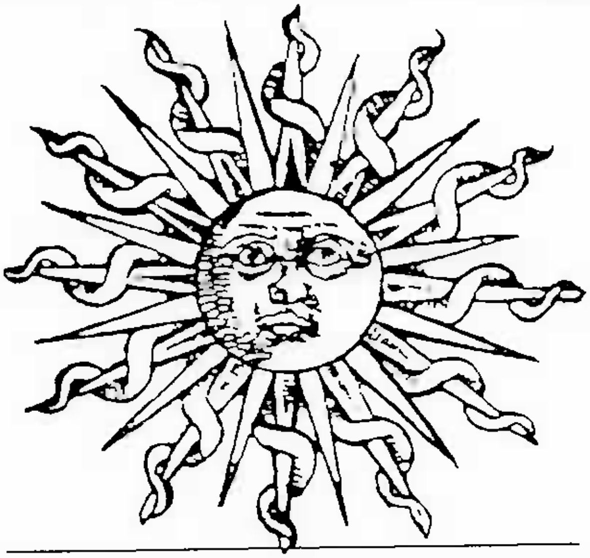

Arid Lands

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Mycorrhizae in Stressed Environments: Effects on Plant Growth, Endophyte Development, Soil Stability and Soil Water

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ABSTRACT

Vesicular-arbuscular mycorrhizal (VAM) fungi are involved in the formation or preservation of soil structure and in the uptake of bound soil water by plants. Together with their well-known function in mediating and enhancing mineral nutrition of their host plant, they are thus agents of resource conservation as well as of crop production. Under severe photosynthate stress, such as heavy grazing, VAM colonization is impaired. When this occurs, an interrelated chain of events may be initiated with adverse effects on agricultural plant-soil systems.

INTRODUCTION

Almost all agricultural plants form symbiotic associations with vesicular-arbuscular mycorrhizal (VAM) fungi which colonize plant roots (mycorrhiza = fungus root). External fungal hyphae reach soil microsites outside the rhizosphere and extend the depletion zone for immobile nutrients around the root. By making these nutrients available to the host plant, VAM fungi can enhance plant growth dramatically in nutritionally marginal soils (1). Perhaps for this reason, VAM research has focused in the past on P-nutrition effects. More recent work shows that VAM fungi are involved in virtually all aspects of interchange between plant and soil (2, 3).

This interchange, a stabilizing factor in the plant-soil system, attains additional significance in direct proportion to the degree of fragility of the ecosystem under consideration (4, 5). Fragility is influenced by stress, as exemplified by the condition of semidesert grasslands in North America, where frequent drought and continual abuse by man has resulted in accelerated soil erosion, brush invasion and reduced forage production (6).

The role of the VAM symbiosis in reacting to and counteracting stresses in semi-arid grasslands under grazing stress is complex (7-13). As obligate symbionts, VAM fungi are directly affected by the ability of their host plants to supply them with photosynthetically fixed carbon (14). If adversely affected by overgrazing (8), deterioration of the fungal component of the mycorrhiza may trigger a little-understood chain of reactions. These reactions are based on the dual function of the fungus as a pipeline for mineral nutrients to its host plant and as a conduit of carbon from the host to the soil (15-18). This latter function is perhaps the least understood (19), and involves mutual trophic interchange of VAM fungi with the soil biota (18). There is increasing evidence that the products of this interchange (extracellular polymers) are instrumental in stabilizing soil by aggregate formation (20, 21). Soil structure influences water-holding capacity and moisture availability (22). The interaction between the availability of water and phosphorus (23) involves VAM fungi in the uptake of both (24, 25). While an alleviation of drought stress in the presence of VAM fungi has been attributed to the effect of soil moisture on P diffusion in the soil (25), evidence is emerging that VAM fungi may be able to utilize soil water not available to the non-VAM plant (26), and that the amount of this water is proportional to plant growth enhancement by VAM fungi (27).

Thus, the level of stress under cultural control (for example, grazing) may have effects on the stressed system (plant-microbe-soil association) that are not immediately obvious. It is conceivable that critical threshold levels of utilization may be exceeded, even under careful management, if key interactions between the biotic and abiotic components of the system are not fully understood and considered. If the system is subject to stress not under control (for example, drought) as well, the effects of cultural stress will be aggravated. Arid and semiarid lands occupy a substantial portion of the North American continent. Since much of the land available for agricultural expansion (or rehabilitation) falls into this category, there has been increasing interest in understanding and identifying mechanisms that have evolved to enable plants to cope with these stresses (28). The mycorrhizal plant symbiosis is such a mechanism. We suggest that the use of VAM fungi may be developed as a technology to improve water utilization practices and to help reduce catastrophic losses of topsoil in agricultural lands. This is important, because erosion rates exceed acceptable levels on more than 200 million acres in the United States alone (29).

