevis*, and *A. morrowiae* were grouped towards the P-available vector on the primary axis ($r = 0.67$; $p \leq 0.05$), where agroecosystem SMCII with high P concentration was placed. In contrary, the highest amount of AMF morphospecies was distributed in agroecosystems with low P-availability ($r = -0.77$; $p \leq 0.05$). On the other hand, *Claroideoglomus* sp. 1, *Funneliformis* sp. 1 and *Glomus* sp. 1, were grouped on the secondary axis, related to the soil pH ($r = 0.59$; $p \leq 0.05$), where the agroecosystems SMCI had the highest pH values were placed (Fig. 3; Table 5).

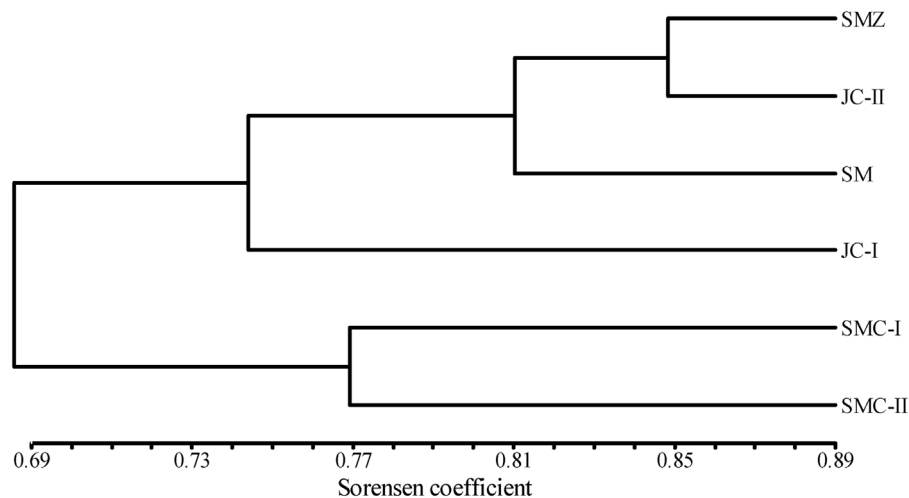


Fig. 2. Dendrogram that shows the similarity of the arbuscular mycorrhizal fungal species composition among the six “poblano pepper” (*Capsicum annuum* L.) agroecosystems sampled from the Puebla State (Mexico). Abbreviations: SM = San Martinito; JCI and JCII = Juárez Coronaco I and II; SMZ = Santa María Zacatepec; SMC-I and SMC-II = San Mateo Capultitlán I and II.

3.3. Soil physical and chemical properties

Some soil parameters showed significant ($P < 0.01$) differences among sampled agroecosystems. The pH values ranged from moderately acid (SM and JCII) to neutral (SMCI and SMCII). The agroecosystem with highest management input (SMCII) had the high concentration of available P and significantly ($p \leq 0.01$) differed when compared to SM, JCII and SMZ agroecosystems. Overall, all agroecosystems showed low EC and very low soil N-concentrations. The textural classification varied from sandy loam (SMZ, SMCI, and SMCII) to sandy clay loam (SM and JCI). Although the SOM concentration was high in the agroecosystem with low input management (SM), it was not significantly different from those with high input management (Table 5).

4. Discussion

The native communities of AMF associated with “poblano” pepper showed variations depending on the agronomic management of the agroecosystem and soil properties. The intensive crop management, including excessive use of fertilizers and pesticides, is perceived to be necessary by farmers in order to be more productive and to make the crop more economically viable; thus, such agronomic practices are very common in most productive agricultural regions in Mexico (Appendini, 2001). In addition to the environmental concerns these practices may raise, it meant that it was extremely difficult to identify sites of “poblano” pepper production with low input management. In that, only one “poblano” pepper farm with low inputs was identified for this study.

The Sorensen's coefficient demonstrated that composition species of AMF communities from the agroecosystems with low and moderate input management (SMZ, JCI, and SM) differed from those with high input management (SMCI and SMCII). For example, *Scutellospora* species were not found at SMCI and SMCII. In contrast, *Acaulospora bireticulata*, *A. splendida*, *E. infrequens*, *G. minutum*, *P. coralloidea*, and *P. aff. franciscana* were only recorded in agroecosystems with low and moderate input management (SM or JCI). This suggests that these species may be specialists under certain ecological conditions, as proposed for other AMF morphospecies (Oehl et al., 2010; Öpik and Moora, 2012). The presence of such species, in soils with low and moderate input management, has been previously reported in grasslands, agricultural crops, and temperate forest (Oehl et al., 2010; Verbruggen et al., 2012; González-Cortes et al., 2012). The later suggests that AMF species may differ in their benefits to different plant species and consequently, their potential role within an agroecosystems (Oehl et al., 2004).

