Mycorrhiza (2011) 21:183–193
DOI 10.1007/s00572-010-0322-6

ORIGINAL PAPER

Soil–strain compatibility: the key to effective use of arbuscular mycorrhizal inoculants?

Ricardo A. Herrera-Peraza · Chantal Hamel · Félix Fernández · Roberto L. Ferrer · Eduardo Furrazola

Received: 26 May 2009 / Accepted: 23 May 2010 / Published online: 16 June 2010

Abstract Consistency of response to arbuscular mycorrhizal (AM) inoculation is required for efficient use of AM fungi in plant production. Here, we found that the response triggered in plants by an AM strain depends on the properties of the soil where it is introduced. Two data sets from 130 different experiments assessing the outcome of a total of 548 replicated single inoculation trials conducted either in soils with a history of (1) high input agriculture (HIA; 343 replicated trials) or (2) in more pristine soils from coffee plantations (CA; 205 replicated trials) were examined. Plant response to inoculation with different AM strains in CA soils planted with coffee was related to soil properties associated with soil types. The strains *Glomus fasciculatum*-like and *Glomus etunicatum*-like were particularly performant in soil relatively rich in nutrients and organic matter. *Paraglomus occultum* and *Glomus mosseae*-like performed best in relatively poor soils, and *G. mosseae* and *Glomus manihotis* did best in soils of medium fertility. *Acaulospora scrobiculata*, *Diversispora spurca*, *G. mosseae*-like, *G. mosseae* and *P. occultum* stimulated coffee growth best in Chromic, Eutric Alluvial Cambisol, *G. fasciculatum*-like and *G. etunicatum*-like in Calcaric Cambisol and *G. manihotis*, in Chromic, Eutric Cambisols. *Acaulospora scrobiculata* and *Diversispora spurca* strains performed best in Chromic Alisols and Rodic Ferralsols. There was no significant relationship between plant response to AM fungal strains and soil properties in the HIA soil data set, may be due to variation induced by the use of different host plant species and to modification of soil properties by a history of intensive production. Consideration of the performance of AM fungal strains in target soil environments may well be the key for efficient management of the AM symbiosis in plant production.

Keywords Adaptation · Effectiveness · Soil properties · Soil type · Soil classification · AM inoculant · Consistency of response

R. A. Herrera-Peraza
Instituto de Ecología y Sistemática, IES, CITMA, Havana, Cuba

C. Hamel (✉)
Semiarid Prairie Agricultural Research Centre, AAFC, PO Box 1030, Swift Current, SK S9H 3X2, Canada
e-mail: Chantal.Hamel@agr.gc.ca

F. Fernández · R. L. Ferrer · E. Furrazola
Department of Biofertilizer and Plant Nutrition, Instituto Nacional de Ciencias Agrícolas, San José de las Lajas, La Habana, Cuba

Introduction

The arbuscular mycorrhizal (AM) symbiosis has evolved in most terrestrial environments as an efficient system of phosphorus uptake in plants (Brundrett 2009). But despite increasing fertilizer costs and disappearing world phosphorus reserves (Gilbert 2009), progression in the use of the AM symbiosis in plant production has been slow. Although the causes of this poor performance have been diverse, it is true that the conditions for the expression of mycorrhizal effectiveness are poorly known, leading to inconsistency in response to AM inoculation (see Ryan and Graham 2002).

According to principles in ecology, the success of an AM symbiosis depends not only on the plant and fungal genotypes, but also on the conditions of the environment. The functional specificity that exists between plants and AM fungi has been documented (Helgason et al. 2002;

Leake et al. 2004; Klironomos 2003). The soil environment certainly imposes a strong selection pressure on AM fungi (Hamel 2007; Helgason and Fitter 2009), but the influence of the soil on AM genotypes is ill understood (Feddermann et al. 2010).

The factors controlling the effectiveness of an AM fungal strains must be understood before reliable AM inoculation technologies for field crops can be produced, and the soil is likely a key determinant of AM fungi effectiveness. We know that plants influence importantly AM fungi through the provision of C substrate, but the influence of the soil on these fungi should not be overlooked. The soil not only provides mineral nutrients to AM fungi, but also constitutes the chemical and physical environment where both these fungi and their plant associates live.

There is much evidence supporting the hypothesis of a large influence of soil properties on AM fungi (Hamel et al. 1994; Frey and Ellis 1997; van Aarle et al. 2002; Johnson et al. 2005; Mechri et al. 2008; Gryndler et al. 2009). The properties and environment of a soil may have different influence on different AM isolates. Liming the soil decreased root colonization by *Acaulospora laevis*, but increased root colonization by *G. invermaium* in the same study (Sano et al. 2002) showing that different AM species have different soil pH optima. The adaptation of AM fungi to specific soil pH caused AM strains to exist only within a range of soil pH levels (Oehl et al. 2005). Soil OM, available N-to-P ratio, bulk density, and pH drive changes in AM fungi community composition (Fitzsimons et al. 2008). It appears that AM strains may survive and function well only within a range of soil environmental conditions.

The effectiveness of AM symbioses created through plant inoculation may depend on the adaptation of the AM fungal strains used to the soil where they are introduced. We tested this hypothesis using data generated by an important research effort made between 1991 and 1993 in Cuba to develop AM fungi inoculation technologies. Here, we used multivariate analysis of data from 130 inoculation trials to reveal relationships existing between the plant response to inoculation with different AM fungal strains and soil properties. One analysis was performed on data from 62 experiments conducted in soils from high input cropping systems that yielded 343 data points (each one being the average of three, four or five replicates) expressing the responses of different crop plants to various AM strains formulated in MicoFert®. Another analysis was performed on data from 68 experiments conducted in more pristine coffee plantation soils that yielded a total of 205 data points (which were averages of four replicates) representing coffee plant response to different AM strains.

