

Evaluation of commercial inorganic and organic fertilizer effects on arbuscular mycorrhizae formed by *Glomus intraradices*

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ADDITIONAL INDEX WORDS. *Allium cepa*, *Rosa*, endomycorrhizae, container production, phosphorus

SUMMARY. Formation and function of arbuscular mycorrhizae (AM) are affected by levels of fertility in soil or fertilizers applied to soilless container mixes. For AM fungi, phosphorus (P) is the main element influencing colonization of host plant roots. The question addressed in this study was whether inorganic or organic fertilizers were more compatible with the formation and function of AM. Several controlled-release inorganic (CRI) fertilizers were compared with several organic (OR) fertilizers at different rates ($\frac{1}{2}\times$ to $4\times$ the recommended rate) to determine (1) threshold levels of tolerance by the AM fungus *Glomus intraradices* in relation to root colonization, and (2) growth responses of 'Guardman' bunching onion (*Allium cepa*) and 'Orange Cupido' miniature rose (*Rosa* spp.) plants grown in a soilless potting mix or sandy loam soil. AM colonization in soil was greatly decreased or totally inhibited by CRI fertilizers with high P content at the $2\times$ rate or greater, whereas colonization was decreased but never eliminated by low-P OR fertilizers at the $3\times$ rate or greater. Shoot growth of onions was similar

with or without AM inoculation when fertilized with CRI, but in general was only enhanced by OR fertilizers if inoculated with AM fungi, compared to the noninoculated controls. Shoot and root growth of onions were significantly increased by AM inoculation when OR fertilizers were used at the $1\times$ rate. In contrast, root growth was not increased by the combination of CRI fertilizers and AM fungal inoculation. Inoculation of miniature roses grown in sandy loam amended with 25% peat and perlite and fertilized with all the CRI or OR fertilizers resulted in high AM colonization, but without much AM-induced growth increase except where OR fertilizers or CRI fertilizers with low P were used. In a soilless potting mix, growth of miniature roses was less with OR fertilizers at the rates used than CRI fertilizers, but mycorrhiza formation was greater in the former unless P was low in the latter. These results indicate that release of nutrients from organic fertilizers, as a result of microbial activity, favors AM establishment and function more than most inorganic fertilizers unless P levels of the latter are low.

Of all factors affecting the establishment and function of arbuscular mycorrhizae on plants, fertilizer level is among the most important. Of the major and minor fertilizer elements, phosphorus is the most important (Menge et al. 1978a). High P levels in plant tissues inhibit colonization of roots (Menge et al., 1978b; Sanders, 1975). The question often asked is what kind and how much fertilizer is appropriate to favor AM establishment and function? Choice of fertilizer is often based on specific formulations of major elements of nitrogen (N), P, and potassium (K), but often without regard to the source or fertilizer release pattern unless totally soluble formulations are used. When soluble fertilizers are used, high P formulations usually inhibit AM formation. Many soilless mixes come to growers fully charged with fertilizers that can prevent AM colonization (Datnoff et al., 1991).

For reasons of conservation and to avoid soil and water contamination with excess fertilizer nutrients, controlled-release inorganic fertilizers have been developed. Many of these, however, are soluble fertilizers formulated within prills to delay or control the release. With most, soluble nutrients are released

due to osmosis through the prill wall. Often, excessive amounts of fertilizer are released that may leach through the medium without being absorbed by the plant roots; unless plants are fertilized again, nutrient deficiencies may occur. More recently, prilled products have been made that release fertilizers in response to temperature-induced changes in the permeability of the prill; the construction of the prill wall determines the release pattern. These products have resulted in more even nutrient supply to plants over time.

There has been an increase in the development and use of organic fertilizers in recent years, partly because of the availability of organic materials in the waste stream, and partly for use in organic farming. Organic substrates used require microbial breakdown to release nutrients that can be used by plants. The result of this process is a progressive release of compounds that are used by both microbes and plants. Many of these products also involve a composting phase of some or all of the components. Thus, plants respond differently to different products, presumably depending on the type and level of nutrients available. Those organic fertilizers that are formulated from undecomposed components require microbial degradation to forms that can be taken up by plant roots. Those that have been decomposed at least partially before being formulated may require further decomposition, but often provide earlier nutrient availability to plants than those that have not been decomposed at all before formulation.

