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Survey of vesicular–arbuscular mycorrhizae in lettuce production in relation to management and soil factors

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SUMMARY

The occurrence of vesicular–arbuscular mycorrhizae (VAM) root colonization and spore number in soil was assessed for 18 fields under intensive lettuce (*Lactuca sativa* L.) production in California during July and August of 1995. Data on management practices and soil characteristics were compiled for each field, and included a wide range of conditions. The relationship between these factors and the occurrence of VAM in these fields was explored with multivariate statistical analysis. VAM colonization of lettuce tended to decrease with the use of chemical inputs, such as pesticides and high amounts of P and N fertilizers. Addition of soil organic matter amendments, the occurrence of other host crops in the rotation, and soil carbon:phosphorus and carbon:nitrogen ratios, were positively associated with VAM colonization of lettuce roots. The number of VAM spores in soil was strongly correlated with the number of other host crops in the rotation, the occurrence of weed hosts and sampling date, but was more affected by general soil conditions than by management inputs. Higher total soil N, C and P, as well as CEC, were inversely related to soil spore number. A glasshouse study of the two primary lettuce types sampled in the field showed no significant differences in the extent of root colonization under similar growing conditions. The results of this study are compared with other studies on the effects of management and soil conditions on mycorrhizal occurrence in agriculture.

INTRODUCTION

Vesicular–arbuscular mycorrhizae (VAM) can improve plant acquisition of soil minerals by soil exploration (George *et al*. 1992; Jakobsen *et al*. 1992) and can better enable a plant to withstand environmental stresses (Hirrel & Gerdemann 1980; Dueck *et al*. 1986; Tobar *et al*. 1994). VAM activity in the soil can lead to increased soil aggregation, which improves drainage and soil quality (Bethlenfalvay & Barea 1994). VAM interact with pathogens and other rhizosphere inhabitants affecting plant health and nutrition (Linderman 1988; Baby & Manibhushanrao 1996). Although VAM fungi are ubiquitous in soils, there is tremendous variation in their abundance, even within agricultural soils.

A number of agricultural management practices affect the soil environment and thereby, mycorrhizal activity. Management factors, such as pesticide use, tillage practices, fertilizer amendments and cropping sequence; and soil factors, such as pH and nutrients, have been assessed for their effects on VAM colonization, VAM diversity and dominance, VAM symbiotic effects on plant growth, and/or spore species composition of the field soil. Few studies, however, have addressed the relationship of a wide range of management and soil factors to VAM colonization on roots and spore numbers in the soil.

This survey assessed the relative importance of agricultural practices and soil conditions that might affect VAM colonization of roots and spore number in soils under intensive lettuce (*Lactuca sativa* L.) production in the Salinas and Hollister Valleys of California. In this region, diverse soil types exist and lettuce is produced using a range of agricultural practices, so that a wide variety of circumstances, including differences in pest and fertility management practices, tillage, field crop history, soil texture, pH, CEC, and N, P and C content were considered in the analysis. Multivariate statistics were used as an exploratory device to assess the relative importance of these factors to VAM colonization and spore number in these fields.

Lettuce is well known as a VAM host, and in order to sample a broad range of agricultural systems, two

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lettuce types (crisphead and greenleaf) were included in this study. A glasshouse trial was conducted to determine if there were differences in the extent of VAM root colonization between two representative varieties of these lettuce types when grown in a field soil known to be conducive to high VAM colonization in lettuce.

The objectives of this study were: (i) to assess the degree of VAM colonization and spore number in growers' fields in a region of intensive vegetable production, and relate these differences to management practices and soil characteristics; (ii) to identify variation in VAM colonization due to different lettuce types grown on the various fields; and (iii) to target practices that encourage the ocurrence of VAM in soils.

