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Separation of Vesicular-Arbuscular Mycorrhizal Fungus and Root Effects on Soil Aggregation

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ABSTRACT

Mycorrhizae influence soil stability, but relative contributions by plant or fungal endophyte to aggregation are little known. We studied the effects of both symbionts together and of each alone on water-stable soil aggregate (WSSA) formation. Split-root soybean [*Glycine max* (L.) Merr.] plants were grown in containers. One side of the split root was colonized by the vesicular-arbuscular mycorrhizal (VAM) fungus *Glomus mosseae* (Nicol. & Gerd.) Gerd. and Trappe; from here the VAM hyphae penetrated through a screen (44- μ openings) to a root-free chamber. On the other side of a solid barrier, the non-VAM portion of the root was in contact through a screen with control soil free of roots and VAM hyphae. Thus, the four treatments, VAM roots (roots and hyphae), VAM hyphae, non-VAM roots, and control, were contained in the same experimental unit. Root length and mass were greater in the VAM-root than in the non-VAM-root chamber, whereas the density of VAM hyphae in the soil was lower in the VAM-root than in the VAM-hyphal chamber. The relative amount of WSSA was highest with VAM roots, lowest in the control chamber, and intermediate and similar with non-VAM roots and VAM hyphae. This incidence of WSSA was lower in all of the chambers at harvest (8 mo.) than in the starting material due to slaking. The composition of WSSA showed that the differences in WSSA between treatments was due to a variable slowing of the slaking process by the mycorrhizae. Non-VAM roots and VAM hyphae had similar effects on soil aggregation.

THE LEVEL OF SOIL AGGREGATION is a crucial determinant of soil structure (Hamblin, 1991). The symbiotic components of VAM-fungi-colonized roots have been shown to be important to soil structure (Jastrow and Miller, 1991; Tisdall, 1991), but the relative

magnitude of their contributions to aggregate stability have not been measured directly. Fungi in general are more effective in binding soil particles than bacteria (Harris et al., 1966). The soil hyphae of VAM fungi are of particular interest in this process, because they comprise the largest portion of the soil microbial biomass (Hayman, 1978) and can penetrate in excess of 90 mm of root-free soil (Camel et al., 1991). Tisdall and Oades (1982) included VAM hyphae in their hierarchical model of soil aggregate structure as a major mechanism for binding microaggregates into macroaggregates, but did not consider that different types of roots may vary in their associations with VAM fungi (Baylis, 1975). Since such differences in the degree of host-endophyte association could contribute differently to the aggregation process, Miller and Jastrow (1990) investigated root and VAM-fungal interaction with WSSA formation in the field. They used a path model relating root lengths and fungal structures of fine and very fine VAM or non-VAM roots to the geometric mean diameter of WSSA. Evaluation of their findings by partial regression analysis indicated that VAM-hyphal effects on the stability of wet-sieved macroaggregates was greater than the effects of fine roots. In contrast, a study (in pot cultures) by Thomas et al. (1986) showed that the contribution of roots to the overall effect was the stronger of the two, based also on regression analysis of root and fungal effects on WSSA formation. However, these authors could not make an unambiguous direct comparison of the effect of roots with and without VAM colonization due to the large difference in the size of VAM and non-VAM plants and in the extent of soil penetration by their root systems.

The purpose of this experiment was to assess the

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Abbreviations: VAM, Vesicular-arbuscular mycorrhizal; WSSA, water-stable soil aggregate; WRRS, Western Region Research Center, WUSA, water-unstable soil aggregate.

effects of VAM roots, VAM mycelia, and non-VAM roots on WSSA formation directly by use of a split-root system in a multi-chambered growth container that permitted measurements on the separated root-system components of the same plant.

MATERIALS AND METHODS

Experimental Unit, Design, and Statistics

Plastic pots (3.8L) were separated into halves by a solid barrier. The halves were divided again by screens (44- μm openings), creating a four-chambered growth container (Fig. 1). Plant root systems were split across the solid barrier and confined by the screens to occupy only two of the chambers. One side of the split-root system was inoculated with a VAM fungus. The screen permitted only the passage of VAM hyphae and soil solution, but not of roots. The soil in the four chambers therefore contained the following components of the root system: (i) VAM roots and hyphae, (ii) VAM hyphae, (iii) non-VAM roots, and (iv) no plant or VAM-fungal contributions, except possibly root exudations. The soil of the fourth chamber was considered to be an internal control for the others. Thus, the four treatments of the experiment were all contained within the same experimental unit: a potted, split-root soybean plant.

