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AGRICULTURAL PRACTICES MINIMISE THE BENEFITS FROM VESICULAR-ARBUSCULAR MYCORRHIZA FORMATION

L.F. Robertson, L.E. Chinnery and S.B. Persad-Chinnery, Department of Biology, The University of the West Indies, POB 64, Bridgetown, Barbados.

ABSTRACT. Plants colonised by vesicular-arbuscular mycorrhizal (VAM) fungi have been shown to be more efficient in nutrient uptake, to be more drought resistant and to have enhanced resistance to pests and diseases than non-mycorrhizal plants. VAM fungal spore populations were determined for each of the soil associations in Barbados. Non-mycorrhizal corn (*Zea mays*), pepper (*Capsicum annuum*) and bean (*Phaseolus vulgaris*) seedlings were transplanted into soil sampled from each association. The numbers of spores and the levels of mycorrhizal colonisation of the roots of the transplants were greater in the non-agricultural soils. This suggests that agricultural practices are reducing the mycorrhizal potential of soils. These results are discussed in relation to the development of sustainable agricultural practices.

INTRODUCTION

Vesicular-arbuscular (VA) mycorrhizae are mutualistic symbiotic relationships formed between most crop plants, except Brassicaceae, and soil fungi classified into six genera within three families of the order Glomales (*Entrophospora* and *Acaulospora* - Acaulosporaceae; *Scutellospora* and *Gigaspora* - Gigasporaceae; *Glomus* and *Sclerocystis* - Glomaceae) (Morton and Benny, 1990). On the basis of presumed homology between their spores and the azygospore found in the Mucoraceae, the Glomales were classified in class Zygomycetes. However, Rosendahl and Dodd (1995) and others now believe that the resting structures found in the Glomales may represent structures that are not homologous to those found in the Zygomycetes and that these structures can not be used to link the Glomales to the true fungi. Further, information from sequences of the 18S ribosomal genes of Glomales indicate that they form an ancient group, arising before the Ascomycetes and the Basidiomycetes (Rosendahl and Dodd, 1995).

To date less than 200 species of vesicular-arbuscular mycorrhizal (VAM) fungi have been identified. However, Morton *et al.*, (1995) have suggested that there may be as many as 2592 species in the genus *Glomus* alone. Their calculation is based on combinations of the morphological characters of the spore wall on which the taxonomy of the Glomales is founded.

Plants colonised by VAM fungi have been shown to have enhanced nutrient uptake, especially of phosphorus (Harley and Smith, 1983), and fewer incidences of micronutrient deficiencies (Abbott and Robson, 1984; Persad-Chinnery and Chinnery, 1996). Such plants show increases in growth (Smith, 1980; Gianinazzi-Pearson *et al.*, 1989; Nielsen, 1990), plant disease resistance (Morandi *et al.*, 1984; Feldmann *et al.*, 1989; Caron, 1989), drought tolerance (Mosse and Hayman, 1971; Davis *et al.*, 1992), and reproduction (Koide *et al.*, 1988).

The growth promoting effect of VAM fungi can be attributed to enhanced phosphorus availability to the host plant, especially when these plants are grown in P-limited soils. Baas and Kuiper (1989) found the physiological effects on plants as a result of VA mycorrhiza formation similar to those of P additions to soils low in this mineral. Conversely, soils with high P levels do not promote VA mycorrhiza formation (e.g. Menge, 1978). Phosphorus diffuses slowly in soil (Buckman and Brady, 1960) and depletion zones develop around roots especially in soils with low P concentrations. VAM fungi extend the surface area of the roots and as such, the mycorrhizal root system can explore a greater volume of soil beyond the depletion zone for P, and other nutrients. The small diameter of the hyphae allows the fungus to explore smaller pore spaces than roots. There have been studies suggesting that VAM fungi can transform unusable forms of P (i.e. adsorbed and organic phosphates) and make them available to the plant (Brundrett, 1991).

In natural ecosystems VAM fungal populations vary due to plant growth stage, season and soil factors (e.g. pH, salinity). Such fluctuations are measured either by quantifying the number and species of asexual spores or by determining the intensity of VAM fungal colonisation within roots during a growing season. The use of pesticides, some cropping practices (e.g. tillage, monoculture) and fertilization also promote such changes and may decrease the diversity of VAM fungi and reduce the beneficial effects that these fungi have on plant growth (Sieverding, 1989; Rabatin and Stinner, 1989). The use of pesticides, fertilizers and farming practices in Barbados and the effects that these agro-chemicals and practices may have on native VAM fungal populations and mycorrhizal associations was reviewed by Persad-Chinnery *et al.*, (1992).