ASPECTS OF MYCORRHIZA-ENVIRONMENT INTERACTIONS

Grazing Effects on VAM Development

General Considerations. The response of plants to nutrients is of interest in the management of semiarid rangelands (30, 31). While N is frequently the major limiting factor (32), the role of P is also important (33) and complex, especially in semiarid environments (34) due to interactions between water and P availability (23). While VAM fungi generally enhance plant growth, growth depression of the host can also result from VAM colonization (35, 36). This may occur at available soil P levels lower than those inhibiting VAM-fungal colonization (37), but higher than those favoring growth enhancement (38). At such soil P levels, the host is capable of meeting its P requirements without enhanced uptake by the endophyte, but since the latter is obligately dependent on its host for photosynthate, it becomes a parasite depressing plant growth (36). When the availability of photosynthate is lowered, VAM colonization is inhibited (14, 39). Grazing may thus affect plant nutrition and growth directly, or indirectly through its effects on the VAM-fungal symbiont. The interaction is complex, as it may depend on the intensity of grazing and on the levels of available soil P at the time of grazing.

Photosynthate stress has an effect on N_2 fixation by legume root nodules similar to that on VAM fungi. Defoliation has been shown to decrease nodule mass and activity (40), while higher rates of N_2 fixation enhance photosynthesis (41). The high P requirement of N_2 fixation makes this process sensitive to P availability, a condition satisfied by VAM fungi (42). Thus, when nodulated legumes form part of a grazing system under N and P stress, interactions among the three symbionts of the legume association must be considered. When N and P stress are relieved through fertilization, colonization of host plants by both microsymbionts is inhibited (43). Long-term effects of continuous inhibition of the VAM mycoflora are not well known.

Colonization of Grasses by VAM Fungi: Field Observations. Surveys of the effect of grazing pressure on the development of the VAM symbiosis were conducted at three sites during the summer of 1982. The sites are characterized as arid to semiarid, with annual average rainfall ranging from 400 millimeters at the Mandan, North Dakota, site, to 200 to 300 millimeters at Medell Flat, near Reno, Nevada, to 250 millimeters at the lower elevations of the Santa Rita Experimental Range near Tucson, Arizona. The communities, characterized as northern mixed prairie (44), big sage brush-grassland (45) and a mesquite-dominated, semidesert grass-shrub ecosystem (46), serve as experimental grazing areas and contain permanent grazing enclosures. Samplings of the vegetation were made from these enclosures (Table 1) and from grazed areas immediately adjacent to the enclosures.

The results showed that moderate grazing produced no significant differences in VAM-fungal colonization compared to no grazing at the Mandan site. At all three sites, heavy grazing resulted in a significant decrease in colonization in most of the grass species sampled. The degree of inhibition varied, with one group of plants at the Mandan site showing < 40 percent, others > 50 percent inhibition. A similar pattern of variation was observed at the Reno site, where colonization levels without grazing were generally higher than at Mandan. An interesting effect of grazing at the Tucson site was the significant decline in colonization of roots intensely colonized in the ungrazed condition, but no change when colonization of the ungrazed plants was low. This pattern was also found in the data obtained at Mandan. Colonization of the only two annual grasses contained in this survey, *Bromus tectorum* and *Panicum capillare*, was markedly reduced by grazing.

Table 1. Colonization of grasses by VA mycorrhizal fungi as a result of grazing at different arid sites.

Site/Species	Colonization (%)[a]			Inhibition[c](%)
	Heavy grazing[b]	Moderate grazing[b]	No grazing[b]	
Mandan, North Dakota				
Agropyron smithii	48^{x}	71^{y}	75^{y}	36
Bouteloua gracilis	35^{x}	41^{xy}	54^{y}	35
Koeleria cristata	38^{x}	83^{y}	87^{y}	56
Poa compresa	38^{x}	52^{y}	54^{y}	30
Stipa comatu	38^{x}	71^{y}	85^{y}	55
Stipa viridula	32^{x}	82^{y}	90^{y}	65
Reno, Nevada				
Agropyron desertorum	63		88*	28
Bromus tectorum	33		76*	57
Oryzopsis hymenoides	40		86*	53
Sitanion hystrix	53		83*	36
Stipa comata	33		82*	60
Stipa thurberiana	40		88*	55
Tucson, Arizona				
Bouteloua curtipendula	30		33	9
Bouteloua filiformis	40		44	9
Eragrostis lehmanniana	10		12	17
Heteropogon contortus	42		89*	53
Panicum capillare	34		98*	65
Tichachne californica	66		90*	26