The question to growers and mycorrhiza researchers alike is which type of fertilizer is the most compatible with mycorrhizal fungi that might be present or introduced into the crop production system. Therefore, the purposes of this study were to determine whether a selection of commercial CRI fertilizers were more compatible with AM fungal colonization by *G. intraradices* than progressive-release OR fertilizers, and which functioned best regarding mycorrhiza-induced growth enhancement compared to growth of nonmycorrhizal control plants under low-P conditions.

Materials and Methods

In three separate experiments, we used several commercial fertilizers (Table 1), both OR and CRI, to examine their effects on establishment

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and function of mycorrhizae and on plant growth. The CRI fertilizers used represented an array of formulations and nutrient-release patterns. The OR fertilizers used were formulated from different components; some had been composted prior to formulation; all as formulated had relatively low N:P:K.

EXPERIMENT 1. This study consisted of a factorial combination of five commercial fertilizers (Table 1) applied at six rates (including the nonamended control) to 'Guardsman' bunching onions, each with and without AM fungal inoculation. Fertilizers were tested at the recommended full label (1×) rate, 1/2×, 2×, 3×, and 4× label rate. Long Ashon's Nutrient Solution (LANS) (Hewitt, 1966) was used as a liquid fertilizer control and was applied with a reduced P level of 11 mg·L⁻¹ (ppm). Control treatments received LANS, beginning immediately after thinning of onion seedlings and applied weekly thereafter to ensure seedling establishment in the nutrient deficient sandy loam soil used. The amount of elemental P supplied for each fertilizer formulation at the recommended 1× rate is given in Table 1.

Mycorrhizal fungal inoculum consisted of *G. intraradices* spot-cultured for 4 months with 'Guardsman' bunching onions grown in 1:1 alluvial loam:sand (by volume) (pH 6.5, 11 mg·L⁻¹ P).

Inoculum consisted of the sandy loam passed through a 2 mm sieve and mixed with small fragments of colonized onion root pieces [0.25 to 0.50 cm (0.098 to 0.197 inch) long]. Pre-study evaluation of the inoculum indicated an average of 8 loose spores/g soil, hyphal fragments and densely colonized root pieces. Overall inoculum potential was 18 propagules/g soil as determined by the most probable number (MPN) method (Woomer, 1994). About 5 cm³ (0.5 tablespoon) were incorporated into the medium in each tube under the seed germination zone. Root and soil washings from the *G. intraradices* pot-culture were prepared by passing them through a 38-µm sieve (Tyler equivalent 400-mesh) and Whatman #1 filter paper. Immediately after seeding, this filtrate was added to the nonmycorrhizal control pots at 20 mL (0.68 fl oz) per tube to qualitatively standardize the rhizosphere microflora of both AM treatments.

Alluvial loam and sand from an uncultivated Willamette Valley source were mixed 1:1 (by volume) and yielded pH 6.5 with 11 mg·kg⁻¹ P. This mix was pasteurized with aerated steam [65 to 70 °C (149.0 to 158.0 °F) for 1.5 h, and then air-cooled and stored for at least 1 week before testing (Meyer and Linderman, 1986). All fertilizer treatments, except the liquid fertilizer controls, were

incorporated into the sandy loam by mixing in a stainless steel dry twin-shell blender. Half of each mix was removed and mixed with the AM fungal inoculum (approximately 5 cm³ per final container volume). Super-Cell Cone-Tainer tubes (Steuwe and Sons, Corvallis, Ore.) were filled with 140 cm³ (8.5 inch³) of the mix amended with specific fertilizers at specified rates as well as treated or not with AM fungal inoculum (eight replicates per treatment), then lightly moistened with water.