MATERIALS AND METHODS

Field study

Eighteen production fields planted with lettuce were sampled for VAM colonization and soil spore number *c*. 2 weeks prior to harvest on farms in the Salinas and Hollister Valleys in the Central Coast region of California, during July and August 1995. Different fields, representing unique combinations of management practices and soil conditions were sampled during a 7-week period (Table 1). The first sample time was in Week 1, the next in Week 4 and the last in Week 7. Roots were collected from 15 randomly sampled lettuce plants from a *c*. 200 m^2 area of each field. These were washed with tap water, cleared with 5% KOH, and acid stained with 0·05% trypan blue lacto-gycerol solution (modified from Phillips & Hayman 1970). Colonization was determined by assessing five slides with ten 1 cm root segments from each plant under 100–400× magnification and scoring the intensity of colonization from 0 to 4, where $0 =$ no colonization, $1 = 1$–25% colonization, $2 =$ 26–50% colonization, $3 = 51$–75% colonization and $4 = 76$–100% colonization for each root segment. These scores were averaged for each plant. Field colonization was the mean of these plant scores. For Fig. 1, the means were converted to percentages by taking the midpoint of each scoring interval. Bulked soil from five 15 cm deep soil cores were taken randomly from beds within the field site. Soil moisture was determined by weighing moist field soil, then drying at 105 °C for 48 h and weighing again. For each field, three 10 g subsamples from the bulked moist soil were wet sieved in a manner modified from Gerdemann & Nicholson (1963) so that soil aggregates were broken to ensure a better recovery of spores from finer textured soil samples (McKenney & Lindsey 1987). The 45–250 μ fraction was subject to centrifugation in a 50% sucrose solution to separate the spores (Jenkins 1964). These were counted under a dissecting microscope at 80×. Air-dried soil was analysed for total carbon and total nitrogen by combustion gas analysis (Pella 1990), total phosphorus by microwave acid digestion/dissolution (Sah & Miller 1992), as well as Olsen phosphorus based on alkaline extraction (Olsen *et al*. 1954), CEC by barium acetate saturation and calcium exchange (Rible &

Table 1. *Brief summary of fields sampled, including soil type, lettuce cultivar, management system and sample period. 'Certified organic' refers to certified compliance with Californian organic production laws*

Field number	Soil type	Cultivar	Certified organic	Sample period
1	Clay loam	Tierra (GL)	Yes	3
2	Clay loam	Tierra (GL)	Yes	3
3	Clay loam	Two Star (GL)	Yes	1
4	Loam	Coastal (GL)	Yes	2
5	Loam	Coastal (GL)	Yes	2
6	Clay loam	Vanguard†	No	1
7	Sandy loam	Vanguard†	No	3
8	Clay loam	Montemar†	No	3
9	Clay loam	Salinas*	No	2
10	Loam	Montemar†	No	3
11	Sandy loam	Montemar†	No	3
12	Clay	Coastal 105*	No	1
13	Sandy loam	Hacienda (GL)	No	1
14	Clay loam	Salinas*	No	2
15	Sandy loam	Verano*	No	1
16	Sandy loam	Coastal 115*	No	1
17	Clay loam	El Dorado*	No	2
18	Clay loam	Two Star (GL)	No	2

* 'Salinas' type.
† One parent common to 'Salinas'.