In this study the mycorrhizal potential of soils in Barbados was assessed by determining VAM fungal spore density and assessing the colonisation of roots of phytometers by VAM fungi.

METHODS

Soil samples were collected from sites (Table 1) within each of the ten soil associations, including both variants of the grey brown association, recognised in Barbados (Vernon and Carroll, 1966). At each site three subsamples were collected. One was placed in a plastic bag for subsequent extraction of spores. The other two were transferred to 15.5 cm plant pots with as little disturbance as possible. The soil sampling was accomplished in a single day.

Seedlings to be used as phytometers were prepared by germinating seeds in an autoclave sterilised mixture of equal volumes of soil, sand and vermiculite in 96 well seedling trays. Three unrelated species were used - corn (*Zea mays* L.), pepper (*Capsicum annuum* L.) and bean (*Phaseolus vulgaris* L.). In order to have seedlings of suitable size of each species, the pepper seeds were germinated first, after the first two leaves had unfolded the beans were planted. Two days later the corn was planted.

Three seedlings of each species were transplanted into one set of pots. Four corn achenes soaked in aerated water for 24 hr were planted into the second set of pots.

One plant of each species was carefully removed from each of the first set of pots and a corn seedling from each of the second set of pots at 2, 3 and 4wk after planting. The roots were cleared in KOH, stained with Chlorazol black E (Brundrett *et al.*, 1994), and examined for VAM fungal colonisation. This was quantified by the method used by Brundrett and Abbott (1995). The length of the colonies (mm) was measured with a compound microscope. These values were converted to a percentage of the root portion examined. Brundrett and Abbott (1995) found this method to be particularly suitable when colonisation levels were low.

Spores were extracted from two 50g samples of each soil by wet sieving, decanting and sucrose centrifugation (Brundrett *et al.*, 1994). The bottom sieve was 45μm to ensure collection of the small spores of some *Glomus* spp. The spores were examined and counted under a dissecting microscope (x40).

Table 1. Locations of soil samples collected from each soil association (1-9 Coral region formation; 10 Scotland district formation).

Sample Number	Association	Location
1	Red Brown Association (60s)	Easy Hall, St.Joseph
2	Yellow Brown Association (50s)	Groves, St.George
3a	Grey Brown Association (Sandy Variant) (40s)	Porters, St.James
3b	Grey Brown Association (Leeward Coast Variant)(40s)	Rock Dundo, St.James
4	Black Association (30s)	Content, St.Lucy
5	St.John's Valley Association (64s and 65s)	Wakefield, St.John
6	St.George's Valley Association (20s)	Carmichael, St.George
7	St.Philip Plain Association (10s)	Lowlands, St.Lucy
8	Red Sand Association (70s)	Allmens, St.Lucy
9	Coastal Association (80s)	Hope, St.Lucy
10	Scotland District Soils	Greenland, St.Andrew

RESULTS

The highest spore populations were found in the Scotland District soils (SDS) and the Coastal Association (80s) and these were significantly greater than that of the sandy variant of the Grey Brown Association (40s) (Fig.1).

The seedlings transplanted into the first set of pots showed increased colonisation over time (Fig. 2). The overall % colonisation being 9.3, 19.6 and 21.6 in weeks 2, 3 and 4 respectively. At all sample dates for all soil samples, the corn plants were more highly colonised than either beans or pepper (Fig. 2). The highest mycorrhizal potential was exhibited by the soils of the Scotland District (10) and the Coastal Association (9). The soils with low mycorrhizal potential were mainly those in agricultural areas, e.g. Yellow Brown (2) and Grey Brown (3a) associations.

The corn plants in the second set of pots were all mycorrhizal after two weeks and those planted in the soils of the Scotland District and the Coastal Association were the most highly colonised at all three sample dates. There was much more variation between root samples in these pots than in the other set and statistical differences between soils were not detected.

DISCUSSION

All three methods of assessing the mycorrhizal potential of the soils gave similar results with the non-agricultural soils of the Scotland District and the Coastal Association having more resting spores and higher levels of VAM fungal colonisation of the phytometers. This suggests that agricultural practises may be minimising the benefits from mycorrhiza formation.