Materials and methods

Approach

Our study is based on the results of 62 inoculation trials using soils from Cuban plains with a history of high input agriculture (HIA) management (Table 1) and 68 trials conducted with pristine or semi-natural soils, which were under low-input under-story coffee production, typically from mountainous areas (CA) (Table 2). The inoculation trials conducted using soils of the HIA and CA groups were evaluating AM fungal strains (Table 3) for their ability to enhance plant growth. Different crops were grown in HIA soils and coffee plants were grown in CA soils. These experiments are described in Tables 1 and 2 and in the text below. Additional information on these experiments can be found elsewhere (Fernández 1999). In all these experiments, plants were inoculated with different AM fungal strains with potential for use in inoculants, and their performance at stimulating plant growth was recorded. The indicator of AM fungal strain performance varied between experiments (Tables 1 and 2) as they were not initially meant for the meta-analyses reported here. Thus, the responses to inoculation generated by these experiments were standardized by calculating the relative response to inoculation (RI) in each single inoculation trial as:

$$\mathrm{RI} = (\mathrm{P_i} - \mathrm{P_c})/\mathrm{P_c}{*}100$$

where P_i represents the performance of inoculated plants and P_c represents that of non-inoculated control plants for the variable considered in an experiment. The RI values used in the two analyses were the average of the replicates of each inoculation treatments. In the HIA-related experiments, 343 RI data points were generated, and the CA-related experiments yielded 205 RI data points.

The CA- and HIA-related data sets were examined, seeking a possible relationship between soil properties and the functionality of AM fungal strains, as expressed by RI, in the different CA soils (Table 4) and HIA soils (Table 5). These two groups of data (CA- and HIA-related) were analyzed separately. Means of plant response to inoculation with different AM fungal strains in CA or HIA soils used constituted the response data sets, and corresponding soil fertility descriptors, pH and levels of P, K, Ca, Mg, and OM, constituted the explanatory data sets. Soil type names were used as labels for each line (i.e., as objects) in both data sets, which were subjected to canonical correspondence analysis (CCA). The CCA were conducted using 1,000 runs in PC-ORD v. 4.34. Relative increments in plant performance in response to inoculation were normalized by transformation into classes (<−30%, −30% to −5%, −5% to 5%, 5% to 20%, 20% to 40%, 40% to 80%, 80% to 100%,

Table 1 Experiments conducted in Cuba from 1991 to 1993 to test different arbuscular mycorrhizal (AM) strains formulated as MicoFert® inoculants in different crop plants grown in different soils from high input agriculture (HIA) fields

Experiment number	Number of factors (description)	Center	Plant species and cultivar	Propagule	Substrate sterilization	Cultural system	Experimental design	Performance indicator	Duration (month)
1	1 (AMF)	INIVIT	Banana (*Musa paradisiaca* L.) Gran Enano	Micropagated	Formalin[a]	Containers	5 R of 20 plants	Shoot fresh weight	3.0
2	1 (AMF)	IES	Banana (*Musa paradisiaca* L.) Gran Enano	Micropagated	Methyl bromide	Containers	4 R of 1.3 kg	Shoot dry weight	4.4
3, 4	1 (AMF)	ISPCAM	Banana (*Musa paradisiaca* L.) Gran Enano	Micropagated	Autoclave	Containers	4 R of 1.5 kg	Leaf area	3.0
5	1 (AMF)	IES	Banana (*Musa paradisiaca* L.) Parecido a Rey	Micropagated	No	Field plots	2 of 0.45 ha	Shoot height	6.0
6	1 (AMF)	EEC	Tangerine Cleopatra (*Citrus* spp.)	Seeds	Sterile	Nursery	4 R of (5×4.5 kg)	Shoot height	8.0
7	1 (AMF)	EEC	Tangerine Cleopatra (*Citrus* spp.)	Seeds	No	Nursery	4 R of (5×4.5 kg)	Shoot height	10.0
8–10	1 (AMF)	IES	Tangerine Cleopatra (*Citrus* spp.)	Seeds	No	Nursery	10 R of 4.5 kg	Leaves per plant	17.0
11	1 (AMF)	ENF	Mango (*Mangifera indica* L.) Manga Blanca	Seeds	No	Nursery	10 R of 4.5 kg	Plant height	12.0
12	1 (AMF)	EEPB	Guava (*Psidium guajaba* L.) Cotorrera	Seeds	No	Nursery	10 R of 4.5 kg	Shoot dry weight	4.0
13	1 (AMF)	ENF	Papaya (*Carica papaya* L.) Maradol Roja	Seeds	Formalin	Nursery	20 R of 2.5 kg	Shoot dry weight	2.5
14	1 (AMF)	ENF	Papaya (*Carica papaya* L.) Maradol Roja	Seeds	No	Nursery	25 R of 2.5 kg	Seedling height	2.5
15, 16	1 (AMF)	ENF	Papaya (*Carica papaya* L.) Maradol Roja	Seeds	Formalin	Nursery	25 R of 2.5 kg	Seedling height	2.5
17, 18	1 (AMF)	ENF	Maracuyá (*Passiflora edulis* Sims.) Flavicarpa	Seeds	No	Field plots	9 R of 20 m²	Number of fruits per plant	24.0
19, 20	1 (AMF)	IES-ENF	Maracuyá (*Passiflora edulis*) Flavicarpa	Seeds	No	Containers	4 R of 2.5 kg	Stem length	9
21	1 (AMF)	ISACA	Pineapple (*Ananas comosus* (L.) Merrill.) Cayena Lisa	Micropagated	No	Containers	5 R of 0.5 kg	Leaf area	3.7
22, 23	1 (AMF)	INIVIT	Tomato (*Lycopersicun esculentum* Mill.) Clinton	Seeds	No	Seed-bed	4 R of 1 m²	Seedling height	3.0
						Field plots	4 R of 32 m²	Fruit yield	
24–29	2 (AMF and fertilization treatments)	INCA	Tomato (*Lycopersicum esculentum* Mill.) INCA-17	Seeds	No	Field plots	4 R of 33.6 m²	Fruit yield	3.0
30–35	2 (AMF and cultivars)	IES	Garlic (*Allium sativum* L.) Criollo & Vietnamita	Explant	No	Field plots	4 R of 35 m²	Bulb yield	3.6
36	1 (AMF)	IES	Red bean (*Phaseolus vulgaris* L.) CC-25-9R	Seeds	No	Field plots	4 R of 3.2 m²	Grain yield	3.0
37	1 (AMF)	IES	Soybean (*Glycine max* (L.) Merr.)	Seeds	No	Field plots	4 R of 12 m²	Grain yield	3.0