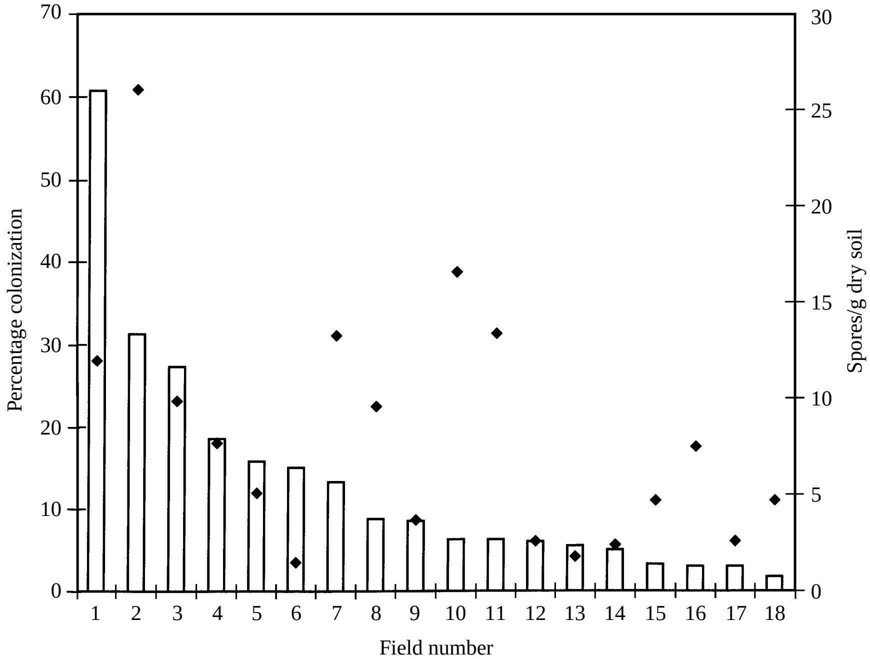

Fig. 1. Range of VAM colonization (□) of lettuce roots and soil spore numbers (◆) from 18 on-farm fields in the Salinas and Hollister Valleys of California. Each bar is the mean of 15 plant samples. Each diamond is the mean of three soil subsamples.

Quick 1960) and pH in 1:1 soil:water paste. These measurements were made by the analytical laboratory of the Division of Agriculture and Natural Resources of the University of California. Soil texture was ascertained from soil maps (USDA/SCS 1978). Growers answered questions about field history and management practices. Grower information included the current lettuce cultivar, as well as the field crop history for at least 3 years; whether tillage practices were low or high disturbance, i.e. whether semi-permanent beds were maintained for several years, or the entire field was disked several times a year, and how many passes were used; the amount and kind of N and P fertilizer applied to the lettuce crop, as well as any amount and kind of organic materials added to the soil in the last year; whether fungicides, insecticides or herbicides were used in the field; and the identity of the dominant weed species.

Field conditions and management regimes differed between fields so that each field presented a unique combination of factors. A brief description of the soil, crop and management, as well as sampling time for each field is provided in Table 1. Soils ranged from clay to sandy loam. Just under a third of the farms were operating as California certified organic growers, which means that organic sources are used for soil fertility and pest control. Another field was in transition to organic production, but not yet qualified for certification. Plant age ranged from 43 to 72 days. Soil P was at least sufficient in all soils, and pH was neutral to slightly alkaline. Most growers used some pesticides, though no fields had been soil-fumigated due to an extremely wet spring. Minimum tillage was primarily used in fields with drip irrigation systems. All growers used some form of N fertilizer, although four applied no mineral P. Organic matter amendments were added to eight of the fields within the previous 8 months. The full range of management practices and soil conditions that were considered for their possible association with the occurrence of VAM in the field in the multivariate analyses are given in Table 2.

Relative contribution of these environmental and management factors to VAM colonization of lettuce and spore number in the field were assessed with canonical correlation analysis (CCA) using SAS (Statistical Analysis Systems Institute 1990). CCA is used to identify and quantify the associations between two sets of variables, where the dependent variables may be intercorrelated. Dependent variables were VAM colonization score and spore number/g dry soil. These data were log transformed to satisfy normal distribution. Independent variables included for analysis are listed in Table 1. CCA creates a series of canonical variables derived from input values for all the variables. When there is a high correlation

Table 2. *Range and distribution of factors considered for their effect on VAM in 18 fields in California under intensive lettuce production*

Management practices		Soil and environmental conditions	
Factor	Range	Factor	Range
Crop age	43–72 days	Sample periods	3
Use insecticide/nematicide	15 fields	pH	6·0–8·6
Use fungicide	12 fields	CEC	17·5–45·0 meq/100 g soil
Use herbicide	8 fields	Total N	0·08–0·23 %
Use conservation tillage	6 fields	Total C	0·70–2·22 %
Number of tillage passes	3–13	Total P	503–1759 μg/g soil
N fertilizer	3·4–302·4 kg/ha	Olsen P	31–129 μg/g soil
P fertilizer	0–212·8 kg/ha	Total N:P	71·6–254·3
P:N fertilizer	0–1·75	Total C:P	424–2739
Used transplants	2 fields	Total C:N	5·9–10·83
Organic matter amendments	0–22·4 Mg/ha	Total N:Olsen P	923–4483
VAM host crops in rotation	25–100 %	Total C:Olsen P	6726–42561
Previous host crop	11 fields	Flood-affected fields	3
Winter crop cover	7 fields	Weed species in field	0–4

between input variables and canonical variables, it is feasible to assign an identity to each series of correlation values that represents the association between dependent and independent input values. Field means or ordinal values, representing simple intervals, were entered for each variable of every field so that there were no missing values considered in the analysis. Because the number of independent variables was too large for a correlation matrix of this sample size, a series of CCAs was used to assess the relationship of management and soil factors to the measurements of VAM in the 18 fields in a variety of combinations, so that those factors consistently found to have little relationship to the incidence of VAM in this study could be dropped from the final correlation matrix.