The strong correlation between spore numbers and root colonisation was unexpected, since colonisation is commonly from hyphal fragments which contribute most of the inoculum in many soils. Otherwise, the data clearly show that three weeks growth of the transplanted phytometers was sufficient to obtain useful results and that the transplanted plants, with their developed root systems, were more informative than those derived from the soaked corn achenes. That the corn phytometers became more highly colonised than those of the other two species does not necessarily mean that corn is the best species to use.

VAM fungi are not only affected by the soil and the host plant when grown in an agricultural field, they are also subject to agricultural practices. Among those practices that may be detrimental are tillage, crop rotation, and the use of organic manure, inorganic fertilizers and other agricultural chemicals.

Recently there has been emphasis on cropping with reduced tillage. This has been advocated mainly because tillage promotes soil erosion, reduces soil moisture and promotes the prolific growth of saprophytic bacteria rather than fungi. Dibb *et al.*, (1990) reported that tillage alters the distribution of VAM fungi in the soil profile and can lead to reduced VA mycorrhiza efficiency and lower spore densities. Due to the predominance of clay in the agricultural soils of Barbados there is a tendency for the soil to compact and self-decompact. Compaction too, can alter the occurrence of VAM fungi in the field hence, a balance of tillage and compaction must be sought to minimize their negative effects on VAM fungi.

Crop rotation where a VAM fungal host is alternated with a non-host species is very likely to lead to a reduction in the number and species diversity of VAM fungi in the soil. Rotating crops that are mycorrhizal is suggested if the population of VAM fungi is to exert a significantly beneficial effect on agricultural production. Harinikumar and Bagyaraj (1989) reported stimulated mycorrhizal root colonization and sporulation when a suitable crop rotation was carried out.

Continuous monoculture has been shown to have a decreasing effect on the abundance of VAM propagules in the soil while intercropping supports a diversity of VAM fungal types (Sieverding, 1991). However, in Barbados continuous monoculture of sugarcane does not seem to have caused a reduction in the formation of VA mycorrhizae (Chinnery *et al.*, 1987). This contradictory finding indicates that further studies need to be conducted since different species of VAM fungi may react differently when associated with particular crops. A fallow period is normally necessary for fields that have been extensively monocultured as a means of replenishing the diversity of VAM fungal populations. Fallow, or lay aside, is not normally practiced in Barbadian agriculture.

Brechelt (1989) found that increased amounts of fresh organic manure led to a decrease in mycorrhizal efficiency due to the increased P levels in the soil. Composted manure has been shown to improve the effectiveness of VAM fungi (Sieverding, 1991). In Barbados, de Boer (1992) reported that compost consisting of filter-press mud, bagasse and fly-ash leads to an increase in sugarcane yields when compared to N-K fertilizer application. It is possible that the compost promotes VA mycorrhizal associations and thus better yields.

Intensive use of inorganic fertilizers may decrease the quantity of VA mycorrhizal fungi in some tropical soils and it has been consistently shown that increased P levels tend to demote the formation of mycorrhizae. For example, Sieverding (1989) found that P fertilizers applied to fields at concentrations greater than 50 kg P ha^{-1} reduced the formation of VA mycorrhizae. Abbott and Robson (1984) reported that high P and N levels decreased VAM infection within roots. Addition of fertilizers, especially phosphates, to soil creates situations where the crop plants depend less on VAM fungi for growth and, at very high phosphorus levels, root systems are normally sparsely infected. Ellis *et al.*, (1992) found that root colonization of soybean and sorghum by VAM fungi was greatest when fertilizer was not applied to the soil. In Barbados, no P fertilizer is used on the main crop - sugarcane. Persad-Chinnery *et al.*, (1992) calculated that the average amount of P fertilizer applied to non-sugar agro-ecosystems was approximately 40 kg phosphate per hectare per year. This value is approaching the levels that will impact negatively on VAM fungi.

There have been few studies on the effects of pesticides on VAM fungi and the formation of VA mycorrhizae, a topic last reviewed by Trappe *et al.*, in 1984. Results from greenhouse pot culture experiments and to a lesser extent, field experiments suggest that agricultural chemicals, used at recommended doses could have effects upon VAM fungi ranging from minor to severe (Trappe *et al.*, 1984). Many pesticides exert effects on non-target organisms. For example, an insecticide may kill non-target insects, including biological control agents, or may have deleterious effects on beneficial fungi and bacteria.