Onion seeds were placed (three per tube) into tubes and covered with 10 cm³ (0.6 inch³) more of each mix. Immediately after seeding, microbial sieving solution was added to the nonmycorrhizal control pots at 20 mL per tube to qualitatively standardize the rhizosphere microflora of both AM and nonAM treatments. Soil was then manually misted to moisten the whole tube volume. Onion plants were thinned to one plant per tube two weeks after emergence and arranged on a greenhouse bench in a randomized block design. There were eight replicate onions per fertilizer per rate, each inoculated or not with the AM fungus. Greenhouse temperatures were maintained on a 24/18 °C (75.2/64.4 °F) day/night cycle, with 14-h daylengths of 600 to 800 µmol·m⁻²·s⁻¹ (at canopy level) provided by supplemental lighting with

Table 1. Fertilizer formulations and sources, and phosphorus (P) and nitrogen (N) concentrations used in experiments to evaluate interactions with the arbuscular mycorrhizal (AM) fungus *Glomus intraradices*.

Fertilizer formulation ^{a,y}	Recommended (1×) rate (g·L ⁻¹) ^x	Elemental N supplied/plant [mg·kg ⁻¹ (ppm)] ^w	Elemental P supplied/plant (mg·kg ⁻¹) ^v	Expt. no.
Inorganic controlled release				
Osmocote 14-14-14 (14N-6.2P-11.6K)	3.6	302	133	1, 2, 3
Osmocote 18-6-12 (18N-2.6P-9.1K)	3.6	389	57	3
Apex 14-14-14 (14N-6.2P-11.6K)	4.2	353	155	2, 3
Apex 16-5-9 (16N-2.2P-7.5K)	4.2	403	55	3
Apex 21-2-11 (21N-0.9P-9.1K)	4.8	605	25	3
Scotts High N 21-4-7 (21N-1.8P-5.8K)	3.0	378	32	2, 3
WoodAce 14-12-14 (14N-5.3P-11.6K)	2.4	202	76	1, 2, 3
Organic base				
Bandini 6-2-4 (6N-0.9P-3.3K)	2.5	90	13	2, 3
BioGro 7-7-2 (7N-3.1P-1.7K)	2.5	105	46	1, 2, 3
BioSol 6-1-3 (6N-0.4P-2.5K)	2.5	90	7	1, 2, 3
Mixture organic/inorganic				
Best Regain 6-2-6 (6N-0.9P-2.5K)	3.0	180	16	1, 2, 3
Water soluble				
Plant Marvel 13-2-13 (13N-0.9P-10.8K)	2.5	195	13	3
LANS (using 1/4× P)	NA ^u	168	11	1, 2

^aWoodAce and Regain are no longer manufactured.

^yManufacturers: Scotts Company, Marysville, Ohio (Osmocote, Scotts High N); J.R. Simplot, Lathrop, Calif. (Apex, Best Regain); Vigoro, Winter Haven, Fla. (WoodAce); Spectrum Brands, St. Louis, Mo. (Bandini); BioOregon, Warrenton, Ore. (BioGro); Rocky Mountain Bio-Products, Denver, Colo. (BioSol); Plant Marvel Laboratories, Chicago Heights, Ill. (Plant Marvel).

^xRecommended rates adjusted for plant and size considerations where given by manufacturer; 1.0 g·L⁻¹ = 1.69 lb/yard³.

^wTheoretical N concentration supplied to each plant in a 0.6-L (0.63-qt) plastic pot at the 1× rate. Final concentration/pot based on: %N × 10 × rate × 0.6 g·L⁻¹.

^vTheoretical P concentration supplied to each plant in a 0.6-L plastic pot at the 1× rate. Final concentration/pot based on: %P × 10 × rate × 0.6 g·L⁻¹.

^uRate application not applicable as with other fertilizer blends; rates adjusted to provide desired P level in final solution for each

high intensity halide vapor lamps.

Plants were harvested 8 weeks after emergence. Roots were washed clean of soil, severed from the shoot at the base of the bulb, weighed and subsampled for root clearing and staining procedures to quantify AM colonization. Remaining roots and shoots were oven-dried at 65 °C (149.0 °F) for dry weight measurements. Roots were cleared and stained following a modified Phillips and Hayman (1970) protocol where lactophenol was replaced with lactoglycerin and colonization was assessed on a stereoscope using the grid-line intersect method (Giovannetti and Mosse, 1980).

