Fitting plants to soil through mycorrhizal fungi: plant nutrition in host-endophyte combinations evaluated by the diagnosis and recommendation integrated system

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Summary. Vesicular-arbuscular mycorrhizal (VAM) fungi improve plant growth in marginal soils. This study was conducted to determine the effects of three species of VAM fungi on plant nutrition in two cultivars of corn (*Zea mays* L.) and one of sunflower (*Helianthus annus* L.). Plants were grown in pot cultures under controlled (greenhouse) conditions in a soil high in K, Mg, and P, and low in Ca and N, and were supplied with amounts of VAM-fungal inocula in which equal numbers of infective propagules had previously been determined. Analysis of variance showed highly significant main effects and interactions due to both factors (plant and fungus) for N, P, Ca, and Mg. For K, only plant effects were significant ($P < 0.043$). The uptake of nutrients was selectively enhanced or inhibited by one or the other VAM fungus relative to non-VAM control plants. In sunflower, N concentration was markedly enhanced (73%) by the mixed inoculum of the three fungi, even though individual effects were not significant. Evaluation of leaf nutrient analyses by the Diagnosis and Recommendation Integrated System (DRIS) revealed the utility of this system to rank nutritional effects by VAM fungi in an order of relative nutrient deficiency. The DRIS therefore is seen as a useful tool in evaluating and selecting VAM fungi for the alleviation of specific nutrient disorders.

Key words: DRIS – *Helianthus annus* – Plant nutrition – VAM – *Zea mays*

An argument for "fitting plants nutritionally to soils", rather than fitting soils to plants, was presented by Brown

and Jones (1976) more than 15 years ago. These authors summarized reports of differential plant responses to nutrient stresses and noted that nutrients in soils range from deficient to toxic, while plant responses vary widely in their efficiency and tolerance of such conditions. They suggested that this information could be used to fit a crop to a specific soil, since soils and crops must be compatible for maximum yield, and stated that efficient plants respond to stress by altering their metabolism to ameliorate stress, while inefficient ones do not and therefore develop nutrient deficiencies or toxicities. During the past decade, work on plant-soil relationships (Guzmán-Plazola and Ferrera-Cerrato 1990; Linderman 1988a) showed that the nutrient-response mechanisms ascribed by Brown and Jones to plants are modified by the healthy plant's ever-present fungal symbionts, the vesicular-arbuscular mycorrhizal (VAM) fungi.

In different arable soils VAM fungi may show distinct populations (Land et al. 1989), which can vary with soil type (Lambert et al. 1980), crop management (Johnson et al. 1991a), and successional stage (Johnson et al. 1991b). Root systems are typically colonized by more than one VAM-fungal species (Daft 1983), but host-endophyte preference in establishing plant-fungus combinations (McGonigle and Fitter 1990) and in plant response (Hetrick et al. 1990; Krikun et al. 1990) has been demonstrated. The response may be either positive (Kothari et al. 1990) or negative (Johnson et al. 1992). In the latter case, the loss of C by the host plant (Bethlenfalvay et al. 1982; Johnson et al. 1992) may become a gain of C to the host soil (Gupta and Germida 1988; Thomas et al. 1986), to the ultimate benefit of the plant-soil system as a whole (Jastrow and Miller 1991).

Whether differences in VAM-fungal populations encountered in similar soil types and climates are due to host plant or host soil factors (Haas and Menge 1990), crop VAM dependence and the efficacy of VAM biotypes are essential components for fertilizer management (Krikun et al. 1990). In view of the demonstrated ability of VAM fungi to enhance or inhibit the uptake of specific nutrients (Bethlenfalvay et al. 1989) and to conteract

nutrient toxicities (Heggo et al. 1990), their impact on efforts to fit plants to soils must be considered. Success in such efforts will depend on (a) progress in the production of host-free inocula (Janardhanan et al. 1990), (b) an understanding of the mechanisms of competition between native and introduced inocula (Sen et al. 1989) and their respective effects on plants (Hetrick and Wilson 1990), (c) the elucidation of the physiology of host-plant and endophyte preference (Smith and Gianinazzi-Pearson 1988), and (d) the development of techniques to diagnose VAM effects on plant nutrition, such as attempted here.