Glasshouse study

The two lettuce types sampled in this survey were grown under similar conditions in a glasshouse to check if differences in VAM colonization of lettuce types would confound the results of the survey since greenleaf types were most often grown in certified organic fields, and crisphead types in the others. Cultivars for this glasshouse study were chosen to represent adequately those in the field study. Most crisphead cultivars were of the 'Salinas' type or had at least one 'Salinas' parent (Table 1). The greenleaf cultivar, Two Star, was chosen because it was sampled from both certified organic and conventional farms. From a field in which both high colonization and spore counts had been measured (i.e. field 3, Fig. 1), steel cylinders 15 cm in diameter and 38 cm deep were used to remove undisturbed intact cores from the bed. The cylinders were arranged in a glasshouse in a completely randomized block design. In eight of these cylinders, the crisphead cultivar, Salinas 88, was planted, and in eight others, the green leaf cultivar, Two Star. Eight seeds were placed in each cylinder, and were thinned to one plant per cylinder 3 weeks later. Fertilizer was not added. Glasshouse temperatures ranged from 16 (night) to 28 °C (day). Photoperiod was *c.* 12 h, and was dependent on the natural light from February to April in Davis, CA. Water was applied equally to all pots on a daily basis, or as needed, to maintain soil moisture at approximate field capacity in all cylinders, as indicated by tensiometers placed in representative cylinders of each block. Plants were harvested 7 weeks after planting. Roots were cleared, stained and assessed as in the field survey. Comparative VAM colonization of the cultivars was determined through ANOVA with SAS.

RESULTS

Field study

In the 18 fields, a wide range of VAM colonization of lettuce roots, and of spore number in soil, was found (Fig. 1). Root colonization ranged from 2 to 60 %, but over half the fields had $<$ 10 % root colonization, and only one had $>$ 50 % colonization. This field had been converted to vegetable production from an abandoned orchard, and had been cultivated under organic management for only a few years. Fields with the highest levels of colonization were all under certified organic production. Spore number also varied between fields, and did not follow the same trends as root colonization. Spore number ranged from 1·5 to 26/g dry soil, although most fields had $<$ 10 spores/g dry soil. However, all but one field with root colonization over 10 % had $>$ 5 spores/g dry soil.

Table 3. *Management and soil factors most affecting VAM colonization of lettuce* (n = *18*)

Factor	Effect	Correlation coefficient
Greater soil C:P	+	0·68
Greater soil N:P	+	0·66
Fungicide use	–	0·66
Higher P fertilizer	–	0·61
Older crop age	+	0·55
More VAM hosts in rotation	+	0·52
Higher N fertilizer	–	0·51
Insecticide use	–	0·51
Greater soil C:N	+	0·50
Herbicide use	–	0·48
Previous host crop	+	0·46
Total soil P	–	0·45
More organic matter applied	+	0·44
Use of transplants	–	0·43
Higher soil pH	+	0·43
Higher soil spore number	+	0·42
Fertilizer N:P	+	0·31
Finer soil texture	+	0·29

Table 4. *Management and soil factors most affecting VAM spore number in soil* (n = *18*)

Factor	Effect	Correlation coefficient
More VAM hosts in rotation	+	0·66
Later sample date	+	0·60
Higher total soil N	–	0·50
Winter cover	–	0·49
Higher total soil C	–	0·48
Insecticide use	–	0·44
Higher root colonization	+	0·42
Greater number weed species	+	0·41
Previous host crop	+	0·40
Higher total soil P	–	0·34
Higher soil CEC	–	0·33
Higher soil pH	+	0·30
Fertilizer N:P	+	0·28
Finer soil texture	–	0·25
Herbicide use	–	0·22
P fertilizer	–	0·22
N fertilizer	–	0·21
Fungicide use	–	0·12