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[a] Percent colonization of root length by VAM fungi was determined by microscopic examination of stained root segments on statistically meaningful sample sizes (7). Differences were evaluated by Duncan's multiple range test (Mandan) and student's t-test (Reno and Tucson). Numbers followed by the same letter are not significantly different ($p>0.05$). Asteriks indicate a significant difference ($p<0.05$) between heavy and no grazing.

[b] The absence of grazing pressure indicates sampling from permanent cattle exclosures. Moderate grazing at the North Dakota site represents levels comparable to pre-agriculture conditions. Heavy grazing represents continuous use, or use during the growth season of the rest-rotation cycle preceding this survey.

[c] Inhibition denotes the decrease in root length colonized by VAM fungi due to heavy grazing.

The data are not sufficient to make generalizations. Grasses display considerable variability in their dependence (47) on VAM fungi for maximum growth (11, 48). It is conceivable that any of the following little-understood factors interact in determining the responses noted: the physiology of host-endophyte preference (49), the response of host plant to photosynthesis stress (28), the environmentally conditioned dependence of host on endophyte (50, 51), and the source-sink relationships of phosphorus and carbon exchange between the symbiotic partners (14, 38). Finally, grazing pressure on individual grass species within the same sampling site may vary due to herbivore predilections and plant resistance (52). It appears, however, that the severity of stress impacts on the development of the symbiotic association (8). Possible results of this impact on the environment, as mediated by mycorrhizae, are beginning to be delineated in the literature (2, 25). They include, in addition to adverse effects on plant nutrition, such complex ecological phenomena as competition (53), succession (54), soil stability (19, 21, 55) and water utilization (56-58).

The Effect of VAM Development on Soil Structure

General Considerations. In contrast with the voluminous literature on the beneficial effects of VAM fungi on plant growth, only a few studies have so far considered the impact of the mycorrhizal plant on the soil. This literature was briefly reviewed by Thomas et al. (19). The authors cited agree that the counterflow of nutrients from plant to soil is facilitated by the presence of mycorrhizal fungi, and that the effect of this enhanced flow is measurable in terms of increased cohesion of soil particles. Approaches and methodologies, however, differ from author to author, indicating a need for interdisciplinary collaboration on this problem area by plant and soil scientists and soil microbiologists.

Interactions between the Fungus-Root and Soil Aggregation: Experimental Demonstration. The dependence of plants on their VAM endophytes for maximal growth under a given set of conditions varies, and increases with the coarseness of the host's root system. To demonstrate VAM effects on soil aggregation, we chose onion (*Allium cepa* L.), a plant highly dependent on its fungal endophyte, and grew it with or without a VAM fungus (*Glomus macrocarpum* Tul. and Tul.) for a 5-month test period in a sieved (3-millimeter), silt-clay loam soil (Typic Xerorthent) in greenhouse pot cultures (19). Plants, soil and soil fungi were evaluated periodically (20 harvests) for changes in the following parameters (Figure 1, Table 2): plant biomass, percent VAM-fungal colonization of roots (59), fungal density in the soil (15), soil aggregation (Figure 1), soil bulk density, pore-size distribution (60) and permeability (61). Predicted values for all parameters at the start and end of the test period were obtained from regression analyses of the actual data vs. time. The differences between these initial and final values were calculated as percentages of change (Figure 1, Table 2).

A qualitative representation of actual plant and fungal biomass and of the mass of soil aggregates presents a comparison of the VAM and non-VAM plant-soil systems at the last harvest (Figure 1). Lower CO_2-fixation and photosynthate-transfer capabilities of the markedly smaller shoots and roots of non-VAM plants strongly suggest that their input of reduced C to the soil was commensurately smaller than that of VAM plants. Carbon input to the soil occurs as exudation from roots and hyphae, and through the decomposition of plant and fungal materials. This carbon is utilized by soil microorganisms to increase their biomass and to produce extracellular polymers that cement soil particles and bind small aggregates into larger units (17, 62, 63). This was apparent in the soil of VAM plants (Figure 1) whose growth was enhanced markedly (400 percent, dry mass) as a result of colonization by *G. macrocarpum*. The relative abundance of the largest aggregates ($<$ 2.0 millimeters) increased while that of most other smaller particles decreased significantly with time (Figure 1). In contrast, only the smallest particles ($<$ 0.12 millimeters) increased in abundance in the soil of non-VAM plants, while the larger aggregates, as a class, tended to decrease. The slopes of regression lines for the change in the abundance of the largest and smallest aggregates with time were significantly ($p<0.05$) different for VAM and non-VAM plants. Thus, in the presence of the VAM fungus the soil aggregated, while in its absence there was a trend toward disaggregation.