EXPERIMENT 2. Based on results of Expt. 1 and other unreported studies, we examined an expanded range of commercial fertilizers (Table 1) for their effects on *G. intraradices* colonization of onion. Fertilizers were mixed into the same sandy loam soil mix, using only the recommended rate (1×) for each product. Low-P LANS was again applied as a liquid fertilizer control. The AM inoculum used for this experiment, inoculation procedures, and growing conditions were the same as described for Expt. 1. Plants were arranged on a greenhouse bench in a randomized block design, grown for 8 weeks, then

harvested as described for Expt. 1, and root colonization and plant dry weight were determined.

EXPERIMENT 3. ‘Orange Cupido’ miniature rose (PP10820; Yoder Brothers, Inc., Barberton, Ohio) was used in this experiment employing the same expanded range of fertilizers applied in Expt. 2 (Table 1), but including additional lower P formulations of some fertilizers (12 products total). A soluble liquid fertilizer, Plant Marvel 13N-0.9P-10.8K-6.0Ca-3.0Mg (Plant Marvel Laboratories, Inc., Chicago Heights, Ill.), adjusted to supply 200 mg·L⁻¹ N and 13.5 mg·L⁻¹ P, was used to replace the LANS formulation used in Expt. 1 and Expt. 2. All fertilizers except Plant Marvel (PM) were mixed at a 1× rate into one of two growth media. The first growth medium consisted of the same sandy loam mix used in Expt. 1 and Expt. 2, which was also amended with 25% (by volume) of a mixture of 1 peat (Lake-land Peat; Sun Gro Horticulture, Inc., Hubbard, Ore.); 1 perlite (Supreme Perlite, Portland, Ore.). The second growth medium used was Grower’s Gold B (Sun Gro Horticulture, Inc., Hubbard, Ore.), a soilless potting mix consisting of 60% peat, 20% perlite, 20% pumice, dolomitic limestone, and

a wetting agent but without fertilizer charge.

Two-node cuttings of miniature roses were first rooted in Oasis cubes (Smithers-Oasis USA, Kent, Ohio) after being dipped in rooting hormone (Dip-N-Grow; Astoria-Pacific, Inc., Clackamas, Ore.), placed under mist for 3 to 4 weeks, then transplanted into square black plastic pots [10.2-cm (4-inch) diameter, 0.6-L (0.63-qt) capacity] containing the fertilizer × AM inoculum mixes. The same *G. intraradices* inoculum used in Expt. 1 and Expt. 2 was used to inoculate roses by placing 12 cm³ (≈1 tablespoon) of inoculum in a depression of the medium in the center of each pot prior to transplant. Rooted cuttings were placed directly on the inoculum. Filtered inoculum washings, as described in Expt. 1, were applied at 50 mL (1.7 fl oz) per pot immediately after transplant to standardize the microflora between the mycorrhizal treatments and controls. Plants were arranged on a greenhouse bench in a randomized block design and grown under the same conditions as onions. Stems of plants were pruned twice during the study and harvested 10 weeks after transplant. Pruning promoted vegetative growth, and few flower buds formed. Harvested plants

Table 2. Contrast analyses probability values describing comparative effects of organic (OR) and controlled-release inorganic (CRI) fertilizers and mycorrhiza (AM) treatments on onion or mini-rose biomass and root colonization by *Glomus intraradices* in different potting media.