VAM fungi, as non-target organisms, may be affected by fungicides which may inhibit spore germination, mycelial development or sporulation. Rabatin and Stinner (1989) found that triazole fungicides suppress root colonisation and sporulation. Nemec (1980) tested eleven fungicides on two *Glomus* species. Amongst these captafol at rates of 2.2, 4.5 and 9.0 kg ha^{-1} and captan at rates exceeding 9.0 kg ha^{-1} reduced both colonisation and sporulation. All rates of benomyl, whether applied to seeds or mixed into soil, were toxic to VAM fungi (Nemec, 1980) as are most systemic fungicides (Jalali and Domsch, 1975). Maneb and chlorothalonil at rates of 11.2 and 22.4 kg ha^{-1} reduced sporulation of *G. mosseae*. Copper based fungicides, used to control phycomycetes and downy mildews, have also been reported to have a growth reducing effect on VAM fungi (Graham *et al*., 1986; Nemec, 1980; Menge, 1982). All of the fungicides mentioned have been approved for use in Barbadian agro-ecosystems.

Herbicides are used to control the presence of undesirable plants and may have indirect harmful effects on VAM fungi. When a plant is killed its mycorrhizal association breaks down and the extraradical mycelium has to infect another plant. If there are few or no plants remaining after the herbicide treatment then the survival of these fungi may be threatened. Alternatively the herbicide may lead to a shift in the dominant vegetation such that the dominant plant species is non-mycorrhizal or weakly mycorrhizal and this too may threaten the survival of VAM fungi.

Bellamy (1993) found that sugarcane growth in Barbados was reduced when 2,4-D or Dowpon were used to control weeds compared to manual weeding. This effect could have resulted from negative effects on VAM formation or other beneficial organisms (e.g. nitrogen-fixing bacteria). Chinnery *et al*., (1987) previously showed that sugarcane is highly mycorrhizal. Paraquat (gramoxone) has been found to reduce VAM fungal colonisation of roots and sporulation but generally herbicides do not have fatal effects on VAM fungi (Rabatin and Stinner, 1989). Dehn *et al*., (1990) tested the effects of herbicides on hyphal growth and VAM fungal infection. Alachlor used at recommended rates depressed hyphal growth of *G. fasciculatum*, *G. etunicatum*, and *G. mosseae*.

Insecticides may have no effect or either cause promotory or inhibitory effects on growth and sporulation of VAM fungi. Trappe *et al*., (1984) reported that carbofuran at 22 kg ha^{-1} and oxamyl as a foliar spray did not have any effect on sporulation of VAM fungi. A promotory effect may be realized if the insecticide eliminates predators of these fungi. If soil organisms like collembola and nematodes that graze VAM fungal hyphae and spores are killed, increased fungal growth and sporulation may result. Alternatively, insecticides that kill soil organisms responsible for dispersing spores may contribute to changes in species diversity in a field. Generally most insecticides are applied to foliar parts of the plant and when used at recommended rates should not affect VAM fungi. However, they may be used at concentrations above the recommended rate or at a frequency greater than that recommended (Ferdinand, 1988; Chinnery and Gibbs, 1991). Buildup of insecticide residues in the soil could lead to deleterious effects on VAM fungi. Most insecticides, especially the newer types, have not been tested to evaluate their effects on VAM fungi and VA mycorrhizae. However, we have recently started a series of experiments at the University of the West Indies.

There is no way of knowing which of the above caused the results obtained. However, they are cause for concern. If sustainable agriculture is to be achieved, we need more information on the effects of agricultural practices on VAM fungi and VA mycorrhizae. Also, the indigenous VAM fungal populations need to be investigated. The effectiveness and competitive ability of each species must be evaluated and the most effective VAM fungi for a particular crop determined. Then, seedlings can be colonised in the nursery before introduction into the field or it may be possible to inoculate entire fields with suitable species of VAM fungi. VAM fungi if managed as a biofertilizer can lead to a reduction in fertilizer inputs to agro-ecosystems and yet maintain high crop yields. Disease resistance, drought tolerance and the other benefits listed above should also stimulate interest in managing and effectively utilizing VAM fungi in agro-ecosystems. Savings on production costs and thus the potential for increased profits are reasons why farmers may well be interested in maintaining the benefits of these fungi.