The conclusion from the analysis of aggregate size distribution was confirmed by changes in pertinent soil physical characteristics. As a function of time, only the soil of non-VAM plants

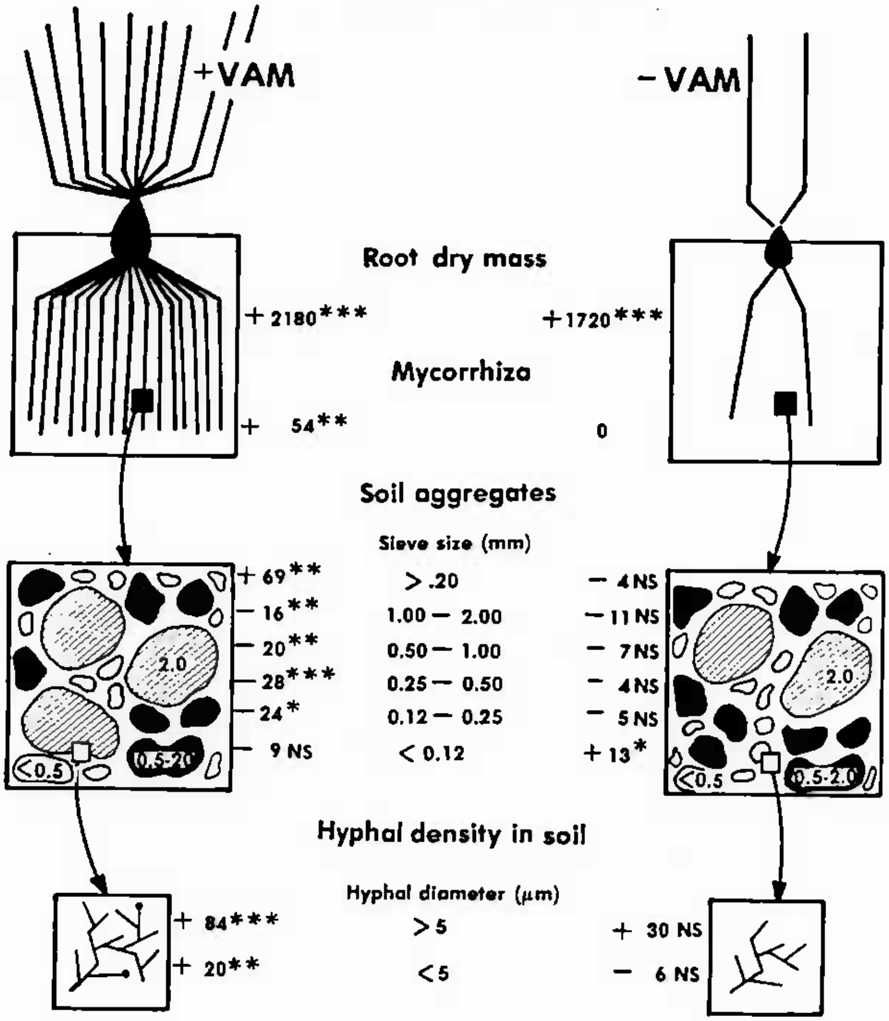

Figure 1. A qualitative representation of actual plant dry mass, fungal density (m hyphae/g soil) and relative abundance of soil aggregates (% of total soil) in VAM and non-VAM plant-soil systems at the end of a 5-month test period. Fungal hyphae > 5 μm in diameter are primarily those of the VAM fungus, while those < 5 μm belong primarily to saprophytic soil fungi. Numbers (other than dimensions) represent % changes in parameters between beginning and end of the test period. The significance of regression analyses for each parameter changing with time is indicated as ***, $p < 0.01$; **, $p < 0.05$; and *, $p < 0.10$; NS, $p > 0.10$. Soil aggregation was determined at each harvest when soil moisture content of the pot cultures was 16%. After removing roots and comminuting (< 10 mm) the soil, water-stable aggregates were separated by gentle, mechanical agitation under water using five stacked sieves with 2.0, 1.0, 0.5, 0.25 and 0.12 mm openings. The mass of aggregate fractions collected from each sieve, and that passing through the smallest sieve openings, was expressed as a percentage of total sample mass placed on the sieve stack.