Table 1 (continued)

Experiment number	Number of factors (description)	Center	Plant species and cultivar	Propagule	Substrate sterilization	Cultural system	Experimental design	Performance indicator	Duration (month)
			G7R-315						
38	1 (AMF)	IES	Soybean (*Glycine max* (L.) Merr.) G7R-315	Seeds	No	Field plots	4 R of 12 m²	Grain yield	3.0
39	1 (AMF)	EEPB	Leucaena (*Leucaena leucocephala* (Lam.) DeWit) Perú	Seeds	Autoclave	Containers	3 R of 1.5 kg	Shoot dry weight	8.0
40, 41	1 (AMF)	IES	Sugar cane (*Saccharum* spp.) C-120-78	Explant	No	Field plots	3 R of 60 m²	Stem yield	10.0
42	1 (AMF)	EEPB	Sorghum (*Sorghum bicolor* (L.) Moench.) Forraje	Seeds	Autoclave	Containers	3 R of 1.5 kg	Shoot dry weight	8.0
43	1 (AMF)	IES	Sorghum (*Sorghum bicolor* (L.) Moench) V-6	Seeds	Methyl bromide	Field plots	3 R of 1 m²	Grain yield	4.0
44, 45	2 (AMF and soil sterilization)	INCA	Rice (*Oryza sativa* L.) J-104	Seeds	Sterile and not sterile	Containers	4 R of 2.5 kg	Panicles weight	3.0
46, 47	2 (AMF and soil sterilization)	INCA	Wheat (*Triticum aestivum* L.) Anahuac 75	Seeds	Sterile and not sterile	Containers	4 R of 2.5 kg	Panicles weight	3.0
48	1 (AMF)	EEPB	King grass (*Pennisetum purpureum*×*P. americanum*)	Explant	Autoclave	Containers	3 R of 1.5 kg	Shoot dry weight	8.0
49	1 (AMF)	EEPB	Hierba Guinea (*Panicum maximum* Jacq.) Tobiatá	Explant	Autoclave	Containers	3 R of 1.5 kg	Shoot dry weight	8.0
50	1 (AMF)	EEPB	Brachiaria (*Brachiaria decumbens*) CIAT-606	Seeds	Autoclave	Containers	3 R of 1.5 kg	Shoot dry weight	8.0
51, 52	2 (AMF and soil types)	INIVIT	Potato (*Solanum tuberosum* Sw.) Desiree	Tubers	Formalin	Containers	4 R of 2.5 kg	Number of tubers per plant	3.0
53, 54	2 (AMF and fertilization treatments)	INCA	Potato (*Solanum tuberosum* Sw.) Desiree	Seeds	No	Containers	4 R of 30×25×15 cm. L×w×h box	Tubers yield	3.0
55	1 (AMF)	INIVIT	Malanga (*Colocasia antiquorum* Schott.)	Explant	Formalin	Containers	5 R of 2.5 kg	Number of corms per plant	3.0
56	1 (AMF)	INIVIT	Cassava (*Manihot esculenta* Crantz.) Señorita	Explant	Formalin	Containers	5 R of 2.5 kg	Shoot dry weight	8.0
57, 58	2 (AMF and soil types)	INIVIT	Sweet potato (*Ipomoea batatas* (L.) Lam.) CULTIVAR CEMSA 85–48	Explant	Formalin	Containers	5 R of 2.5 kg	Number of tubers per plant	3.0
59–62	2 (AMF and soil types)	INIVIT	Yam (*Discorea alata* L.) Belep	Explant	Formalin	Containers	5 R of 2.5 kg	Shoot fresh weight	4.0