The objectives of this experiment were: (1) to compare differences in nutritional host-plant responses to three VAM-fungal species and their combination in a soil not deficient in P, (2) to utilize a diagnostic method (Walworth and Sumner 1987; Bethlenfalvay et al. 1990) for the evaluation of the relative order of nutrient deficiency and nutrient balance, and (3) to demonstrate differences in the capability of VAM fungi (or their combination) to affect plant nutrition.

Materials and methods

Experimental design and statistics

A preliminary experiment was carried out to assess the incidence of infective propagules in inocula of three VAM fungi. It was a 3×4 factorial with four replications, and with fungal species (3 levels) and inoculum concentration (4 levels) as factors. The main experiment was conducted to determine host response to root colonization by the three fungi individually and collectively, relative to a non-VAM control. The main study was a 3×5 factorial, with host plants (3 levels) and VAM fungi (5 levels) as factors. There were five replications of each treatment for a total of 75 potted plants as experimental units. The results were evaluated by analysis of variance and Duncan's multiple range test. To give a more precise reading of the statistical evaluations of these plant responses than that provided by the convenient but arbitrary 5% levels (Nelson 1989), we included the actual probability values (P-value) associated with the F statistic of the analysis of variance with each treatment group.

Biological materials

Two corn cultivars (Zea mays L., cv. Zac-58 SM 18 Precoz, and cv. H-30, a hybrid) and one sunflower cultivar (Helianthus annus L., cv. Scikus) were used. Zac-58 was of the native race Cónico-Norteño (Wellhausen et al. 1951), and H-30 was a hybrid from the germplasm collection of the Centro de Genética, Colegio de Postgraduados (CP). Mycorrhizal plants were inoculated with one of the three VAM fungi Glomus etunicatum Becker and Gerdeman (Ge), Glomus mosseae (Nicol. & Gerd.) Gerd. and Trappe (Gm), Glomus pallidum Hall (Gp), or with all three of the fungi (Mix). Non-VAM plants served as controls (Cont).

Preliminary experiment

In the preliminary experiment, infectivities of the inocula were determined by the infection unit method according to Franson and Bethlenfalvay (1989). Increasing amounts of the inocula (1, 4, 16, or 64 g), containing VAM propagules in soil, were combined with the sand-soil mix used in the main experiment to make up a total mass of 100 g.

Sorghum (Sorghum bicolor L.) test seedlings selected for uniformity were grown for 14 days in growth tubes containing the 100 g of soil. Infection units per unit root weight were determined after staining the roots with trypan blue. The relationship between infection units and soil inoculum concentration was used to determine the amounts of inocula needed to produce a desired uniform density of infection units. Inocula

equivalent to 50 infection units per 10 mg of root mass were used in the main experiment, as determined from the relationship between infection units and soil inoculum concentration (Fig. 1).

Main experiment

The growth medium was a mix of washed river sand and soil (1:1, v:v) with a final texture consisting of 75% sand, 10% silt, and 15% clay. It had organic matter content of 0.8% and pH 8.3. Nutrient concentrations were: total N, $0.6 \mathrm{~g} \mathrm{~kg}^{-1}$, $NaHCO_3$-extractable (Olson) P, $21 \mathrm{~mg} \mathrm{~kg}^{-1}$, and Ca, K, and Mg (cmol kg^{-1}), 30.3, 0.7, and 5.8, respectively. The soil was low in organic matter, N and Ca, and high in K, Mg, and P, and was not fertilized during the experiment. A P-sufficient soil was selected because the strong VAM P-response often masks other effects in P-deficient soils. Soil P concentrations are generally favorable for mycotropic (VAM-enhanced) plant growth near Olson-P levels of $10 \mathrm{~mg} \mathrm{~kg}^{-1}$ (Bethlenfalvay et al. 1983).

Plastic pots containing 1.5 kg of growth medium were watered once a week to field capacity (drip) with distilled water. Plants were grown in a greenhouse at Montecillo (near Mexico City) from November to December (corn, 45 days; sunflower, 40 days). Day/night (12 h/12 h) temperature variations were small (25–30 °C). Plant and soil nutrient status was determined by standard analytical methods by the Soil Fertility Unit, Centro de Edafología, CP, Montecillo, Mexico. Root colonization by VAM fungi was determined by staining with trypan blue (Phillips and Hayman 1970).