Because VAM colonization and spore number tended to show different relationships to field and management factors, separate canonical correlation matrices were constructed to best represent each of these two sets of measurements. Correlations between the dependent variables and canonical variables were greater than 0·97 in both analyses, and the matrices showed similar results for common independent variables. The rankings of canonical correlation coefficients from the analyses of the most important management and soil variables associated with VAM colonization and spore number are given in Tables 3 and 4, respectively. These show results from the final correlation, which was performed without the management and soil variables consistently found to be poorly correlated with either of the dependent variables in order to retain a matrix of the appropriate size.

Multivariate analysis showed that VAM colonization and spore number were affected to different degrees by various management practices, and did not always respond similarly (Tables 3 and 4). The use of insecticides decreased both the extent of colonization and the spore number in the soil. Fungicides, on the other hand, and, to a lesser extent, herbicides, appeared to have a more negative effect on colonization than spore number. This was true of P and N fertilizers as well, where larger applications of both P and N fertilizers decreased colonization. Both spore number and root colonization were reduced at higher ratios of fertilizer P:N. The application of organic matter amendments to soil tended to increase root colonization, but showed lack of relationship with soil spore number, so that it was not included in the final matrix in Table 4. A large proportion of VAM host plant species in the crop rotation was positively associated with VAM spore number in soil, and showed strong correlation with root colonization as well. Similarly, if the previous crop was a VAM host, the sampled lettuce crop was more likely to have higher VAM root colonization, and the soil to have higher spore numbers. Higher soil spore numbers were also associated with the presence of a greater number of weed species in the field, but no relationship was found with VAM colonization of the lettuce, so it was not included in the final matrix in Table 3. Fields with winter crops, however, tended to have fewer spores than those left fallow during the winter, though no relationship with subsequent colonization was found. Colonization was higher in older lettuce plants than in younger ones. Later calendar dates showed a greater increase in the number of spores in the soil than root colonization. Transplanted lettuce tended to have lower colonization levels than direct-seeded plants, but spore number was not affected. Tillage methods showed little effect on either measurement of VAM in these systems, and so were not considered in the final CCA. Similarly, the effects of flooding and lettuce type were also dropped from consideration. Overall, host dynamics, pesticide use and fertilizer management appeared to be the most important agricultural practices affecting the VAM association in lettuce fields.

The soil factors measured in this survey also showed differing degrees of importance in relation to VAM colonization and spore number in the fields (Tables 3 and 4). Nevertheless, soils with higher total P tended to have both fewer spores and lower levels of root colonization, and as mentioned above, none of the fields in this survey were P-deficient. In this study, measurements of total P were more highly correlated with VAM colonization and spore number than measurements of Olsen available P, and therefore total P was used in the final CCA analysis. Colonization tended to be greater with a high ratio of total C or N to total soil P, but spores showed greater correlation with total C and N than the ratios of these elements in soil. Higher ratios of total soil C:N actually showed an inverse relationship with soil spore number. Higher soil CEC was also negatively correlated with soil spore number, though it had very little impact on colonization. Finer textured soils tended to have more VAM colonization in the lettuce crop, while coarser soils were associated with a larger number of spores in the soil. Higher soil pH was positively correlated with both colonization and spore number. The soil factors most strongly correlated with VAM in these fields were the soil C, N and P contents and their relative proportions to one another.

Glasshouse study

The comparison of greenleaf and crisphead lettuces showed no significant differences in the extent of colonization between the lettuce types. Mean colonization was 37·0% (S.E. 3·6) in the green leaf variety, and 34·1% (S.E. 6·1) in the crisphead variety. Lettuce type, consequently, is not considered to affect the results of this survey.

DISCUSSION

Background

Previous studies comparing low input and organically managed farming systems with conventional farm management systems have shown that the former tend to have more VAM spores in the soil, more diverse populations of VAM fungi and/or higher levels of VAM colonization of crop roots than the latter (Werner *et al.* 1990; Douds *et al.* 1993; Ryan *et al.* 1994). These results were variously attributed to differences between the systems in P fertilizer source, chemical pesticide use and/or crop rotations.