INIVIT Instituto Nacional de Investigation de Viandas Tropicales, Villa Clara, *IES* Instituto de Ecología y Sistemática, La Habana, *EEC* Estación Experimental de Cítricos de Jagüey Grande, Matanzas, *EEPB* Estación Experimental de Pastos Barajagua, Cienfuegos, *ENF* Estación Nacional de Frutales del Instituto Nacional de Cítricos y Frutales, La Habana, *ISPCAM* Instituto Superior Pedagógico de Camagüey, *ISACA* Instituto Superior Agrícola de Ciego de Avila, *INCA* Instituto Nacional de Ciencias Agrícolas, *AMF* strains individually tested for their effect on plant growth by comparison to a non-inoculated control treatment (see list in Table 3), *R* number of replicates

[a] Formalin, soil drenched with a 3% (*v*/*v*) formalin solution; methyl bromide, 3 kg m^{-3} of soil; autoclave, 1 h at 0.12 MPa

Table 2 Experiments conducted in Cuba from 1991 to 1993 to test different arbuscular mycorrhizal (AM) strains formulated as MicoFert® inoculants in coffee plants grown in different coffee plantation soils (CA)

Case	Number of factors (description)	Field site	Cultivar	Cultural system	Experimental design
1–6	2 (AMF and VC)	Jibacoa	Catuaí Amarillo	Bags	4 R of 1 m^2
7–12	3 (AMF, VC, and PSB)	Veguitas	Caturra Colombiano	Seedbed	4 R of 49 m^2
13	2 (AMF and VC)	Jibacoa	Caturra Colombiano	Bags	4 R of 100 m^2
14, 15	3 (AMF, VC, and BNF)	Veguitas	Caturra Colombiano	Bags	4 R of 100 m^2
16, 17	4 (AMF, VC, BNF, and PSB)	Veguitas	Caturra Colombiano	Bags	4 R of 100 m^2
18–21	1 (AMF)	La Villa	Caturra Colombiano	Bags	4 R of 100 m^2
22–25	2 (AMF, and P fertilization)	Bachiplán	Catuaí Amarillo	Bags	4 R of 100 m^2
26, 27	2 (AMF and organic ammendment)	Cancán	Catuaí Amarillo	Bags	4 R of 100 m^2
28, 29	2 (AMF and VC)	Santiago	Catuaí Amarillo	Bags	4 R of 100 m^2
30–32	1 (AMF)	Tomatera	Catuaí Amarillo	Bags	4 R of 100 m^2
33–36	3 (AMF, VC, BNF)	Tope de Collantes	Catuaí Amarillo	Bags	4 R of 100 m^2
37, 38	3 (AMF, PSB, and BNF)	Tope de Collantes	Catuaí Amarillo	Bags	4 R of 100 m^2
39, 40	2 (AMF, PSB)	Tope de Collantes	Catuaí Amarillo	Seedbed	4 R of 49 m^2
41, 42	2 (AMF and PSB)	Topes Collantes	Catuaí Amarillo	Seedbed	4 R of 49 m^2
43–46	3 (AMF, VC, and PSB)	Cancán	Catuaí Amarillo	Seedbed	4 R of 49 m^2
47, 48	2 (AMF and VC)	Jibacoa	Catuaí Amarillo	Seedbed	4 R of 49 m^2
49–52	3 (AMF, VC, and BNF)	Santiago	Catuaí Amarillo	Seedbed	4 R of 49 m^2
53–56	3 (AMF, VC, BNF)	Tercer Frente	Catuaí Amarillo	Bags	4 R of 100 m^2
57–60	3 (AMF, VC, BNF)	Veguitas	Catuaí Amarillo	Seedbed	4 R of 49 m^2
61–64	3 (AMF, VC, PSB)	Veguitas	Catuaí Amarillo	Seedbed	4 R of 49 m^2
65–68	3 (AMF, VC, BNF)	Jibacoa	Catuaí Amarillo	Seedbed	4 R of 49 m^2

Seeds were used as propagules, the soil was non-sterile, plants were grown for 7 months, and all experiments were conducted by EICVC, Estación de Investigationes del Café Jibacoa at different field sites. The performance indicator was leaf area, except for one experiment where shoot dry weight was used

AMF strains individually formulated as MicoFert® and tested for their effect on plant growth by comparison to a non-inoculated control treatment and, in some cases, with a mix of native strains (see list in Table 3), *VC* vermicompost from coffee fruit residues, *PSB* P solubilizing bacteria, *BNF* N-fixing bacteria, *R* number of replicates used

and >100%) before subjecting the data to CCA (Fig. 1). The use of CCA was dictated by the non-linear response of AM fungi to environmental conditions (Bethlenfalvay et al. 1983; Hamel et al. 1997) and the wide ranges of gradients in soil fertility descriptors resulting from the use of soil with contrasting properties (Ter Braak 1986; Legendre and Legendre 1998, p. 600; Ramette 2007).

The relationship between pairs of soil fertility descriptors within each of the CA and HIA soil groups were assessed by regression analysis using JMP v.3.2.6 (SAS Institute, Cary, USA), as a mean to describe nutrient balance in CA and HIA soils.

Soil analysis

The P availability of CA soils was tested using the Bray extracting solution (Bray and Kurtz 1945) and that in HIA soils using the Olsen extracting solution (Olsen et al. 1954). Soil pH in water was determined using a pH meter. Soil OM content was determined by the Walkley–Black method (Jackson 1962). Amounts of exchangeable K, Ca and Mg were determined using 1 M ammonium acetate at pH7 (Jackson 1962). Soil analyses were conducted on samples taken from the top 0–20 cm soil layer at all locations.

At all sites where CA soils were taken except one, a pit was dug, the soil profile was described and the soil was classified according to the FAO-UNESCO system (FAO, ISRIC and ISSS 1998). Soils at other sites had already been described and existing descriptions were used.