Analyses	Probability values (P) ^z		
	Plant biomass		Percent AM colonization
	Shoot	Root	
Expt. 1 (onion) ^y			
-AM: OR vs. CRI	<0.001	0.012	NA ^x
+AM: OR vs. CRI	0.045	0.100	<0.001
OR: -AM vs. +AM	0.021	0.399	NA
CRI: -AM vs. +AM	0.349	0.573	NA
Expt. 2 (onion)			
-AM: OR vs. CRI	<0.001	<0.001	NA
+AM: OR vs. CRI	<0.001	<0.001	<0.001
OR: -AM vs. +AM	<0.001	<0.001	NA
CRI: -AM vs. +AM	<0.003	<0.001	NA
Expt. 3 (mini-rose)			
Sandy loam mix			
-AM: OR vs. CRI	<0.001	0.526	NA
+AM: OR vs. CRI	<0.001	0.318	<0.001
OR: -AM vs. +AM	0.021	0.014	NA
CRI: -AM vs. +AM	0.196	0.318	NA
Grower mix B			
-AM: OR vs. CRI	<0.001	<0.001	NA
+AM: OR vs. CRI	<0.001	<0.001	<0.001
OR: -AM vs. +AM	<0.001	<0.001	NA
CRI: -AM vs. +AM	<0.001	<0.001	NA

^zAnalyses of transformed data

^yAnalyses based on label rate (1×) of each fertilizer to eliminate rate effects in comparisons in Expt. 1

^xNA = not applicable

were processed as described for onions, severing shoots at the soil level. Dry weights of prunings were included in the total shoot dry weights.

DATA ANALYSIS. Data were analyzed separately for each experiment. For Experiment 3, the different potting media were not treated as experimental factors, and the bioassays in each medium were run separately. Plant biomass data were log-transformed and root colonization data were arcsin transformed and subjected to analysis of variance procedures for factorial experiments using Systat 8.0 (SPSS, Inc., Chicago, Ill.). Actual data are presented in the graphs. Due to the highly significant interactions found by analyses, treatment comparisons were limited to pertinent contrast comparisons (Table 2).