The high similarity achieved between the six agroecosystems ($> 75\%$) suggests a certain amount of system stability, with low species turnover (beta diversity). This suggests that the majority of the AMF species identified within each agroecosystem has a wide geographic distribution and some of them are well adapted to agronomical disturbances (low or moderate input management) (Oehl et al., 2010; Verbruggen et al., 2012; Alguacil et al., 2014). Only a few species, were found to be well adapted to a high input management, these included *A. colombiana*, *F. geosporum*, *Glomus* aff. *microcarpum*, *Glomus* sp. 2, and *Glomus* sp. 3.

The low beta diversity also indicates that AMF species assemblage may only be characteristic for the pepper agroecosystems. We suggest that, high input management will result in the disappearance of some AMF species, resulting in more abundant and tolerant AMF species becoming dominant within the system (Oehl et al., 2004; Verbruggen et al., 2012). Furthermore, the intensity of agronomical practices which may select AMF species that are not necessarily the most effective plant growth promoters (Oehl et al., 2004; Trejo et al., 2011), which may alter some ecosystem functions, then making the agroecosystems more susceptible to losses from pests and diseases outbreaks (Coleman and Whitman, 2005; Mace et al., 2012).

Biological species richness is key to the resiliency, sustainability, and productivity of an agroecosystem (Coleman and Whitman, 2005; Mace et al., 2012; Verbruggen et al., 2012). The number of AMF morphospecies recorded in the present study (33) is higher than those estimated from other varieties of *C. annuum*, which ranged from 9 to 17 morphospecies (Cardona et al., 2008; Castillo et al., 2010; Boonlue et al., 2012; Chen et al., 2012; Vays and Vays, 2012).

The agroecosystems SMCI and JCII, with high and moderate input management, respectively, had 35% less AMF species than that agroecosystems with low input management (SM). This reduction in AMF species in relation to intensity of disturbance, is in agreement with reports for a variety of agroecosystems/land use (Oehl et al., 2010; Verbruggen et al., 2012) and crop production systems, including coffee, avocado, and maize (Arias et al., 2012; Trejo et al., 2011; González-Cortes et al., 2012).

We do not have a clear understanding of what a reduction in AMF diversity and species number will mean in the long-term. We suggest that the continuous application of high input of agrochemicals (fertilizers and pesticides) will result in loss of genetic and functional diversity of AMF species, and subsequently, a reduction in soil health, productivity, and species richness (Oehl et al., 2010; Alarcón et al., 2012; Alguacil et al., 2014). Thus, the later also results in alterations of ecosystem services (food production, habitat, water, nutrient, and

Table 3

Spore number (SN), relative abundance (RA), and isolation frequency (IF) of arbuscular mycorrhizal fungi (AMF) in the rhizosphere of six “poblano pepper” agroecosystems in Puebla State (Mexico).