AM inoculum and inoculation

The AM fungal strains used (Table 3) were formulated into MicoFert® (Instituto de Ecología y Sistemática [IES], La Habana, Cuba) inoculants. MicoFert® contains a mixture of AM fungi-colonized soil and colonized root fragments, which are produced on Sorghum (*Sorghum bicolor* (L.) Moench) inoculated with IES-certified AM fungal strains and grown for 90 days in a 3:1 (*v*/*v*) mixture of soil/cachaza, which is an organic amendment from sugarcane residues.

Table 3 Arbuscular mycorrhizal fungal strains used in the experiments conducted in soils with history of high input agriculture or in soils from coffee plantations with their abbreviation and origin

Abbreviation	Name	IES-Nr accession	Origin	Used in HIA cases (number)	Used in CA cases (number)
Aca	*Acaulospora scrobiculata* Trappe	IES-10	CIAT, Cali, Colombia Collection E. Sieverding	1–4, 7, 38–39, 42–43, 48, 56–57	14–17, 28–48
Agg	*Glomus aggregatum* N.C. Schenck & A. Schüßler	IES-4	W. Escambray, Villa Clara, Cuba	7–8, 12–21, 37, 44–47, 49–55	
cl-l	*Glomus clarum*-like	IES-13	UNAM, México, Collection S. Palacios	8, 16–19	
Div	*Diversispora spurca* (C.M. Pfeiff., C. Walker & Bloss) C. Walker & A. Schüßler	IES-3	W. Escambray, Villa Clara, Cuba	1–6, 8, 12–14, 16–21, 37, 40–41, 44–47, 49–55, 58–62	28–46
et-l_1	*Glomus etunicatum*-like	IES-6	Puerta de Golpe, Pinar del Rio, Cuba	8, 16–21, 37, 44–47, 49–55, 58, 62	
et-l_2	*Glomus etunicatum*-like	IES-7	W. Escambray, Villa Clara, Cuba	8, 16–21, 37, 46–47, 49–55, 58–62	57–68
fa-l	*Glomus fasciculatum*-like	IES-1	Turin, Italy. LPA-7 in INRA, Dijon, France	1–8, 10–14, 16–62	1–12, 18–27, 49–68
int_1	*Glomus intraradices* N.C. Schenck & G.S. Sm.	IES-9	UNAM, México, Collection S. Palacios	12–21, 37–39, 42–49, 56–57	
int_2	*Glomus intraradices* N.C. Schenck & G.S. Sm	IES-12	UNAM, México, Collection S. Palacios	5–6, 16–19	
Man	*Glomus manihotis* R.H. Howeler, Sieverd. & N.C. Schenck	IES-2	CIAT, Cali, Colombia Collection E. Sieverding	1–4, 7–14, 16–62	13, 26–46, 49–56
mo-l_2	*Glomus mosseae*-like	IES-14	Los Pinos, Ciudad de La Habana, Cuba	8, 16–19	
Mos	*Glomus mosseae* (T.H. Nicolson & Gerd.) Gerd. & Trappe	IES-8	Est. Nac. Frutales, Gïra de Melena, Cuba	1–4, 7–8, 10–11, 16–19, 22–27, 37–39, 42–45, 48–57	1–13, 18–27, 49–52, 57–68
mos-l	*Glomus mosseae*-like	IES-5	W. Escambray, Villa Clara, Cuba	3, 12–14, 16–19, 37, 49–55, 58–62	1–12, 18–25
NSC	Native strains concentrate	n/a	n/a		47–48, 53–56
Occ	*Paraglomus occultum* (C. Waker) J.B. Morton & D. Redecker	IES-11	CIAT, Cali, Colombia Collection E. Sieverding	7, 16–19, 38–39, 42–43, 48, 56–57	14–17, 47–48

n/a not applicable

The rate of inoculant applied to the experimental plants followed the manufacturer recommendation, i.e., rates of 5 cm^3 $plant^{-1}$ of MicoFert® were used to inoculate seeds smaller than 2 cm and 10 cm^3 $plant^{-1}$ was used for larger seeds and micro-propagated plants. The inoculants were placed in the planting holes. Rates of 0.5 to 1.0 $dm^3 m^{-2}$ of MicoFert® were used in seedbeds.

Results

HIA and CA soils comparison

A range of plant response to inoculation varying from positive to negative were obtained in both HIA and CA soils (Fig. 1).

Examination of the chemical analyses of HIA and CA soils revealed that these soils differed most in their level of OM (Tables 4 and 5). Note that the extracting solution used for Bray index determination extracts larger proportions of P from soils than the Olsen extracting solution (Bationo et al. 1991). The relationships between pairs of soil variables were all positive and relatively strong in CA soils, but weak and sometimes negative in HIA soils (Fig. 2), suggesting the alteration of soils' chemical equilibrium by HIA management.