Evaluation

The nutrient status of plants was assessed by comparing nutrient-concentration data with the nutrient indices derived from the Diagnosis and Recommendation Integrated System (DRIS; see Walworth and Sumner 1987). Nutrient analyses by DRIS are based on a comparison of ratios of element concentrations in the experimental samples with the same ratios (reference norms) from high-yielding, field-grown crops. Because of its reliance on nutrient ratios, the use of DRIS minimizes morphogenic and genotypic effects on the accuracy of deficiency diagnoses, predicts which nutrient is most limiting to yield, and provides an expression for nutrient balance. The lower the sum (irrespective of sign) of the indices, the better balanced are the nutrients. Plant nutrient responses to VAM fungi are evaluated to permit the selection of VAM fungi both for their effect on the alleviation of specific nutrient deficiencies and for their compatibility with a host-plant species or cultivar.
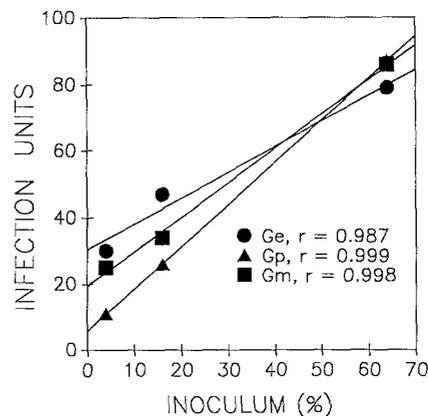
Fig. 1. Relationship between inoculum concentration and infectivity. Different amounts (4, 16, and 64 g) of VAM soil inoculum were mixed with 100 g of sterilized soil. Infectivity was determined as VAM infection units produced in these soil mixtures after 14 days per unit root mass (10 mg). Discrete infection units correspond to viable VAM propagules in the soil. Data points are the means of four replications. Abbreviations ara as in Table 1

Reference norms for corn developed by Summer (1981) were used. Means and CVs for the norms were: p/n, 0.108, 33; n/k, 1.74, 45; ca/n, 0.200, 34; mg/n, 0.098, 46; k/p, 6.52, 39; ca/p, 2.43, 45; mg/p, 1.71, 69; k/ca, 3.31, 59; k/mg, 7.73, 74; and mg/ca, 0.492, 35, respectively. The indices for N, P, K, Ca, and Mg were calculated according to Sumner (1981) as:

N index = [f(N/K) − f(P/N) − f(Ca/N) − f(Mg/N)]/4
P index = [f(P/N) − f(K/P) − f(Ca/P) − f(Mg/P)]/4
K index = [f(K/P) − f(N/K) + f(K/Ca) + f(K/Mg)]/4
Ca index = [f(Ca/N) + f(Ca/P) − f(K/Ca) − f(Mg/Ca)]/4
Mg index = [f(Mg/N) + f(Mg/P) − f(K/Mg) + f(Mg/Ca)]/4.

The functions were calculated using two equations:

$$f(N/K) = [(N/K)/(n/k) − 1] (1000/CV) \text{ when } N/K > n/k, \text{ and}$$
$$f(N/K) = [1 − (n/k)/(N/K)] (1000/CV) \text{ when } N/K < n/k,$$

where capital letters refer to the nutrient concentrations of the sample tissues, lower case letters to the concentrations of the reference norms, and CV to the coefficient of variation of the concentration-ratio norms.

Reference norms (means and CV) used for sunflower were those of Grove and Sumner (1982): n/p, 12.80, 13; n/k, 0.125, 21; n/ca, 0.75, 29; n/mg, 6.55, 29; k/p, 7.86, 31; p/ca, 0.24, 30; p/mg, 0.52, 33; k/ca, 0.92, 49; k/mg, 4.18, 49; and ca/mg, 2.18, 20, respectively. The calculation of DRIS indices, though slightly modified, were analogous to those for corn.