The plants were grown in a completely random design. Ten replicates with intact screens at harvest were selected for evaluation; soil and VAM parameters were evaluated for each of the four chambers in all replicates. Analysis of variance, *t*-tests, and ranking by Duncan's multiple-range test (at $P < 0.05$) were used in data comparisons.

Soil and Biological Materials

A calcareous silty clay loam soil (fine-loamy, mixed, thermic Calcixerollic Xerochrept, 12% sand, 68% silt, and 20% clay) of the Balcom series, Yolo County, California, was obtained from the field in an air-dried state and was crushed and sieved to particle size ≤ 3 mm. The sieved soil was mixed with fine (75–250 μm) sand (soil/sand, 2:1 v/v; 1:51 w/w) to reduce swelling and shrinking of the soil during wetting and drying,



Fig. 1. Four-chambered growth container for the separation of Vesicular-arbuscular mycorrhizal (VAM) roots from VAM hyphae (by a 44- μm screen) on one side of a solid barrier, and non-VAM roots from control soil (screen) on the other.

a process that presumably could disrupt VAM hyphae crossing the screens. The soil-sand mix was autoclaved (2 h, 120 °C) to eliminate VAM-fungal propagules. Organic matter content of the soil-sand mix was 10.0 mg g^{-1} .

A nonnodulating isolate of soybean (cv. Clark) was inoculated with the VAM fungus *Glomus mosseae* (Nicol. & Gerd.) Gerd. and Trappe, isolate WRRC no. 1. This isolate was exotic with respect to both host plant and host soil in this experiment. Its conditions of origin were characterized previously (Bethlenfalvay et al., 1983). The inoculum (15 g of dry soil containing ≈ 700 VAM spores and 200 colonized root fragments) was mixed identically into the experimental soil (1.5 kg chamber $^{-1}$). Identical portions of autoclaved inoculum were added to the uninoculated chambers to maintain uniform soil texture. A VAM-free filtrate of the VAM inoculum was applied to all chambers to equalize the nonVAM microbiota (Ames et al., 1987).

Growth Conditions

One seedling, with taproots truncated at 7 d, then grown for 21 d to develop lateral roots, was transplanted into the four-chamber pots with roots equally distributed in soil on the two sides of the solid barrier. Plants were grown for 8 mo in a greenhouse at Albany, CA. Flowers were routinely removed to retard the onset of senescence. The greenhouse was maintained between 18 and 25 °C. Sunlight was supplemented by 1000-W General Electric coated metal halide lamps, providing 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation for 16 h per light period.

Pots were watered from below using nutrient solution, with uptake monitored by pot weight corrected for plant weight as previously determined. Moisture content was taken to saturation ($\approx 24\%$ moisture) during a 3-d period, then allowed to fall to 16 to 19% (mean value for the four chambers) during a 3- to 4-d period. The relative distribution of moisture in the four chambers was monitored by calibrated soil moisture blocks (Model 5201, Soilmoisture Equipment Corp., Santa Barbara, CA; Watermark Model 200, G.F. Larson, Co., Santa Barbara, CA) embedded in the soils of some of the pots. At the end of a watering cycle the soils in the rooted chambers were usually slightly drier than in the nonrooted chambers. Nutrient concentrations in the solution were: 2mM $\text{Ca}(\text{NO}_3)_2$, 1 mM K_2SO_4 , and 0.25 mM MgSO_4 ; micronutrients were equivalent to one-quarter-strength Hoagland's solution.

Sampling and Assays

The soil was watered to field capacity before harvest to equalize soil moisture content in the four chambers. To facilitate uniform drying of the soils in the four chambers, the shoot was excised. The containers were permitted to dry until soil moistures were below the plastic limit (14% water content, see Sowers, 1965) to minimize the artificial formation of WUSA through handling (Kemper and Rosenau, 1986). The soil was removed from the pots, and passed through a sieve (6-mm openings) three times to recover roots and root fragments and to set an upper limit for the size of cohesive soil particles. Soils from all chambers were processed by the same procedure. Slight differences in the friability of soils of rooted or root-free chambers due to residual differences in mean water content (11.8% rooted; 13.1% root free; soil samples oven-dried for 24 h at 110 °C) at harvest were noted nevertheless. As a consequence, passing the soils of the rooted and root-free chambers through the sieve required slightly different compressive forces.