Soil influences on plant response to inoculation

Canonical correspondence analysis (CCA) revealed relationships between plant response to inoculation with different AM fungal strains and soil chemical properties in CA (P=0.001), but not in HIA (P=0.413) systems (Fig. 3). Perpendicular projections of plant response to inoculation with the various AM fungal strains on vectors describing soil fertility descriptors indicates at which relative levels of fertility AM fungal strains function better. In CA soils fa-l and et-l_2 produced their best response in

Table 4 Properties of soils from high input agriculture (HIA) fields

Experiment number	Soil type	pH	OM	P[a]	K (cmol kg^{-1})	Ca	Mg
1, 22–25, 57–58	CC	6.9	1.46	8.5	59.7	48.0	4.32
12	CC	6.5	nd	73.9	89.1	26.9	10.53
42–43	CC	5.5	3.48	16.2	74.8	0.4	0.06
19–20	CCE	7.7	1.48	12.0	134.7	nd	nd
41, 44, 50–52	CE	5.2	nd	16.8	17.5	nd	nd
3–4	FFR	6.7	1.53	51.0	15.1	0.3	0.23
21	FFR	6.7	1.53	22.3	13.0	0.3	1.41
14–16, 38	FR	7.2	nd	48.0	19.9	31.8	6.58
6	FR	7.1	2.43	121.9	74.8	16.5	2.55
7, 11	FR	6.8	2.80	97.5	71.8	17.6	2.65
55–56	FR	6.8	2.40	75.0	59.8	11.9	0.40
53–54, 59–62	FR	6.7	1.83	48.1	42.8	9.6	0.46
8–10, 35–37	FR	6.5	nd	19.0	nd	nd	nd
2	FR	6.1	nd	65.6	nd	nd	nd
32–34	FR	6.1	nd	130.7	82.8	nd	nd
26–31	FR	6.0	2.11	234.0	31.9	8.5	1.62
45	FR	6.0	nd	125.9	nd	nd	nd
13, 17–18	FR	5.9	nd	74.3	nd	nd	nd
39	FR	5.8	2.17	289.0	69.8	9.9	1.49
5	FR	5.7	nd	36.4	91.3	10.0	2.41
40	FR	5.1	2.96	3.7	21.9	4.9	4.10
46–49	GA	4.9	2.20	25.0	10.0	12.1	1.00
Average		6.3	2.18	72.5	54.5	13.9	2.65
CV		0.12	0.29	1.01	0.64	0.94	1.06

CC Calcaric Cambisol, *CCE* Chromic, Eutric Cambisol, *CE* Eutric Cambisol, *FFR* Ferric, Rodic Ferralsol, *FR* Rodic Ferralsol, *GA* Alumic Gleysol

[a] The Olsen solution is used in the analysis of HIA extract soil P less thoroughly than the Bray solution used for CA soils (Bationo et al. 1991)

Table 5 Properties of soils from coffee (CA) plantations

Experiment number	Soil type	pH	OM	P	K (cmol kg^{-1})	Ca	Mg
1–12	ACCE	5.2	3.0	44.8	32.0	8.0	2.4
13	ACCE	5.7	3.8	26.9	19.2	12.8	1.4
14–17	ACCE	5.8	3.0	30.6	16.4	5.1	1.5
18–21	ACCE	5.8	3.5	13.9	27.5	8.6	1.5
22–25	ACCE	5.8	3.0	30.6	16.4	5.1	1.5
26–27	CCE	6.4	4.1	175.0	79.8	11.2	1.3
28–29	CCE	7.1	3.8	175.0	59.8	14.0	1.4
30–32	NRXE	4.9	1.0	12.0	39.9	7.0	1.6
33–36	AC	4.9	1.2	11.8	18.5	1.4	1.4
37–38	AC	4.8	1.5	12.7	10.4	1.5	1.1
39–40	FR	6.8	3.4	62.0	49.7	8.4	1.2
41–42	FR	6.8	3.4	228.1	49.7	8.4	1.2
43–46	FR	7.1	3.8	70.3	59.6	7.8	1.4
47–48	FR	5.8	3.0	56.8	37.6	5.2	1.5
49–52	CC	6.8	4.1	169.8	79.4	23.5	1.3
53–56	CC	7.3	3.8	248.9	112.1	32.0	7.9
57–60	CC	6.0	3.0	116.6	53.3	14.3	2.4
61–64	CC	6.0	3.0	105.7	53.3	14.3	2.4
65–68	CC	6.6	3.5	101.3	48.6	15.3	1.5
Average		6.08	3.10	89.09	45.43	10.73	1.89
CV		0.13	0.29	0.84	0.56	0.67	0.78

AC Chromic Alisol, *ACCE* Chromic, Eutric Alluvial Cambisol, *CC* Calcaric Cambisol, *CCE* Chromic, Eutric Cambisol, *FR* Rodic Ferralsol, *NRXE* Rodic-Xantic, Eutric Nitisol

[a] The Bray solution used in the analysis of CA extract soil P more thoroughly than the Olsen solution used for HIA soils (Bationo et al. 1991)