Table 2. Changes in physical characteristics of soils planted with VAM and non-VAM onions.

Correlated parameters[a]	% change[b] VAM	% change[b] Non-VAM
Bulk density vs. time	0.4 NS	8.2**
Permeability vs. time	5.9 NS	-30.0*
Pore volume vs. bulk density		
Pore size > 75	-24.7 NS	-60.0***
< 75	3.4 NS	12.6***

[a] Undisturbed soil core samples were taken to determine bulk density, pore-size distribution and permeability. The proportion (% total void volume) of soil pores larger or smaller than 75 μm was estimated by saturating and subsequently equilibrating samples at 400 mm water suction according to the capillary model (60). The relative abundance of these large and small voids was calculated and correlated with soil bulk density. Permeability (saturated hydraulic conductivity) of the samples was determined using the falling head technique (61).

[b] Numbers represent the percent change in parameters between initial and final or minimum and maximum values during the test period, as computed from regression analyses. The significance of the regression lines is given as ***, $p < 0.01$; **, $p < 0.05$; *, $p < 0.10$; NS, $p > 0.10$.

increased significantly in bulk density and decreased in permeability (Table 2). The relative abundance of small pores (<75 millimeters) that made up 85 percent of total pore volume increased significantly with bulk density, while that of the large pores decreased. These findings indicate a change with time to a more compact, less porous condition in the soil of non-VAM plants. Apparently, the mycorrhizae (hyphae and roots) tended to counteract the slaking effects caused by periodic wetting and drying. Slaking, a process of disaggregation and dispersal of soil particles, is known to cause a reduction in infiltration and porosity (18). As the stability of pores and particles is essential for optimum growth of plants, we discern a closed chain of cause-effect relationships in the function of VAM fungi in the plant-soil system: the fungi enhance plant growth through increased mineral uptake from the soil; the larger plant has a greater C input into the soil which encourages the activity of the microbiota; the products of microbial metabolism improve soil structure; and better soil structure permits better plant and VAM-fungal growth.

The extent to which the fungal endophyte alone, apart from the root, facilitates the formation of stable aggregates cannot be inferred from our results. The proliferation of hyphae in macroaggregates (Figure 2) emphasizes fungal contributions to aggregate stability. Greater hyphal density in the soil of mycorrhizal plants (Figure 1) also suggests such a role. The effects of soil aggregation in the present experiment may be ascribed to both symbiotic partners, since significant correlations of the increase of large aggregates (>2.0 millimeters) with both root ($p<0.01$) and hyphal ($p<0.10$) development were observed (19). The influence of VAM fungi on particle-size distribution in our experiment is reminiscent of distributions in the field under different cropping systems, where a marked increase in large aggregates with increasing root density can occur over a long period of time (64). Our results show that even over a short period of time VAM fungi can have a positive effect on soil aggregation directly and/or mediated through enhanced host-plant growth.

Mycorrhizae and Soil Water

General Considerations. The capacity of soil to hold water depends on its state of aggregation, and this, in turn, is affected by the soil microbiota (18, 21, 22, 65, 66). As an interface of nutrient-exchange between plant and soil, VAM fungi participate in the developmental processes of both (56). In this capacity, they are apparently involved in water uptake by the plant (24, 26, 27, 57, 58, 67-72) and thus influence physiological processes that depend on plant water status (73, 74).