Results

When considering the effects of VAM fungi on plant nutrition in this experiment (Table 1), one must keep in mind that nutrient levels in the soil were low for N and Ca, and high for P, K, and Mg. Although the same soil was used for all plants, VAM effects modifying plant response to the soil were different in several instances. The

Table 1. Leaf nutrients in plants colonized by the VAM fungi *G. etunicatum* (Ge), *G. pallidum* (Gp), *G. mosseae* (Gm), their mixture (Mix), or in non-VAM controls

Treatment	Nutrient (g kg⁻¹)				
	N	P	K	Ca	Mg
Native corn					
Ge	24.2a	1.46c	36.2a	6.36a	1.62a
Gp	10.2b	1.56bc	43.6a	3.26b	1.66a
Gm	10.9b	1.76a	44.5a	3.42b	1.60a
Mix	9.4b	1.76a	43.4a	3.34b	1.38a
Control	10.5b	1.61ab	37.5a	3.60b	1.48a
P-value	0.0001	0.0139	0.1452	0.0001	0.5201
Hybrid corn					
Ge	22.8a	1.54c	35.8b	5.20a	1.02c
Gp	13.1bc	2.33ab	41.6ab	4.08b	1.38b
Gm	9.2cd	2.16b	44.3a	3.32c	1.24bc
Mix	18.2ab	2.88a	35.9b	3.22c	1.48b
Control	8.6d	2.61ab	41.9ab	5.12a	2.64a
P-value	0.0001	0.0004	0.1033	0.0001	0.0001
Sunflower					
Ge	20.5b	3.05b	36.3a	5.88b	3.44b
Gp	18.8b	3.58a	38.0a	9.86a	4.54a
Gm	16.1b	3.12ab	33.7a	9.94a	4.54a
Mix	36.5a	3.20ab	38.2a	8.56a	3.16b
Control	21.1b	3.06b	38.3a	9.70a	3.68b
P-value	0.0001	0.0648	0.6522	0.0003	0.0010

Numbers are the means of five replications, and (P<0.05) those followed in the column by the same letter are not significantly different

linear portion (3 highest inoculum concentrations) of regression lines, which related the inocula to infectivity (preliminary experiment), were used to determine the amounts of inocula needed to produce uniform levels of infection by each of the VAM fungi or their mixture (Fig. 1).

Native corn

In native corn, VAM colonization did not affect K and Mg concentrations (P>0.05) relative to the nonVAM control. The levels of N and Ca in the Ge-colonized (Ge) plants, however, were not only higher as measured by statistical significance (P<0.05), but were also makedly greater in magnitude (biological significance) than in the controls. None of the measured nutrient concentrations in the Gp- and Gm-colonized (Gp and Gm) plants were significantly (P>0.05) different from the controls, and the plants colonized by a mixture (Mix) of the three inocula did not reflect the effects on N and Ca produced by Ge alone.

In support of the strong effects of VAM fungi generally observed on P nutrition (Stribley 1987), differences between leaf P of the VAM treatments were observed in native corn, even at high soil P. Levels of P were lower (P<0.05) in the Ge plants than in the control, and also in the Ge and Gp plants compared to the Gm and Mix plants. This indicates a differential effect of VAM fungi on plant nutrient-uptake capabilities and the possibility of an exclusion mechanism mediated by some of the VAM fungi when soil P is high. The similarity in P levels of the Gm and Mix plants indicated an appreciable contribution of Gm in the mixed inoculum in this host, in spite of its low levels of root colonization (Table 2).

Hybrid corn

The effects of Ge on hybrid corn were similar to those in native corn, in that N concentration was increased and P inhibited relative to the control (Table 1). However, Ge had no effect on Ca concentration, while in all other treatments Ca was lower than in the control. Unlike in native corn, N concentration in Mix was more than twice as high as in the controls, and second to that of Ge. The N effect in Mix was related to the greater development of Ge in the hybrid vs. the native corn plants (Table 2), suggesting either that the host cultivar influences preferential development of one or the other component of its set of

Table 2. Root colonization by the VAM fungi *G. etunicatum* (Ge), *G. mosseae* (Gm), *G. pallidum* (Gp), or a mixture (Mix) of the three species

Plant	Fungus			
	Ge	Gm	Gp	Mix
		(%)		
Native corn	26 ± 3	5 ± 1	65 ± 4	24 ± 5
Hybrid corn	35 ± 3	6 ± 1	50 ± 7	30 ± 3
Sunflower	29 ± 8	15 ± 4	53 ± 6	25 ± 3

Numbers are means and SE of five replications

endophytes, or that it can respond selectively to different endophytes. The N response in the Mix hybrid-corn treatment may also have been affected by Gp, whose single-species treatment had higher N levels than the control.