Results and discussion

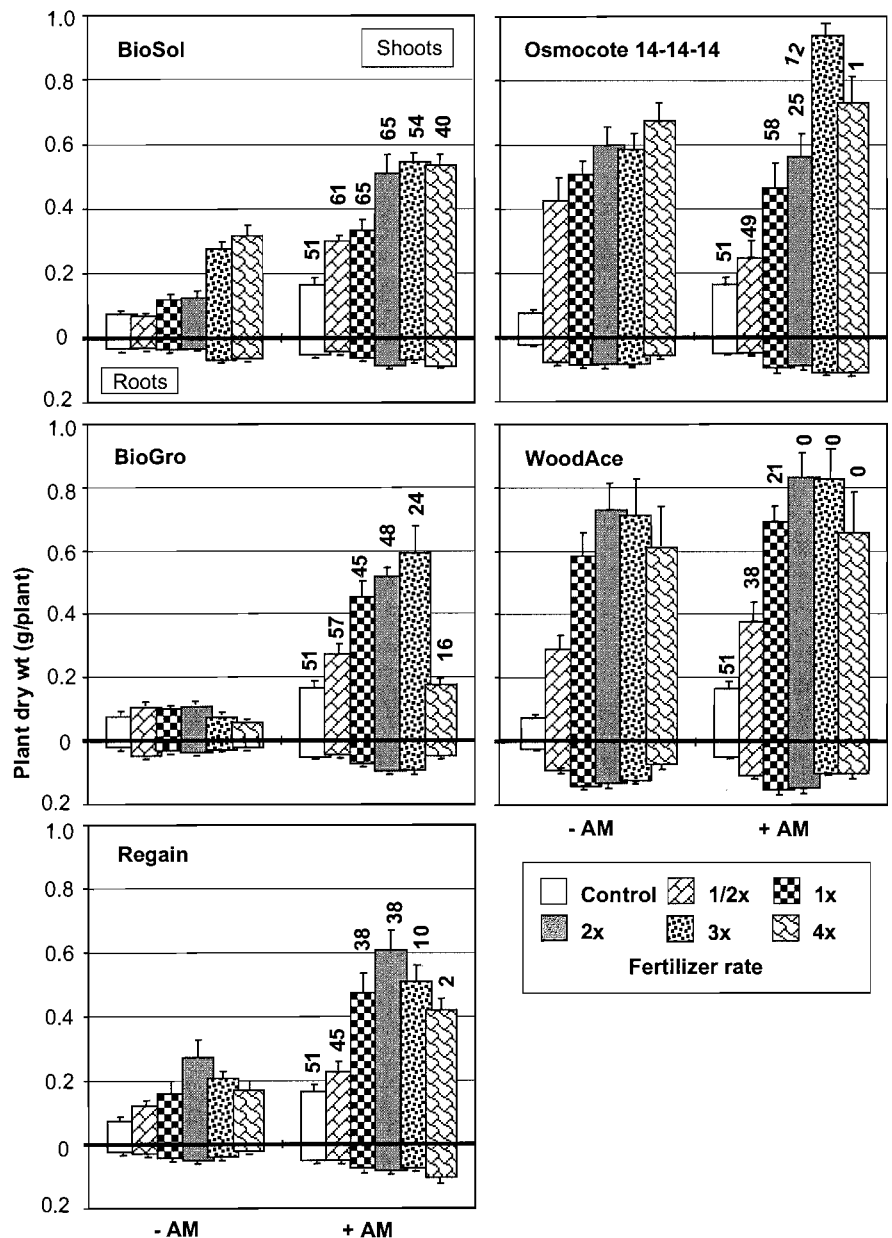
EXPERIMENT 1. In this study involving application of CRI and OR fertilizers at different rates, shoot and root growth of onions were generally greater when CRI fertilizers were used than when OR fertilizers were used, regardless of inoculation with *G. intraradices*. Inoculation of plants fertilized with CRI did not further enhance shoot or root growth. Shoot growth of onions grown with OR fertilizers generally was only increased, compared to nonmycorrhizal control plants, if inoculated with *G. intraradices* ($P < 0.021$) (Fig. 1). Increasing the rate of fertilizer in the growth medium generally increased shoot growth, although the 4x rate of BioGro inhibited shoot growth compared to other treatments other than the control. Plants fertilized with Regain at 3x and 4x rates grew less than those at the 2x rate. Regain, which is a mixture of organic and inorganic components, and BioSol stimulated plant growth in the absence of mycorrhizae over the controls. However, BioGro did not stimulate plant growth at any rate without mycorrhizae. Of significance in this experiment was that Osmocote and WoodAce inhibited AM colonization at the 2x rate and above; WoodAce totally inhibited AM formation at the 2x rate and above. In contrast, the OR fertilizers BioSol and BioGro inhibited AM formation at 3x and above, although not completely even at the 4x rate (Fig. 1). AM colonization with 3x and 4x rates of Regain were reduced compared to the 2x rate.

These results indicate that OR fertilizers have less negative impact on

mycorrhiza formation than CRI fertilizers with a higher available phosphoric acid (P_2O_5) content ($P < 0.001$), which supply moderately high P levels for 2 to 3 months, thereby inhibiting AM formation by *G. intraradices*. However, the OR fertilizers supported much less plant growth than the CRI fertilizers in the absence of mycorrhizae (Fig. 1; Table 2). In the presence of mycorrhizae, growth was enhanced over the nonmycorrhizal controls, but not as much as with the CRI fertilizers at most rates.

EXPERIMENT 2. When we examined a broader range of fertilizers applied at the label recommended rate (1x), results were similar to Expt. 1 in that OR fertilizers generally stimulated onion shoot growth less than CRI fertilizers, ($P < 0.001$ by contrast analysis) and shoot growth was enhanced more when OR fertilizers plus *G. intraradices* were used ($P < 0.001$, Fig. 2). The

Fig. 1. Rates of fertilizers and effects on onion biomass and root colonization by the arbuscular mycorrhizal (AM) fungus *Glomus intraradices* (Expt. 1). Numbers over +AM columns are percentage over +AM length with AM colonization. Control treatment = Long Ashton's Nutrient Solution (LANS). Fertilizer recommended (1x) rates ($g \cdot L^{-1}$) were BioSol 2.5, BioGro 2.5, Regain 3.0, Osmocote 14-14-14 3.6, and WoodAce 2.4 ($1.0 g \cdot L^{-1} = 1.69 lb/yard^3$). Standard error bars indicated for each treatment ($n = 8$); $28.35 g = 1.0 oz$.