AMF morphospecies	Agroecosystems																	
	Low management			Moderate management									High management					
	SM			JCI			JCII			SMZ			SMCI			SMCII		
	SN	RA	IF	SN	RA	IF	SN	RA	IF	SN	RA	IF	SN	RA	IF	SN	RA	IF
Acaulosporaceae	19	5.86	80	21	4.54	100	1	0.39	20	15	10.20	60	9	1.68	80	22	2.26	80
<i>Acaulospora bireticulata</i>	3	0.93	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>A. colombiana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	0.21	20
<i>A. laevis</i>	4	1.24	40	15	3.24	100	–	–	–	1	0.68	20	3	0.56	40	8	0.82	20
<i>A. mellea</i>	1	0.31	20	–	–	–	–	–	–	–	–	–	–	–	–	1	0.10	20
<i>A. morrowiae</i>	8	2.47	80	1	0.22	20	1	0.39	20	1	0.68	20	4	0.74	40	6	0.62	40
<i>A. scrobiculata</i>	–	–	–	–	–	–	–	–	–	12	8.16	60	2	0.37	40	4	0.41	60
<i>A. spinosa</i>	3	0.93	20	–	–	–	–	–	–	1	0.68	20	–	–	–	1	0.10	20
<i>A. splendida</i>	–	–	–	5	1.08	40	–	–	–	–	–	–	–	–	–	–	–	–
Claroideoglomeraceae	71	21.91	100	84	18.14	100	95	37.11	100	34	23.13	100	163	30.35	100	378	38.77	100
<i>Claroideoglomerus claroideum</i>	24	7.41	100	22	4.75	100	31	12.11	100	20	13.61	100	80	14.90	100	72	7.38	100
<i>C. luteum</i>	38	11.73	100	47	10.15	100	55	21.48	80	9	6.12	60	83	15.46	100	303	31.08	100
<i>Claroideoglomerus</i> sp.1	9	2.78	60	15	3.24	80	9	3.52	80	5	3.40	60	–	–	–	3	0.31	20
Diversisporaceae	69	21.30	100	32	6.91	100	13	5.08	80	11	7.48	40	123	22.91	100	161	16.51	100
<i>Diversispora aurantia</i>	51	15.74	100	32	6.91	100	12	4.69	60	11	7.48	40	123	22.91	100	148	15.18	100
<i>D. spurca</i>	18	5.56	60	–	–	–	1	0.39	20	–	–	–	–	–	–	–	–	–
Entrophosporaceae	–	–	–	2	0.43	20	–	–	–	–	–	–	–	–	–	–	–	–
<i>Entrophospora infrequens</i>	–	–	–	2	0.43	20	–	–	–	–	–	–	–	–	–	–	–	–
Gigasporaceae	25	7.72	100	15	3.24	100	19	7.42	80	7	4.76	40	–	–	–	9	0.92	100
<i>Gigaspora candida</i>	5	1.54	40	2	0.43	20	6	2.34	–	2	1.36	20	–	–	–	7	0.72	100
<i>G. margarita</i>	4	1.24	20	–	–	–	–	–	40	–	–	–	–	–	–	2	0.21	40
<i>Scutellospora dipurpurascens</i>	10	3.09	80	8	1.73	80	9	3.52	60	–	–	–	–	–	–	–	–	–
<i>S. pellucida</i>	6	1.85	40	5	1.08	60	4	1.56	60	5	3.40	40	–	–	–	–	–	–
Glomeraceae	140	43.21	100	296	63.93	100	128	50.00	100	80	54.42	100	242	45.07	100	418	42.87	100
<i>Funneliformis constrictum</i>	1	0.31	20	–	–	–	–	–	–	–	–	–	–	–	–	1	0.10	20
<i>F. geosporum</i>	49	15.12	100	95	20.52	100	34	13.28	100	18	12.24	100	155	28.86	100	210	21.54	100
<i>F. mosseae</i>	50	15.43	100	65	14.04	100	71	27.73	100	9	6.12	100	3	0.56	60	52	5.33	100
<i>Funneliformis</i> sp. 1	5	1.54	60	33	7.13	100	1	0.39	20	15	10.20	80	36	6.70	80	35	3.59	100
<i>Glomus microcarpum</i>	–	–	–	–	–	–	–	–	–	–	–	–	1	0.19	20	10	1.03	40
<i>G. minutum</i>	–	–	–	6	1.30	20	–	–	–	–	–	–	–	–	–	–	–	–
<i>Glomus</i> sp. 1	5	1.54	60	61	13.17	100	3	1.17	40	13	8.84	60	14	2.61	40	13	1.33	80
<i>Glomus</i> sp. 2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21	2.15	80
<i>Glomus</i> sp. 3	–	–	–	–	–	–	–	–	–	–	–	–	2	0.37	40	10	1.03	100
<i>Glomus</i> sp. 4	3	0.93	20	–	–	–	2	0.78	40	1	0.68	20	–	–	–	2	0.21	40
<i>Glomus</i> sp. 5	4	1.23	60	–	–	–	–	–	–	–	–	–	9	1.68	40	20	2.05	100
<i>Rhizophagus fasciculatus</i>	21	6.48	100	31	6.70	100	14	5.47	80	5	3.40	60	19	3.54	80	19	1.95	80
<i>Sclerocystis sinoua</i>	2	0.62	40	5	1.08	60	3	1.17	60	19	12.93	80	3	0.56	40	25	2.56	100
Pacisporaceae	–	–	–	13	2.81	100	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pacispora coralloidea</i>	–	–	–	12	2.59	100	–	–	–	–	–	–	–	–	–	–	–	–
<i>P. aff. franciscana</i>	–	–	–	1	0.22	20	–	–	–	–	–	–	–	–	–	–	–	–

Abbreviations: SM = San Martinito; JCI and JCII = Juárez Coronaco I and II; SMZ = Santa María Zacatepec; SMCI and SMCII = San Mateo Capultitlán I and II.

carbon cycling). In addition, resilience of specialist AMF species after being subjected to long-term high input agronomic practices is unclear (Oehl et al., 2009; 2010; Verbruggen et al., 2012).