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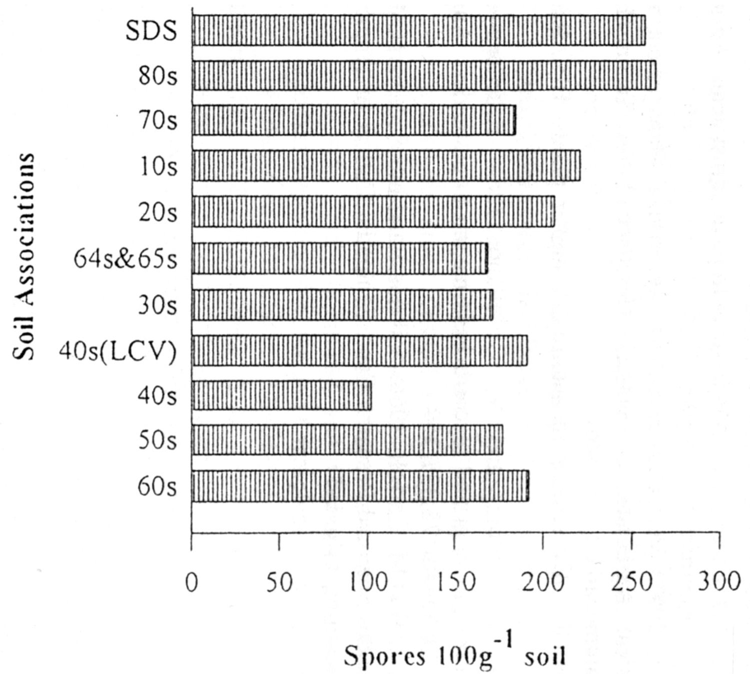

Fig. 1: Number of VAM fungal spores in soil samples from each association.

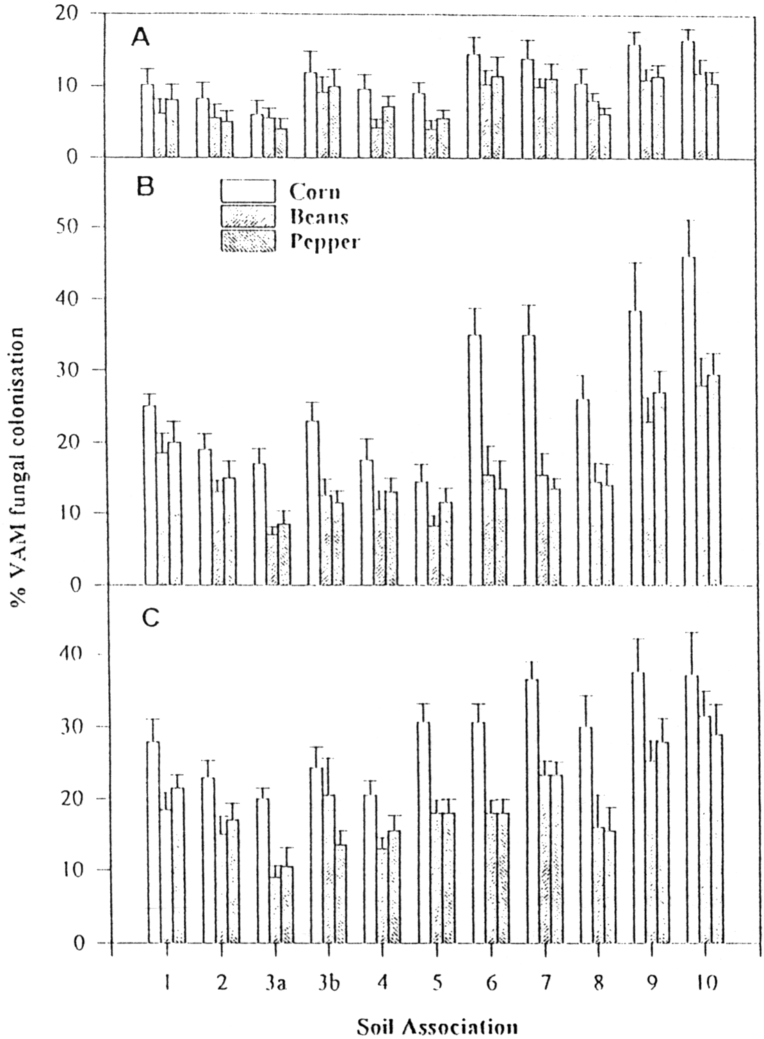

Fig. 2: Percentage VAM fungal colonisation of phytometers grown in each of the soils sampled. (Harvested at A 2, B 3 and C 4 wks)(Error bars are standard errors).