Many common fungicides and soil fumigants are detrimental to VAM (Spokes *et al.* 1981; Menge 1982; Dodd & Jeffries 1989). Insecticides can also decrease root colonization (Spokes *et al.* 1981) and spore number in the soil (Ocampo & Hayman 1980). Herbicides, on the other hand, have more variable effects on VAM. Although there may be no direct effect on the amount of root colonization by VAM (Ocampo & Barea 1985), some herbicides can reduce the speed of hyphal growth through soil (Dehn *et al.* 1990). Herbicides also may affect VAM on crop plants and VAM diversity indirectly by decreasing the abundance and diversity of weed host species (Spokes *et al.* 1981).

Some studies have demonstrated that tillage and soil disturbance may reduce subsequent colonization of plant roots (Evans & Miller 1988; Jasper *et al.* 1989; McGonigle & Miller 1993). However, some of these studies used soils unaccustomed to tillage, so that VAM responses may have differed from soils that were frequently tilled; or spores were not assessed despite their potential importance as sources of inoculum in intensively tilled soils. Even when there is no effect on colonization, P uptake by mycorrhizal plants decreases after tillage, presumably due to the breakup of the fungal mycelium and the increased carbon cost to the plant to regain the soil exploration capacity of an extensive, intact hyphal network (McGonigle *et al.* 1990). Spore species population distribution can also change with tillage (Douds *et al.* 1995).

Fertilizer management has a direct effect on the performance of VAM in a system. Generally, P fertilizer reduces VAM colonization and effectiveness of the symbiosis, though different species of VAM respond variously to P additions (Schubert & Hayman 1986). Fields not previously fertilized with P show a greater decrease in VAM colonization in response to P fertilization than fields with a history of P amendments (Jasper *et al.* 1979), which suggests that management practices impose selective pressures on VAM populations in soils. Sporulation is decreased by P fertilization in many VAM species, and also by N fertilization in some species (Douds & Schenck 1990). The addition of P has been shown to suppress colonization only when N is not deficient in the soil (Sylvia & Neal 1990). In lettuce, increasing N supply in relation to P tends to increase root colonization (Hepper 1983).

Results of studies of organic matter additions on VAM fungi are conflicting, which may be due partly to the variable nature of such additions. Mycorrhizal plants demonstrate more efficient use of P from soil organic matter than non-mycorrhizal plants (Joner & Jakobsen 1995*a*), perhaps because VAM allow a plant to utilize P sources to which it would not otherwise have access (Jayachandran *et al.* 1992). In nutrient-poor soils, VAM can be stimulated by fertilizer or manure amendments as a result of the host plant carbon supply increasing in response to fertilization (Ellis *et al.* 1992).

The degree, as well as the effectiveness, of the VAM association can be influenced by the crop history of the field, as well as the crop cultivar. Crop rotation affects VAM species composition and dominance in the field (Hendrix *et al.* 1995). Even weed dynamics in agricultural fields have been associated with changes in VAM spore populations (Kurle & Pfleger 1994). A crop monoculture can favour some VAM species over others, which will vary in accordance with the host crop (Johnson *et al.* 1991). Continuous monoculture can have a negative effect on VAM colonization compared with fields under crop rotation (Baltruschat & Dehne 1988). Yield declines associated with continuous crop monoculture have been attributed partly to decreased VAM effectiveness caused by limited host diversity (Johnson *et al.* 1992). Similarly, long-term fallow disorder has been attributed to a reduction in VAM species diversity and abundance (Thompson 1987). The abundance of VAM spores is greatest in soils supporting a VAM host crop, decreases with non-host crops and is lowest in fallow soils (Harinikumar & Bagyaraj 1988). Spore production itself is influenced by the plant host species (Struble & Skipper 1988) and different genotypes of the same crop species may also respond differently to VAM (Azcón & Ocampo 1981; Krishna *et al.* 1985). Also, a non-host crop can lead to the decreased colonization of a subsequent host crop (Black & Tinker 1979).