The damp soils were sampled for determination of moisture content, and were then air dried. Roots were washed and blotted, sampled randomly to determine root length (Marsh, 1971) and VAM colonization (staining with trypan blue), and dried (24 h at 70 °C). Hyphal densities in the soil were determined according to Bethlenfalvay and Ames (1987). Hyphal lengths

Table 1. Biological soil parameters as influenced by the vesicular-arbuscular mycorrhizal (VAM) component in each of the four chambered containers (means of 10 replicates).

Parameter	VAM root	VAM hypha	non-VAM root	Control
Root length (m)	179a†		133b	
Colonized root length (m)	111a		1b	
Roots, dry mass (g)	2.2a		1.4b	
Hyphal density (m kg ⁻¹ soil)				
VAM fungi	10.0b	13.0a	4.2c	4.3c
non-VAM fungi	9.2a	8.9ab	8.2ab	7.8b

†Means in each row followed by the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test.

were determined separately for hyphae of diameters greater or smaller than 5 μm ; those of the larger size were adjudged to be VAM (see Ames et al., 1983; Fitter, 1985).

Dry- and Wet-Sieving Procedures

Samples of the air-dried soil were dry sieved (1 min) using a RO-TAP Testing Sieve Shaker (W.S. Tyler & Co., Cleveland, IN). The 1- to 2-mm particle-size fraction was used for wet sieving. Dust from the samples was removed by shaking (15 s) on the 1-mm sieve only. Mean total recovery of all fractions was 99.8%.

Wet-sieving procedures were those described by Kemper and Rosenau (1986), with slight modifications, using a commercially available apparatus (William Heinemann, Twin Falls, ID). The optional slow wetting step (Kemper et al., 1985) was omitted, since preliminary determinations on our 1- to 2-mm soil particles revealed best results for aggregate stability measurements of air-dry moisture content (2.8%). Additional sieving steps were added to the standard procedure to allow each of the WSSA and WUSA fractions to be separated into fine (75–250 μm) sand and silt-clay subfractions. For this purpose, custom-made (William Heinemann) sieves with 75- μm openings were used in addition to the standard sieves with 250- μm openings. Complete disintegration of the aggregates in dispersing solution was facilitated by sonication (10s). All fractions (coarse sand, WSSA fine sand, WSSA silt-clay, WUSA fine sand, and WUSA silt-clay) were recovered, oven dried, and weighed. Mean total recovery was 100.4%.

The relative amounts of all fractions were calculated on the basis of the total soil (relative amount of total soil found in 1–2-mm dry-sieved fraction multiplied by relative amount of dry-sieved fraction found in wet-sieved fraction). Values for total WSSA and total WUSA were the sums of values for the fine

Table 3. Changes in soil parameters relative to the control soil as influenced by the vesicular-arbuscular mycorrhizal (VAM) component in the treatment chamber (means of 10 replicates). Mean percentage change was calculated from individual replicates as [(treatment \times control)/control] \times 100.

Parameter	VAM root	VAM hypha	non-VAM root
Water-stable soil aggregates	50 a†	26 b	15 b
VAM hyphal density	133 b	202 a	-2 c
non-VAM hyphal density	18 a	14 a	5 b

† Means in each row followed by the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test.

sand and silt-clay subfractions. Values for the fine sand content of the total WSSA and WUSA provided an indication of the extent to which these fractions contained newly formed aggregates. Original aggregates should have the composition of the original, unamended Balcom soil, and newly formed aggregates that of the amended composition of the experimental soil.

RESULTS

The VAM-fungal soil mycelium grew more profusely in the absence of roots (VAM-hypha chamber) than in their presence (VAM-root chamber). The VAM hyphal densities of the non-VAM root and control chamber soils represented the dead hyphae from the original autoclaved soil mix (Table 1). Non-VAM hyphal density was significantly ($P < 0.05$) greater than in the control only in the presence of VAM roots. The VAM roots were significantly longer and had larger dry mass than non-VAM roots. Two-thirds of this length of VAM roots was colonized by the fungus. Non-VAM roots showed slight (<1%) VAM contamination in two of the 10 replicates.

The presence of VAM roots, of non-VAM roots, or of VAM hyphae alone affected the WSSA status of the soils differently (Table 2). With both roots and hyphae present, there was a significantly greater incidence of WSSA than in any of the other three treatments. The incidence of WSSA was statistically the same ($P > 0.05$) when only VAM hyphae or non-VAM roots were present in the chamber, suggesting comparable effects on water stability of the soil by roots and hyphae alone. Non-VAM fungi may have contributed to the greater abundance of WSSA in the VAM-root chamber (Table 2), since their hyphal density was significantly greater than in the control (Table 1).