Regardless the agronomic management practice, the similar and high AMF species richness observed in all sampled sites was unexpected. We suggest, that the presence of several annual weeds (data not

Table 4

Diversity measurements of arbuscular mycorrhizal fungi in six “poblano pepper” agroecosystems in Puebla State (Mexico).

Ecological parameters	Agroecosystems					
	Low management		Moderate management		High management	
	SM	JCI	JCII	SMZ	SMCI	SMCII
Richness	23	20	16	17	15	24
Maxima diversity	3.13	2.99	2.77	2.83	2.70	3.18
Shannon-Wiener diversity index ^a	2.49 a	2.46 a	2.11 b	2.52 a	1.90 c	2.13 b
Simpson dominance-diversity index	0.11	0.11	0.16	0.09	0.19	0.18
Pieolou evenness index	0.79	0.82	0.76	0.89	0.70	0.67

^a Means with the same letter in the same column are not significantly different (*t*-Student, $\alpha = 0.05$, modified by Hutchinson).

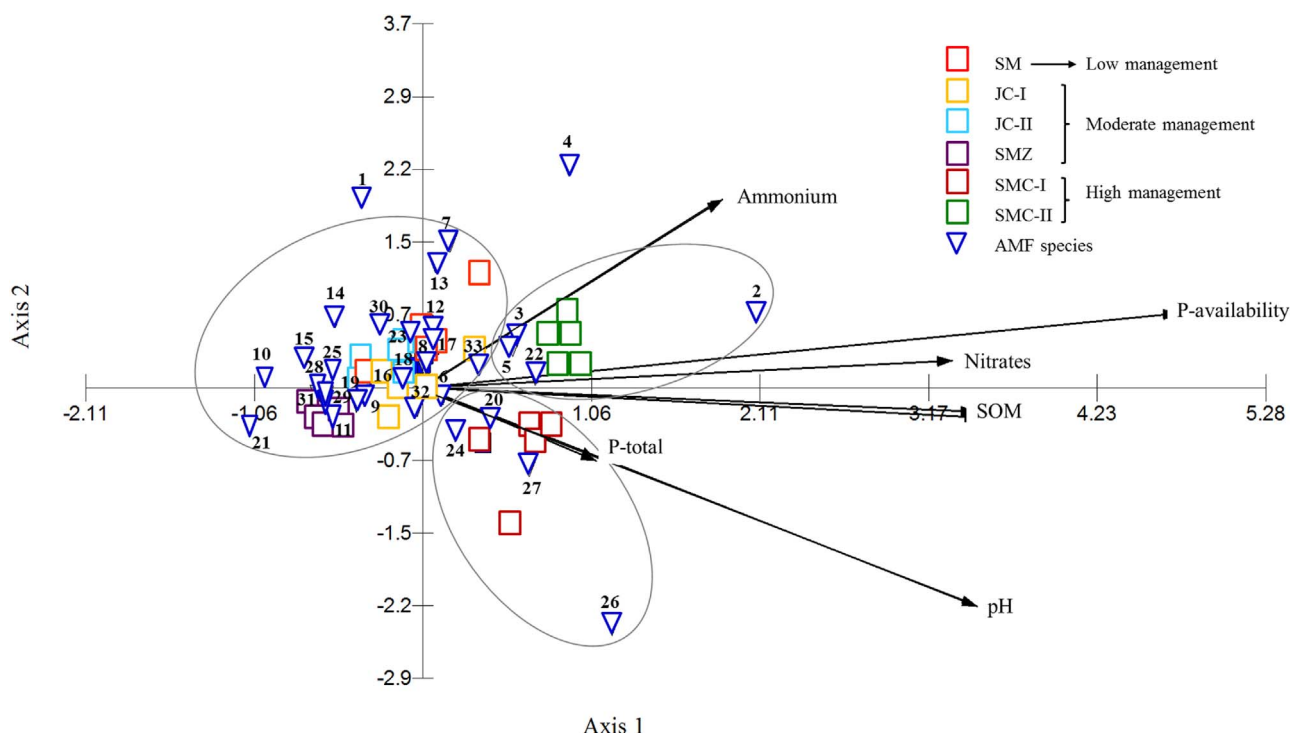


Fig. 3. Ordination diagram that shows the effects of soil properties on the distribution of arbuscular mycorrhizal fungal species from six “poblano pepper” (*Capsicum annuum* L.) agroecosystems at Puebla State (Mexico). Abbreviations: SM = San Martinito; JCI and JCII = Juárez Coronaco I and II; SMZ = Santa María Zacatepec; SMC-I and SMCII = San Mateo Capultitlán I and II; SOM = Soil organic matter. AMF species represented by numbers: 1 = *Acaulospora bireticulata*; 2 = *A. colombiana*; 3 = *A. laevis*; 4 = *A. mellea*; 5 = *A. morrowiae*; 6 = *A. scrobiculata*; 7 = *A. spinosa*; 8 = *A. splendida*; 9 = *D. aurantia*; 10 = *D. spurca*; 11 = *Entrophospora infrequens*; 12 = *Gigaspora candida*; 13 = *G. margarita*; 14 = *Scutellospora dipurpurascens*; 15 = *S. pellucida*; 16 = *Pacispora coralloidea*; 17 = *P. aff. franciscana*; 18 = *Claroideoglopus claroideum*; 19 = *C. luteum*; 20 = *Claroideoglopus* sp.1; 21 = *Funneliformis constrictum*; 22 = *F. geosporum*; 23 = *F. mosseae*; 24 = *Funneliformis* sp. 1; 25 = *Glomus* aff. *microcarpum*; 26 = *G. minutum*; 27 = *Glomus* sp. 1; 28 = *Glomus* sp. 2; 29 = *Glomus* sp. 3; 30 = *Glomus* sp. 4; 31 = *Glomus* sp. 5; 32 = *Rhizophagus fasciculatus*; 33 = *Sclerocystis sinoua*.