Current study

In the lettuce fields sampled in this survey, the use of pesticides, soil fertility management and prevalence of VAM host crop species were the management practices most associated with the measurements of VAM. All conventionally managed lettuce fields used some form of chemical pest control, as did some organic systems that used 'organic' pesticides. The colonization of roots by VAM a showed strong negative correlation with the use of fungicides, insecticides and herbicides; spore number was most negatively associated with insecticides, and only showed a mildly negative response to herbicides and fungicides. The strong effect of insecticides on spore number may be indicative of the importance of soil food web interactions to VAM dynamics in soils. Soil microfauna can be important vectors of spore dispersal, and so may be linked to the spatial and temporal dynamics of VAM activity in soils (Rabatin & Stinner 1989).

Greater applications of chemical fertilizers were strongly correlated with less root colonization by VAM. Spore number in soil had a somewhat stronger relationship with fertilizer N:P ratio than overall rates of chemical fertilizer, although a high ratio of fertilizer N:P increased the likelihood of VAM colonization as well. This may reflect the increased plant demand for P with increasing N supply in lettuce.

Unlike the application of chemical fertilizers, the addition of organic matter amendments to soils was positively correlated with the extent of VAM root colonization in lettuce, as was the soil C:N content. Previous work has shown that mycorrhizal hyphae tend to be longer and more dense in soils with organic amendments (St. John *et al.* 1983; Joner & Jakobsen 1995*b*). There is some evidence that hyphal growth through the soil is mediated through soil organic matter (Warner & Mosse 1980) and that organic matter in soils may be vital to hyphal survival in the soil during periods when there is no living host support (Hepper & Warner 1983). This may affect the inoculum potential of VAM in a soil because hyphae are important infective units for many species of VAM.

The importance of the presence of VAM host crops to VAM fungi is demonstrated by the results of this survey. The increase in spore number with a variety of weed species may be the result of increased host diversity in the field. The use of transplanted lettuce was negatively correlated with colonization, which was most likely due to the delay in field inoculum exposure. This study showed a clear increase in soil spore number throughout the season and with crop age. In natural ecosystems, both VAM colonization and spore number show seasonal variation (Giovanetti 1985) and other agricultural soils also show an increase in spore numbers late in the season (Harinikumar & Bagyaraj 1988) and at crop senescence (Gavito & Varela 1993).

In comparison with other factors in this study, tillage practices were of little importance to the VAM measurements taken in these fields. All the fields in this survey were subject to some degree of disturbance as well as field traffic, so treatment differences in this area of management may not be so pronounced as for other variables.

In general, aside from insecticide use and crop rotation, spore number seemed to be more closely associated with soil characteristics than with management practices. Higher spore density was most likely to be found in soils low in total C, N and P, with a low CEC and coarse in texture. Such soils would tend to have lower nutrient-holding capacities, and might be less able to support hyphal survival without a host than soils with more available carbon resources, so that an investment of carbon by the endophyte in environmentally resistant propagules would gain value in the system as a means of future survival and potential activity. VAM hyphal colonization of roots, on the other hand, shows a strong tendency to be greater with higher soil C:P, N:P and C:N, finer texture and higher pH, which tends to make soil P less available. The soil pH is also an important determinant of VAM species composition (Wang *et al.* 1985) and can affect the performance, or the effectiveness of VAM in benefiting plant growth (Hayman & Tavares 1985). The different responses of VAM spore number and colonization to management practices and soil conditions may reflect differences in the ecological functions of VAM hyphae and spores as environmental conditions alter the costs and benefits of carbon allocation to different fungal structures.

This survey emphasises the importance of carbon sources to VAM in soils, both in the form of host plants and as organic matter amendments. Stimulation of hyphal growth with the addition of organic matter to soils suggests that the occurrence of VAM in agricultural fields may be fostered by soil carbon sources, and that VAM colonization is more complex than a simple relationship between host plant and symbiont. In order to increase the VAM infection potential of a field, this study suggests that one should minimize the use of biocides and chemical fertilizers, while increasing the number of VAM hosts in the crop rotation and the amount of organic amendments to the soil. However, even conventionally managed systems may be able to improve VAM inoculum potential through proper crop rotation. Further studies on the impact of management practices, such as long term tillage effects, crop rotations and fertilizer management practices on VAM functioning in the field, may allow us to use VAM symbiosis more effectively for the benefit of the plant as well as for the soil system.

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