The Mg effect was another example of differences in response of the two corn cultivars to VAM colonization: in native corn the fungi did not affect Mg nutrition, while in the hybrid all VAM treatments had lower Mg concentrations than the control. Patterns of K nutrition were similar in both corn cultivars in that fungal treatments did not vary significantly from the controls (probably reflecting the high soil K levels), though there were differences between K levels among fungal treatments in the hybrid, but not in the native corn.

Sunflower

In sunflower, unlike in corn, Ge did not affect N and P but lowered Ca (Table 1). Uptake of P and Mg were enhanced by Gp, and that of Mg by Gm. The concentration

on N in Mix sunflower was markedly higher (73%) than in the control, although none of the individual VAM treatments differed significantly from the control. This effect is different from that observed in the corn cultivars, where increases in a Mix-plant nutrient level could be related to a similar increase in a single-inoculum plant. We are not aware of a previous report of a similar datum in the literature. The mechanism of this effect is not known.

DRIS analysis

In general, the response to VAM colonization, judged by leaf nutrient concentrations, was most diverse in the hybrid corn and least so in sunflower, suggesting host-plant influence on VAM effects. The magnitudes of nutrient concentrations (Table 1) were mirrored by those of the DRIS indices (Table 3). High and low numbers within a plant-fungus treatment group corresponded to each other for the 2 methods of evaluation. An advantage of the DRIS approach became evident upon ranking the nutrient indices within the plant-fungus response groups (Table 4). Since more negative DRIS indices (Table 3) signify greater nutrient deficiency, ranking of the indices predicts the order of nutrient requirement. Thus, DRIS permitted an evaluation of the relative order of nutrient demand (vs the control) as affected by each fungus for each plant, while conventional nutrient analysis served only to indicate individual, unrelated changes in nutrient concentration.

The comparisons showed K sufficiency to be at such a high level that it was not affected by any of the VAM treatments vs the control (Table 4). Nitrogen status was enhanced by Ge in all three plants and by Mix in sunflower. For P, Mix was associated with a positive shift in native corn and a negative shift in sunflower, while Ge increased the relative P deficiency in hybrid corn. Most of the fungal treatments in native corn were most deficient in P, while those of hybrid corn were most deficient in Mg. The most pronounced effect on Ca was in the Ge-sunflower combination. While the magnitudes of individual treatment effects were delineated equally well by both conventional nutrient analysis and DRIS (Tables 1 and 3), DRIS comparisons (Table 4) provided additional information for the selection of individual VAM fungi or their combination by outlining the relative order of specific nutrient requirements and indicating differences in nutrient balance as influenced by the endophytes (Table 3).

Table 3. Leaf nutrient indices of VAM and non-VAM plants calculated by DRIS

Treatment	DRIS nutrient index					Nutrient balance
	N	P	K	Ca	Mg	
Native corn						
Ge	10	−26	24	10	−18	88
Gp	−6	−15	37	−10	−6	74
Gm	−6	−10	35	−9	−10	78
Mix	−9	−7	36	−7	−13	72
Control	−6	−10	29	−3	−10	58
Hybrid corn						
Ge	13	−17	30	9	−35	104
Gp	−5	3	25	−4	−20	58
Gm	−12	5	34	−8	−19	78
Mix	3	13	18	−17	−17	68
Control	−35	8	14	7	6	70
Sunflower						
Ge	−9	6	40	−19	−18	92
Gp	−29	4	40	−4	−11	88
Gm	−34	4	39	2	−11	90
Mix	6	2	23	−5	−26	62
Control	−13	0	34	−2	−19	64

Treatments as in Table 1. Negative numbers designate nutrient deficiency. Nutrient balance is calculated as the sum of the numbers regardless of sign

Table 4. Nutrient rankings within each plant-fungus grouping according to their respective DRIS indices. The most negative DRIS index corresponds to the greatest relative nutrient deficiency within that grouping