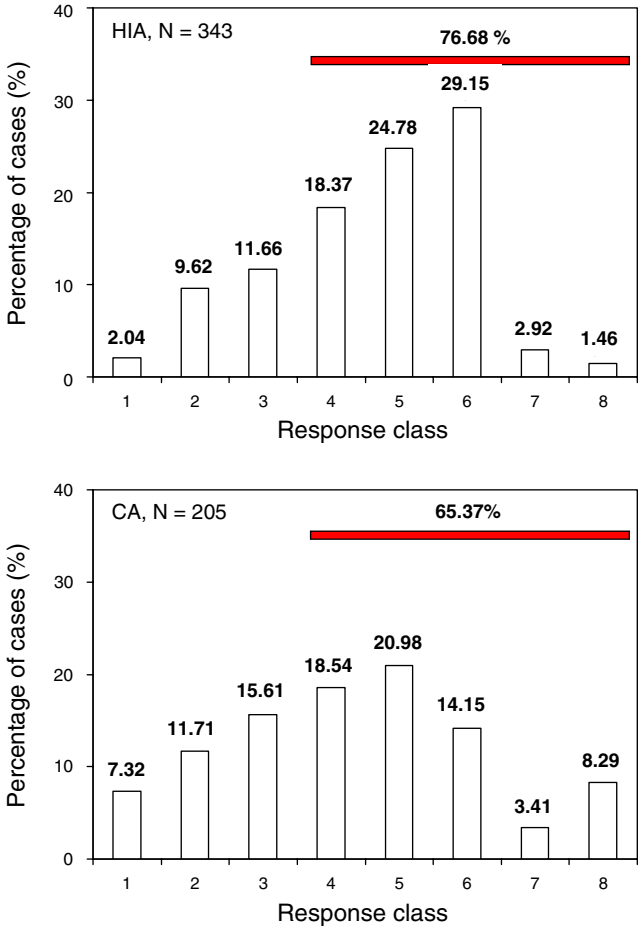

Fig. 1 Percentage of inoculation cases falling in each of eight classes of plant growth responses to AM inoculation observed in the 68 and 62 inoculation experiments conducted in coffee plantation soils (CA) or soils with a history of high input agriculture (HIA), respectively. Growth response less than −30%, in the ranges of −30% to −5%, −5% to 5%, 5% to 20%, 20% to 40%, 40% to 80%, 80% to 100%, and above 100%, were classified as classes 1, 2, 3, 4, 5, 6, 7, and 8, respectively. The percentage of cases where inoculation produced a positive growth response is given on the line drawn above classes 4–8 in each of the HIA- and CA-related panel

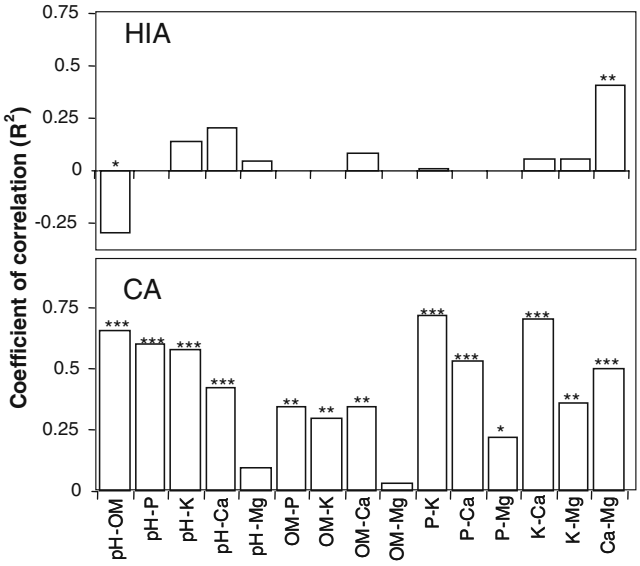

Fig. 2 Coefficients of pairwise correlation (R^2) between soil fertility descriptors with their level of significance, obtained from the analysis of soils from high input agriculture (HIA) and coffee plantation (CA). *Single asterisk*, *double asterisk*, and *triple asterisk* indicate that the correlation is significant at α=0.05, 0.01, and 0.001, respectively

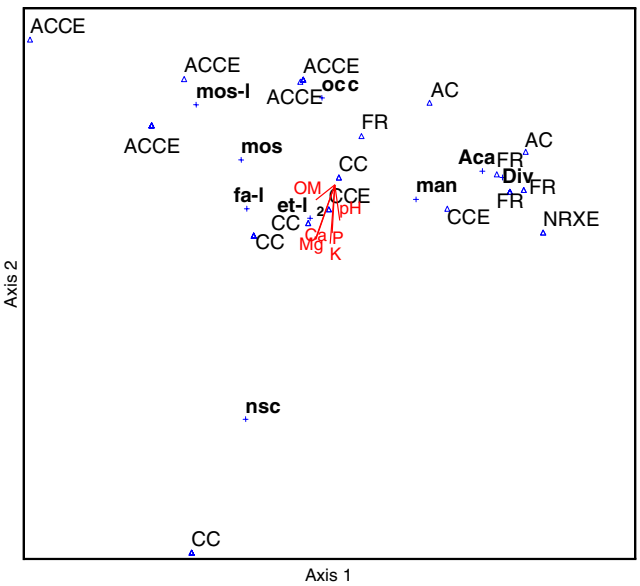

Fig. 3 Ordinations of the relationships between soil fertility descriptors and relative coffee plant growth increment following inoculation with different AM fungal strains, from canonical correspondence analysis (CCA) (P=0.001 for axes 1, Monte Carlo test with 999 iterations; plant response–soil properties correlation=0.888, 0.873, and 0.643 for axes 1, 2, and 3, respectively). The objects (experimental soils) of these analyses are labelled with their taxonomic (FAO) names in the ordination biplot. *OM* soil organic matter, *AC* Chromic Alisol, *ACCE* Chromic, Eutric Alluvial Cambisol, *CC* Calcaric Cambisol, *CCE* Chromic, Eutric Cambisol, *CE* Eutric Cambisol, *FFR* Ferric, Rodic Ferralsol, *FR* Rodic Ferralsol, *GA* Alumic Gleysol, *NRXE* Rodic-Xantic, Eutric Nitisol. See Table 3 for abbreviations of AM fungal strains

soils with relatively high levels of available P; mos and man, in soils with medium P availability; and occ, in soils with relatively low P availability (Fig. 3). Because nutrient levels were all positively correlated in CA soils, it is also true that fa-l and et-l_2 produced better responses in coffee plants grown in soils generally rich in nutrients and OM, in contrast to occ, which produced better responses in relatively poor soils (Fig. 3). Native strains (NSC) functioned best in relatively rich soils.