The relative importance of the fungus and root com-

Table 2. Soil aggregate characteristics as influenced by the vesicular-arbuscular mycorrhizal (VAM) component in the treatment chamber (means of 10 replicates). Differences between the soil at the beginning of the experiment (initial soil) and the harvest soils were determined by *t*-test.

Treatment	Soil parameters				
	Dry-sieved	Wet-sieved			
	1- to 2-mm particles	Coarse sand	Total aggregates†	Water-unstable aggregates	Water-stable aggregates
	-% of total soil (w/w)				
Harvest soil					
VAM root	18.2 b‡	0.7 a	17.5 b	12.4 c	5.1 a
VAM hypha	21.5 a	0.7 a	20.7 a	16.4 a	4.3 b
non-VAM root	18.5 b	0.7 a	17.8 b	13.9 b	3.9 bc
control	21.8 a	0.7 a	21.1 a	17.7 a	3.4 c
Initial soil	14.9*	0.8 NS	14.1*	6.8*	7.3*

* Initial soil was significantly different at $P < 0.05$ from each of the chamber soils at harvest; NS, not significantly different.

† Sum of water-unstable and water-stable aggregates

‡ Means in each column followed by the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test.

Table 4. Net percentage change in soil aggregates during the experiment relative to the starting material as influenced by vesicular-arbuscular mycorrhizal (VAM) component in the treatment chamber (means of 10 replicates).

Parameter	VAM root	VAM hypha	non-VAM root	control
	%			
Water-stable soil aggregates	-30a†	-41b	-47bc	-53c
Water-unstable soil aggregates	82a	141c	104b	160c

† Means in each row followed by the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test.

ponents of the mycorrhiza was put into perspective by the differences in the incidence of WSSA and in hyphal densities compared with the control (Table 3). Apparently, the less dense VAM mycelium together with the larger root ($\approx 50\%$ greater than in the non-VAM chamber, Table 1) produced the highest incidence of WSSA in the VAM-root chamber. Assuming a proportionality between size and aggregating effect and adding effects acting together in the VAM-root chamber, the sum doesn't entirely account for the much greater incidence of WSSA in the VAM-root chamber. This suggests synergism between roots and fungi in this chamber, although differences in root mass and length (VAM vs. non-VAM, Table 1) preclude unequivocal interpretation.

The significantly larger relative amount of WUSA in the soils of the two root-free chambers (Table 2) is ascribed to artifacts introduced by the initial sieving of the damp soils at harvest. The slightly higher moisture contents of the root-free soils may have promoted the formation of WUSA, while manipulation to remove root fragments from the rooted soils probably caused some degradation of WUSA. Evidently, the greater quantity of WUSA in the root-free chambers was responsible for the larger relative amount of total aggregates and, in turn, for the larger relative amount of the 1- to 2-mm dry-sieved fraction recovered from those chambers. The relative amount of coarse sand was intrinsic to the soil texture, which was the same throughout the pots. Thus, as expected, there was no significant difference in this component between chambers.

Relative to the original soil (Table 2), the percentage of total mass present in WSSA had declined in all chambers in the course of the experiment (Table 4), probably because of a combination of factors such as the pressures of root growth, decomposition of organic binding agents, and slaking (see Miller and Jastrow, 1992). The decline relative to the starting material was smallest in the soil of the VAM-root chamber and greatest in that of the control. The total fine sand content of the soil-sand mix at the start of the experiment (42.1%) was 5.5 times greater than the fine sand content of WSSA present in the mix (7.6%), and 2.6 times greater than the sand contained in the WUSA (16.1%) (Table 5). This was so because the fine sand amendment and the autoclaving of the original Balcom soil did not greatly alter the composition of the original aggregates it contained. New aggregates formed during the experiment could be expected to have a composition similar to that of the amended soil rather than the original soil, increasing the overall fine sand content of the aggregate material. This was the case

Table 5. Determination of newly formed aggregates.

	Fine sand content				
	Initial Soil	Soil at harvest			
		VAM root	VAM hypha	non-VAM root	Control
%					
Water-stable soil aggregates	7.6NS	7.6a†	7.2a	6.4b	6.4b
Water-unstable soil aggregates	16.1*	22.4b	28.4a	22.4b	29.3a
Total soil‡	42.1NS	42.1	42.1	42.1	42.1

* Initial soil is significantly different from each of the chamber soils at harvest at $P < 0.05$; NS, not significantly different at $P > 0.05$.