Fungus	Order of nutrient deficiency		
	Native corn	Hybrid corn	Sunflower
Ge	K < N = Ca < Mg < P	K < N < Ca < P < Mg	K < P < N < Mg < Ca
GP	K < N = Mg < Ca < P	K < P < Ca < N < Mg	K < P < Ca < Mg < N
Gm	K < N < Ca < Mg = P	K < P < Ca < N < Mg	K < P < Ca < Mg < N
Mix	K < Ca = P < N < Mg	K < P < N < Ca = Mg	K < N < P < Ca < Mg
Control	K < Ca < N < Mg = P	K < P < Ca < Mg < N	K < P < Ca < N < Mg

Treatment designations are as in Table 1

Interactions

The importance of host-endophyte combination in plant nutrition is underscored by the highly significant plant and fungus effects and interactions of the analysis of variance for four of the five nutrients evaluated (Table 5). This showed that the VAM fungi modified plant nutrient status regardless of soil nutrient status, and that the host plants, in turn, modified fungal effects. To emphasize this point, the meaning of plant-fungus interactions is illustrated in detail for N (Fig. 2) and P (Fig. 3). The data points in these figures represent different data sets and are connected only to emphasize the trend in the changes between interactions.

Since interaction measures the failure of the effect of one factor to be the same for each level of the other factor, it may express itself as a difference in the magnitudes or directions of the responses. Both types of response are shown graphically in the plots of variables (plant or fungus) vs the two response scales used (nutrient concentration or DRIS index). For N (Fig. 2), 'plant-factor' responses diverged both in magnitude and direction with changes in the 'fungus factor' (Fig. 2A), while the fungus factor clearly reversed in direction with changes in the plant factor for Ge and Mix (Fig. 2B). Similar trends were observed for P concentrations (Fig. 3A and 3B). Deviations in the patterns of DRIS interactions (Figs. 2C, 2D, 3C, 3D) from the trends as expressed by nutrient concentrations (e.g. Fig. 3A vs C) were due to the property of DRIS to indicate relative, rather than absolute, nutrient data. Such differences between the methods of evaluation may accentuate and clarify the effects observed (Fig. 2B vs D).

Discussion

Information on differential responses of plants to the various mineral elements should be beneficial for overcoming particular nutrient problems and for developing plants with more efficient nutrient utilization (Clark and Brown 1974). This point was emphasized again (Brown and Jones 1977) in recommending that plants be selected or bred for adaption to problem soils, in preference to a massive use of fertilizers to change the soil to fit the plant. While recent trends seem to prove them right about soil chemistry, they did not consider soil biology (Linderman 1988b) as a factor in matching plants with soils.

As data by us and others show, VAM fungi are an important component of the soil, since they colonize the roots of virtually all crop plants with diverse effects on plant nutrition. Due to the diversity of these effects, selection mechanisms need to be developed before VAM fungi may be used effectively in fitting plants to soil. This

Table 5. Analysis of variance of host-plant and VAM-fungus effects on macronutrients in VAM associations

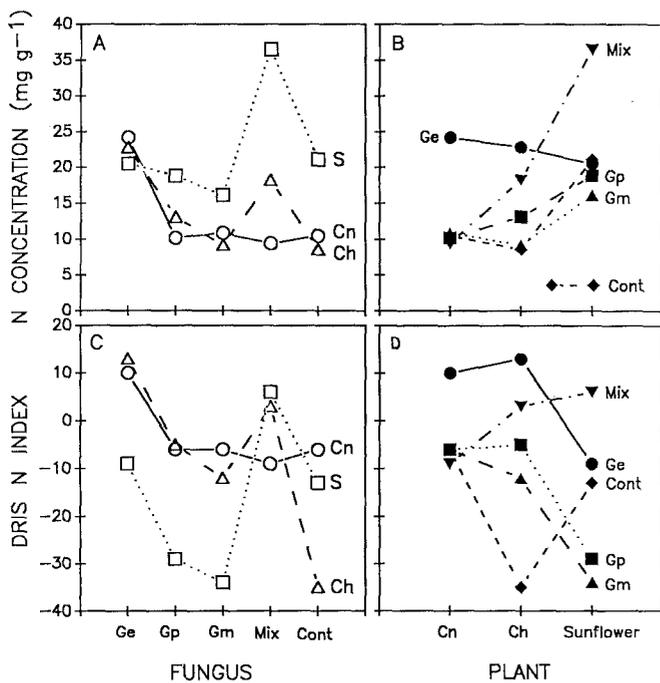| Nutrient	Effect		
	Plant	Fungus	Interaction
N	0.0001	0.0001	0.0001
P	0.0001	0.0001	0.0015
K	0.0430	0.1597	0.1463
Ca	0.0001	0.0005	0.0001
Mg	0.0001	0.0001	0.0001