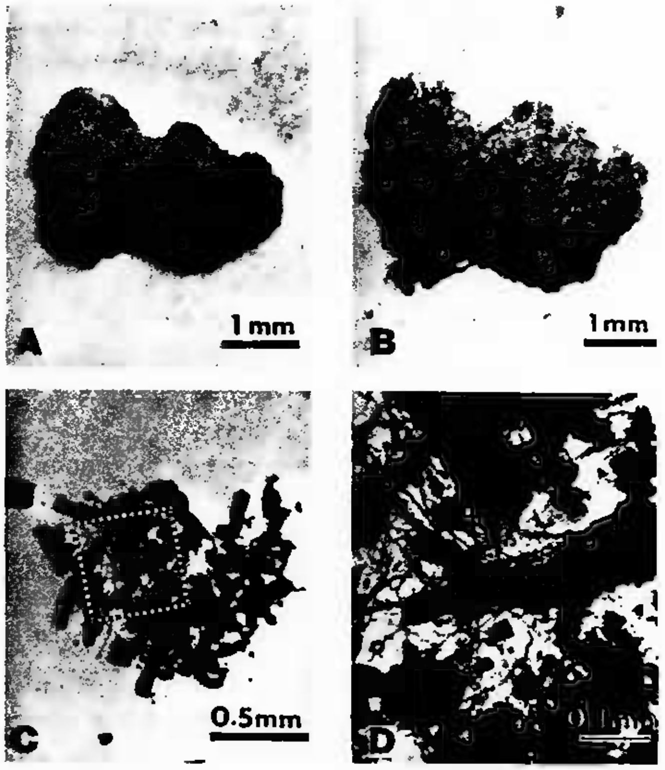

Figure 2. Fungal hyphae in soil aggregates. A. Dry aggregate. B. Same aggregate rapidly wetted. C. Same aggregate after mild ultrasonication. D. Marked area of C enlarged, showing hyphae.

It has been argued that when moisture is limiting, enhanced water uptake by VAM fungi could be detrimental. A larger plant would deplete soil water supplies more rapidly (75) and then succumb to drought or require increased rates of irrigation. However, recent findings suggest (27) that VAM fungi may be able to exploit soil water below the conventional permanent wilting potential (76), that is, bound water, which is not available to the non-VAM plant.

Bound Soil Water, VAM Fungi and Plant Growth: Experimental Demonstration. When grown in soils of different texture, water-holding capacity and water retention (Northern California soils of series Corning, Balcom and Josephine), soybean plants showed markedly different growth responses to VAM fungi (27). This growth response, which ranged from 0 to > 300 percent, was not influenced by nutrient availability, but was correlated significantly (Figure 3) with percent soil water at -1.5 megapascals. Thus, growth enhancement by VAM fungi increased with higher levels of bound soil water.

The suggestion of an involvement of VAM fungi in the uptake of bound soil water was confirmed in a separate experiment. Soybean plants were grown in Balcom soil under a moist or dry watering regime using the fungus *G. macrocarpum* as the endophyte. Non-VAM plants used in comparison received phosphorus fertilizer for optimum growth. Fungal colonization was significantly ($p<0.05$) higher under the wet regime (plants rewatered at field capacity) than under the dry regime (plants rewatered at wilting). After four drought cycles the soil was allowed to dry, and plants were harvested when they failed to recover from wilting after being placed in an incubator at 100 percent relative humidity. Soil water content of VAM soil was significantly lower than that of non-VAM soil when fungal colonization was high, even though the root mass of non-VAM plants