† Means in each row followed by the same letter are not significantly different ($P > 0.05$) by Duncan's multiple-range test.

‡ The fine sand content of the initial soil is a priori the same as that of the chamber soils at harvest.

for the WUSA, whose fine sand content at harvest was greater by 40% in the rooted and by 80% in the root-free treatment soils (Table 5) than at the start of the experiment. This treatment \times treatment increase in WUSA sand content was evidently a reflection of similar increases in the amounts of WUSA in the treatments vs. those in the starting material (Table 4). The fine sand content of the WSSA, on the other hand, did not increase during the experiment; in all chambers it remained statistically the same ($P > 0.05$) as in the WSSA of the initial soil. Apparently, no compensatory new WSSA were formed. A slight ($< 17\%$) drop in the fine sand content of WSSA between VAM-containing and VAM-free chambers was significant $P < 0.05$, Table 5) and paralleled the much larger declines in the amount of WSSA in these chambers (Table 4). This suggests that the WSSA were not entirely homogeneous in composition and a fraction somewhat enriched in fine sand was preferentially susceptible to degradation.

DISCUSSION

Aggregate size and stability are dynamic soil properties that change in response to aggregating and disaggregating forces (Gish and Browning, 1948). Tisdall (1991) recently summarized the effects of the soil biota on the formation and stability of soil aggregates, emphasizing the role of fungal hyphae in this complex process. The effects are manifold: while macroaggregates of soil usually become more stable after the growth of plants (Tisdall and Oades, 1982), the activities of the soil biota contribute both to the production and destruction of aggregates (Jastrow and Miller, 1991), and environmental factors generally tend to act as a disaggregating force (Hamblin, 1991).

Our data on soil aggregation may be evaluated based on the actions of such opposing forces. Slaking, a process of disaggregation of soil particles (Oades, 1984) resulting from the swelling and shrinking of soil due to wetting and drying, and microbial decomposition of organic matter (Gupta and Germida, 1988) can account for the general decline in the aggregate content of our soil during the experiment. Superimposed on this decline, however, were significant differences in WSSA contents of the four treatments, showing that the decline was greatest in the control soil from which roots and VAM fungus were excluded. These data (Table 3) can be interpreted in at

least two ways: (i) a slowing of the slaking process by the mycorrhiza, or (ii) mycorrhiza-mediated formation of new WSSAs compensating for unchecked disaggregation in the control soil.

The first process is suggested by the incorporation pattern of fine sand (added at the start of the experiment) into WSSA and WUSA during the experiment (Table 5): large additions of fine sand to the WUSA were noted, while the fine sand content of the WSSA remained unchanged, at least in the VAM-containing chambers. The finding that biological action by the components of the VAM symbiosis hindered the disintegration of preformed aggregates without causing the formation of new ones may be a function of the methods employed. The test for water stability of aggregates, wet sieving, sets an arbitrary standard, or threshold, for stability. If the degree of stability in a population of aggregates varies (see Tisdall, 1991), the strength of aggregating action by roots or hyphae may or may not be sufficient to make aggregates newly formed from dispersed materials sufficiently cohesive to pass the threshold set by the established conditions of the wet-sieving process. It may, however, suffice to boost cohesiveness in weak macroaggregates above the threshold. The latter mechanism may be operative if these macroaggregates already contain a well-developed system of microaggregates (see Miller and Jastrow, 1992). Such a boost may compensate for the loss of weak macroaggregates to disaggregating forces acting at the same time, depending on the aggregating force of a VAM component.

A distinct separation of the effects of VAM components on soil aggregation may not be possible using different VAM and non-VAM plants because of the disparity in root development. The finding of Thomas et al. (1986) that VAM and non-VAM plants differ in their effects on soil aggregation is not invalidated by our data. The conclusion drawn from the analysis of the results, which ascribed the major part of the VAM contribution to aggregate formation to the root component, is modified. Here, the direct effect of VAM soil hyphae on soil aggregation was shown to be significant and at least equivalent to that of roots alone (Table 3), confirming Miller and Jastrow's (1990) results, and supporting Tisdall and Oades' (1982) concept of VAM contributions to aggregate formation. In terms of energy expended by the plant to create a more favorable rooting environment, the production of VAM hyphae appears to have the advantage over root development. We suggest that this aspect of the VAM contribution to the plant-soil system may equal that of the enhancement of plant growth itself, especially in the context of conservation-oriented, sustainable agriculture.

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