Numbers denote P-values

Fig. 2A–D. Fungus-plant interactions for nitrogen. Interactions between the factors are represented graphically for each factor with N concentration and the DRIS N-index as response variables
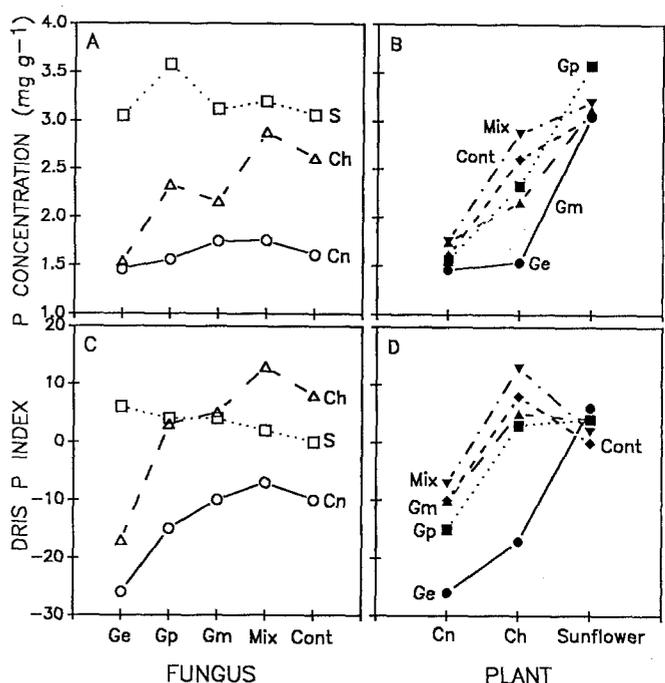

Fig. 3A–D. Fungus-plant interactions for phosphorus. Interactions between the fators are represented graphically for each factor with P concentration and the DRIS P-index as response variables

selection process should be able to determine the compatibility of the fungi with both host plant and host soil, as well as its applicability to the resolution of specific problems in plant nutrition, such as the alleviation of a nutrient deficiency or toxicity, or a combination of these conditions.

With the present data for example, Ge, when grown with native corn, should be further tested to determine its effects on improving N or Ca nutrition in the field, or in alleviating P toxicity (Tables 1, 3). However, the different responses by sunflower to this isolate makes it clear that inferences may not be drawn from one host-endophyte combination to another. The same conclusion probably applies to the host soil too, since soil type influences the development of the VAM fungus and the responses of the host plant to the fungus as well (Bethlenfalvay et al. 1985; Lambert et al. 1980). The present results are therefore applicable only to the soil from which they were obtained, and may be different in another soil because of the abiotic nature of that soil and because of interactions with its biota (Linderman 1988c) and competition with its native VAM fungi (Hetrick and Wilson 1990).

Conclusions

The advantages offered by VAM fungi in supplementing chemical soil treatments are well known, and procedures and principles for the selection of existing isolates have been repeatedly proposed (Abbott and Robson 1982; Medina et al. 1988). Yet, we are still not aware of reports of large-scale selection efforts for naturally occurring VAM fungi, or of the development of specific-purpose VAM-fungal strains by directional selection for subsequent use in alleviating specific nutritional plant disorders on a commercial scale. The nutrient-concentration and DRIS analyses of VAM effects on plant nutrition, as presented here, demonstrate (1) the need for determining the specific effects each VAM-fungal isolate has on each prospective host plant prior to utilization in the field, and (2) the potential for the use of these organisms in improving fertilizer use-efficiency.

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