CA soils belonging to the same taxonomic group appeared in clusters when plotted on the ordination graph (Fig. 3). This clustering suggests that the response to AM inoculation depends on the interaction between the AM strain and the properties of the soil where it is inoculated,

and this relationship can be inferred from the soil type, at least in Cuban coffee plant production. In CA, strain mo-l, mos and occ appear to stimulate better coffee growth in Chromic, Eutric Allivual Cambisol (ACCE), Aca and Div in Rodic Ferrasols (FR, FRR) and in Chromic Alisols (AC), fa-l, et-l_2 and NSC in Calcaric Cambisol, and man in Eutric Chromic Cambisols (Fig. 3).

Discussion

Early studies have shown that plant response to inoculation varied in different soils (Young et al. 1986; Hamel et al. 1997; Zeuske and Weber 2000; Schreiner 2007) and until now, this lack of consistency has hindered the efficient use of AM inoculants in plant production. Our results suggest that AM strains must not only be highly effective, they must also be able to function in the soil environment where they are introduced. Selecting strains based on target soil properties may be the key to consistency in the effect of AM inoculants.

In the more pristine CA soils, the very good relationships between plant response to different AM strains and soil taxa suggests the possibility of choosing AM fungal strains based on soil taxonomic group. This would be very convenient, as soils in agricultural areas have often been described. The soil taxonomic group at a given location is usually known and the appropriate strain among a few strains with high plant growth enhancement potential could be chosen based on this available information, which is simple, rapid and cost-effective. This strategy would be appropriate in regions with relatively low input agriculture such as the Canadian prairie, a major wheat and pulse growing area, where conservation tillage is the common practice and fertilizers have been used with parsimony (Fixen 2006) because water availability is usually the factor limiting yields.

The relationship between plant response to AM strains and soil type was very clear in CA. The levels of the different soil fertility descriptors were well correlated and soils showed a gradient of general fertility ranging from low to high. Relationships were more complex in HIA soils, where correlations between the soil fertility descriptors were poor, in particular in those involving soil P or OM.

Not only nutrient level, but also nutrient balance is an important factor influencing AM symbiotic development and function (Liu et al. 2000; Fitzsimons et al. 2008). Nutrient imbalance may alter the function of indigenous AM fungal strains. Soils with altered nutrient balance may benefit from the introduction of an adapted AM strains. Plant response to inoculation was not less frequent in HIA than in CA soils (Fig. 1), although they were richer in P.

It is true that plant dependence on the AM symbiosis generally decreases with increasing soil fertility (Smith and Read 1997), but a negative impact of soil fertility cannot be assumed to occur. Available N and P scarcity, as well as abundance, may limit AM fungal development (Bethlenfalvay et al. 1983; Chulan and Ragu 1986; Liu et al. 2000; Treseder and Allen 2002). Soil properties influence functionality in AM fungi (Frey and Ellis 1997; Hamel et al. 1997; Carrenho et al. 2007; Arines et al. 1988; Warnock et al. 2007; Mechri et al. 2008). Different AM strains have different ability to function in different soil environments as shown by different AM fungal community composition (Corkidi et al. 2002; He et al. 2004, Fitzsimons et al. 2008), development (Abbott and Robson 1991), sporulation (Baum et al. 2002), and function (Karasawa et al. 2001) in different soils.

It is very important to clarify the suitability of AM fungal isolates employed in connection with soil fertility, as shown here and as pointed out by Zeuske and Weber (2000). It is also important to recognize that the pattern of AM fungal strains proliferation (Hijri et al. 2006; Chao et al. 2010), development and influence on plant growth (Bethlenfalvay et al. 1983) can be unimodal rather than linear, along large soil environmental gradients of multiple factors. The fitness of AM fungi may be limited to a set of specific environmental conditions beyond which they cannot function.

Consistency of response to inoculation with selected AM fungal strains is a prerequisite to adoption of AM inoculation practices in plant production. Thus, it may be important to consider strain–soil compatibility as the AM strains must be introduced in soil environments where their basic requirements are met and where they can function well. It may also be important to consider soil nutrient balance. It is true that the genotype of crop plants may also influence the outcome of AM associations (Klironomos 2003) and ideally, the selection of AM fungal strains should be based on both the target soil and the crop. In HIA systems, the correlation between crop response to AM strains and soil properties could have been confounded by the use of different crop plants. Lack of correlation might also be attributable to soil nutrient imbalance complicating interactions.

Highly effective strains perform generally well on a wide range of crops, and AM inoculation based only on soil type has been successful in Cuba (Rivera et al. 2007).

Conclusions

The reliability of highly effective AM fungal strains seemingly depends on their ability to function under the soil conditions where they are introduced. The choice of effective AM fungal strains based on soil properties may

well be the corner stone for the development of effective use of AM inoculants in plant production systems.

Acknowledgement Collaboration between the two first authors was supported by a grant from the Inter-American Institute for Global Change Research (IAI) CRN, which is supported by the US National Science Foundation (Grant GEO-04523250). RA Herrera-Peraza passed away during the preparation of this article. Most of the HIA data was generated by late RL Ferrer.

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