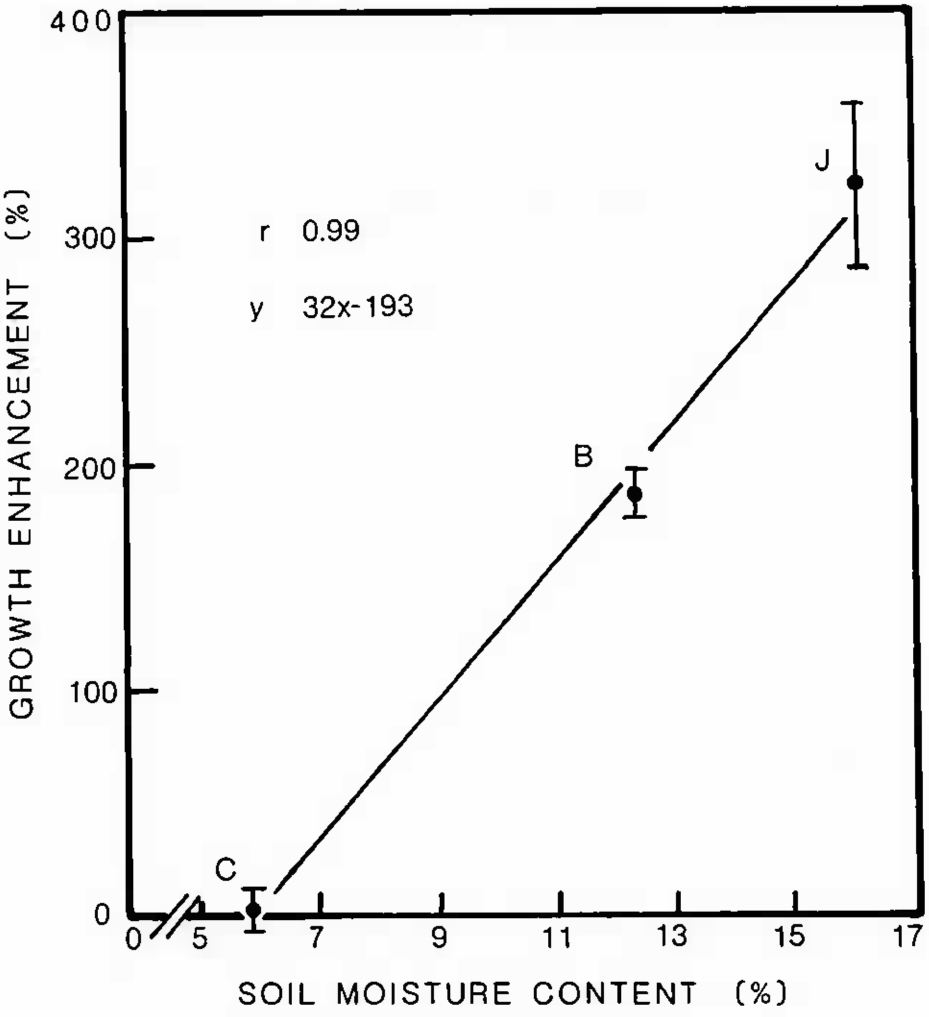

Figure 3. Growth enhancement of soybean plants by the vesicular arbuscular mycorrhizal (VAM) fungus *Glomus mosseae* relative to non-VAM plants as a function of bound soil water, in three northern California soils (Series Corning-C, Balcom-B and Josephine-J). Soil water contents were determined at -1.5 MPa.

was markedly greater than that of VAM plants (Table 3). Under the dry regime, with a lower intensity of colonization, the difference between the water contents of VAM and non-VAM soils was not significant. Significant correlations were also found between the soil moisture contents and percent VAM colonization of the individual replicates for both moisture regimes (Figure 4).

The possibility of a relationship between the uptake of bound soil water and VAM fungi needs much further testing with different host-endophyte combinations, soils, and under various environmental conditions. If substantiated by further evidence, significant applications in agriculture may be envisioned. Physiologically, fungus-mediated uptake of bound soil water would be analogous to the uptake of phosphorus, where the tapping of supplies not available to the plant alone results in a positive growth response (77). The interaction between phospate supply and soil moisture (23) makes a separation of the two phenomena difficult (25). The finding of Nelson and Safir (57) that drought-exposed non-VAM plants could not take advantage of additional phosphorus supplies is significant but needs to be further examined with different phosporus sources under different methods of stress imposition. In the meantime, the mechanism of VAM fungi as mediators of plant water uptake remains controversial (56, 58).

Table 3. Soil moisture content and VAM colonization at wilting in soybean plants.

Moisture treatment[a]	Fungal treatment[b]	
	VAM	Non-VAM
Moist (-0.05 MPa)		
Colonization (%)	73.7 ± 1.2[d]	
Soil water content (%)[c]	4.28 ± 0.13	4.52 ± 0.08*
Root dry mass (g)	1.50 ± 0.39	2.80 ± 0.38*
Dry (-1.00 MPa)		
Colonization (%)	59.3 ± 2.7	
Soil water content (%)	4.12 ± 0.25	4.03 ± 0.28 NS
Root dry mass (g)	.86 ± 0.13	1.86 ± 0.24*

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[a] Plants under the moist and dry regimes were rewatered when soil water potentials were at -0.05 MPa (-0.5 bar) or -1.5 MPa (-15.0 bars), respectively, as determined by permanently embedded soil moisture sensors.

[b] Non-VAM plants received a complete nutrient solution, VAM plants the same solution less phosphorus.

[c] Soil water content was determined when wilted plants did not recover upon being placed in a chamber at 100% relative humidity.

[d] Numbers represent means and standard deviation of six replicates. Asteriks denote significance at the 0.05 level, of the difference between VAM and non-VAM plants.

CONCLUSIONS

We perceive VAM fungi as a two-way transport agent between plant and soil. Fungus-mediated uptake of additional mineral nutrients and water by the host results in plant growth enhancement when these supplies in the soil are limiting. Since they are limiting in dry environments as a rule, the fungi are mutualistic symbionts and are perhaps essential to the survival of plants where drought conditions predominate. The more vigorous mycorrhizal plants can produce an excess of reduced carbon compounds. The transport of this carbon to soil microsites not reached by the root alone is facilitated by extraradical VAM-fungal hyphae. Nutrient transport is particularly significant in arid areas, where root density in the soil is low. The soil microbiota is an important sink for carbon derived from photosynthesis, and is instrumental in cementing soil particles into aggregates. This process is apparently accelerated in the presence of VAM fungi, due to the greater carbon source capacity of the VAM-plant canopy and to the increased transport capability of the VAM root system. Soil aggregation affects water-holding capacity. The bound portion of this water may be more completely utilized by VAM than by non-VAM roots.