shown) associated with pepper crop production, may provide an alternate habitat for AMF (Oehl et al., 2010; Alguacil et al., 2014). Moreover, the agroecosystem SMCII is subjected to crop rotations with maize and beans plants, and these plant species may give better support for AMF propagules.

The AMF alpha diversity varied from 1.9 to 2.5 according to Shannon-Wiener Index, which is higher than that reported for coffee production systems (Arias et al., 2012), similar to those reported for *C. annuum* (Chen et al., 2012) and for sites with other crops, agronomic management practices, and soil type (Oehl et al., 2010). The agroecosystems with high input agronomic management (SMCI and SMCII) showed the lowest AMF diversity and evenness, which may be attributed to the frequent fertilizer application (Oehl et al., 2004, 2010; Alguacil et al., 2014; Bainard et al., 2014). In this regards, *Claroideoglopus luteum* and *F. geosporum* were dominant in the AMF communities found at high input management (29 and 31%, respec-

tively from total spores). These results support our hypothesis since sites with the higher intensity of agricultural inputs are less favorable for AMF communities.

Claroideoglopus and *Funneliformis* produce a large number of spores, and are typically widely distributed across the world (Treseder and Cross, 2006; Dandan and Zhiwei, 2007; Oehl et al., 2010; Carballar-Hernández et al., 2013). In that, they have been reported to form associations with in *C. annuum* and *C. frutescens* in several countries (Cardona et al., 2008; Castillo et al., 2010; Chen et al., 2012; Boonlue et al., 2012; Vyas and Vays, 2012). A positive significant correlation ($r = 0.81, P \leq 0.05$) was found between the relative abundance and the frequency of *F. geosporum*, *C. claroideum* and *C. luteum*, suggesting that the most spore-producing AMF species have wide global distribution. These three AMF species are considered to be generalists and are able to adapt and/or tolerate high input management practices (Oehl et al., 2009, 2010; Öpik and Moora, 2012; Alguacil et al., 2014), which

Table 5
Physical and chemical properties of soil from the rhizosphere collected from six “poblano pepper” agroecosystems in Puebla State (Mexico).