In order to develop the technology for the use of VAM fungi in soil conservation efforts, many little-known aspects of the physiology and ecophysiology of VAM fungi and of the symbiotic VAM association must be elucidated. Adaptation to soil types, host-endophyte preference, source-sink relationships among symbiotic partners within the association and between the association and the soil, and axenic culture of VAM fungi for commercial production of inoculum are research aspects that need to be addressed in detail before VAM fungi can become a useful tool in the service of agriculture on a large scale.

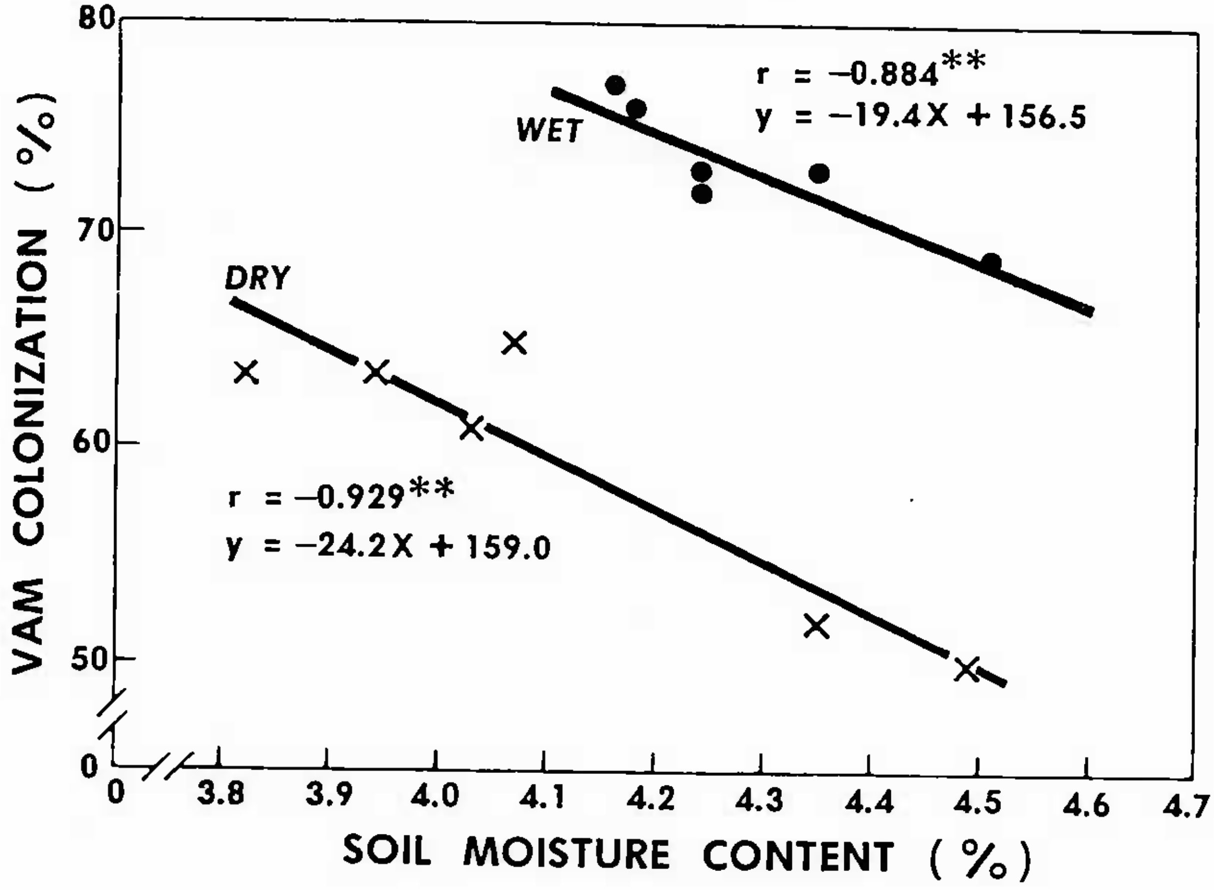

Figure 4. Relationship between the colonization (% root length) of soybean roots by *Glomus macrocarpum* and soil moisture content at permanent wilting.

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