Agroecosystems	Agronomic management	pH	EC (dS m ⁻¹)	SOM (%)	N-NH ₄ ⁺ (mg kg ⁻¹)	N-NO ₃ ⁻ (mg kg ⁻¹)	N-inorganic (mg kg ⁻¹)	P-available (mg kg ⁻¹)	P-total (mg kg ⁻¹)	Soil Texture
SM	Low	5.7 d	0.40 a	0.31 a	16.84 a	5.92 a	22.76 a	22.28 b	390.76 ab	Sandy clay loam
JCI	Moderate	6.7 b	0.14 bc	0.11 bc	1.46 c	1.12 c	2.58 d	50.30 ab	453.02 a	Sandy clay loam
JCII	Moderate	6.2 c	0.11 c	0.08 c	1.48 c	1.02 c	2.50 d	33.24 b	285.34 b	Sandy clay
SMZ	Moderate	6.6 b	0.15 bc	0.12 bc	3.51 bc	2.10 bc	5.61 cd	26.12 b	369.98 ab	Sandy clay
SMCI	High	7.4 a	0.33 a	0.26 a	5.44 b	4.38 ab	9.82 bc	48.99 ab	393.92 ab	Sandy clay
SMCII	High	7.2 a	0.27 ab	0.21 ab	7.30 b	3.58 abc	10.88 b	71.99 a	369.98 ab	Sandy clay

Means with the same letter in the same column are not significantly different (Tukey, $\alpha = 0.05$).

Abbreviations: SM = San Martinito; JCI and JCII = Juárez Coronaco I and II; SMZ = Santa María Zacatepec; SMC-I and SMCII = San Mateo Capultitlán I and II; EC = Electrical conductivity; SOM = Soil organic matter.

is in agreement with our study.

Soil physical and chemical properties affected the composition, abundance, and distribution of AMF species. The soils collected from the six agroecosystems had low EC and SOM, very low available N and P (SEMARNAT, 2002), which we suggest are a direct result of the intensive agronomic management strategies under taken to maximize yield. For example, the agroecosystems with high input management (SMCI and SMCII) had high P-available due to the high inputs of chemical fertilizers.

The analysis of canonic correspondence indicated that pH and P-availability were the main soil parameters explaining both the abundance and distribution of AMF species, especially in the agroecosystems with high input management (high pH and available P concentration). Previous reports indicated that soil P availability has negative effects on composition, distribution, and diversity of the AMF communities (Oehl et al., 2010; Bainard et al., 2014; Jansa et al., 2014). Furthermore, soil pH and chemical properties are key soil factors that exert significant influence on distribution and composition of AMF communities in natural and agroecosystems (Hijri et al., 2006; Bainard et al., 2014).

The canonical correspondence analysis demonstrated that most of the AMF species seems to prefer agroecosystems with low or moderate input management, in which P-availability is low and the pH slightly acid. However, there are some exceptions since *Funneliformis geosporum*, *A. colombiana*, *A. laevis* and *A. morrowiae* were grouped along the vector for P-availability at the primary axis in the agroecosystem SMCII, with high P-availability (72 mg kg⁻¹). In contrast, *C. luteum*, *Funneliformis* sp. 1 and *Glomus* sp. 1 were grouped at the secondary axis, which corresponded to pH (high pH 7.4) of the SMCI agroecosystem. According to Verbruggen et al. (2012) and Alguacil et al. (2014), our study provides further scientific evidence that several AMF species prefer specific habitats for their proliferation, but will also demonstrate a certain tolerance to high input agronomic management, and to soil properties, including high available P content and pH values.

Interestingly, *Scutellospora* species were only observed in agroecosystems with low or moderate input management, and their ecological role is unknown (Oehl et al., 2010). Furthermore, these AMF species did not share habitats with those *Glomus* and *Claroideoglossum* species found at agroecosystems with high input management.

5. Conclusions

Agronomic management affects AMF species composition and community structure. Agroecosystems with low and moderate input management had significantly different AMF species composition when compared to agroecosystems with high input management. High input management affected the AMF community, then, favoring the dominance of some morphospecies, and reducing the diversity and evenness of AMF communities. However, the agronomic management did not affect AMF species richness.

The multivariate analysis gave results that fit the data obtained from the similarity and the diversity-dominance indexes, thus, demonstrating that soil properties (pH and P-availability) and high input management significantly modify both distribution, composition, and diversity of AMF communities. Overall, these two main factors must be taken into account when analyzing or comparing AMF communities in agroecosystems.

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