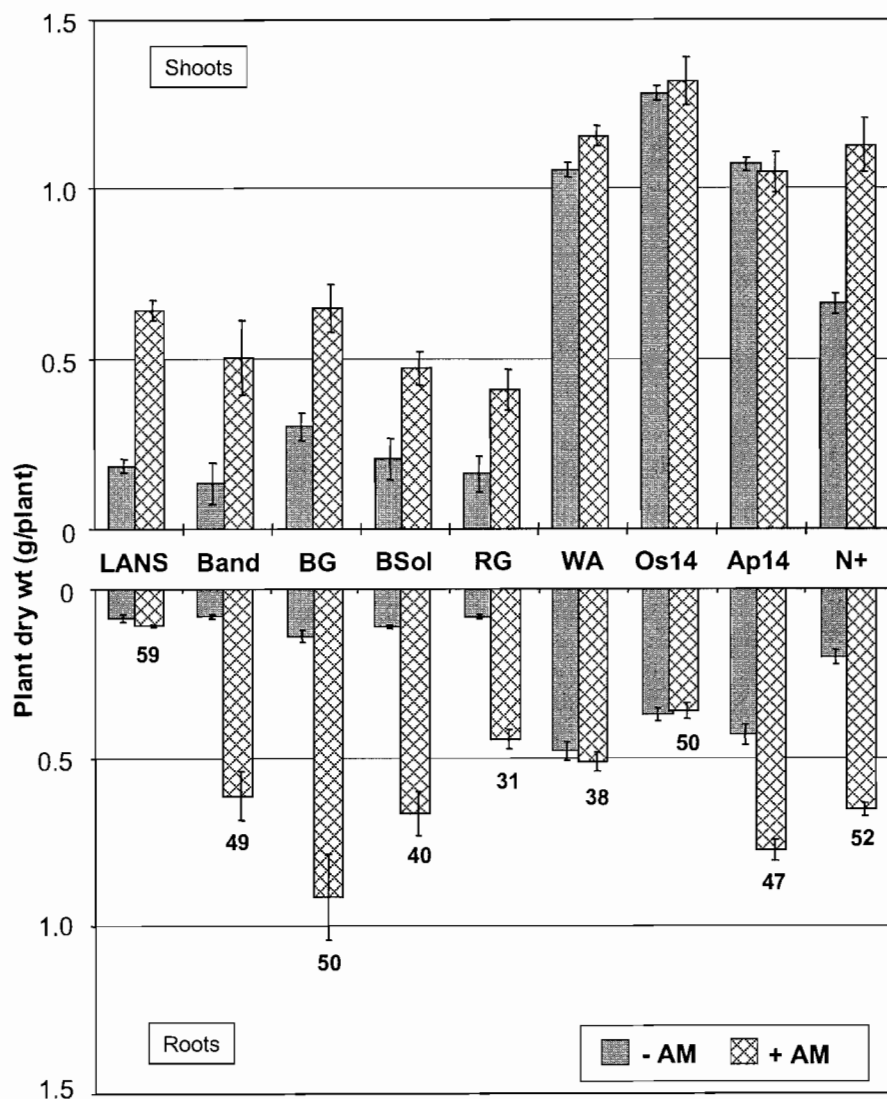


Fig. 2. Fertilizer and inoculation effects on onions grown in a sandy loam medium and root colonization by the arbuscular mycorrhizal (AM) fungus *Glomus intraradices* (Expt. 2). Numbers under +AM columns are percentages of root length with AM colonization. Fertilizer treatments: LANS = Long Ashton's Nutrient Solution; Band = Bandini; BG = BioGro; BSol = BioSol; RG = Regain; WA = WoodAce; Os14 = Osmocote 14-14-14; Ap 14 = Apex 14-14-14; N+ = Scotts 21-4-7. Standard error bars indicated for each treatment ($n = 8$); 28.35 g = 1.0 oz.

magnitude of shoot growth enhancement with mycorrhizae was significantly greater with OR than CRI fertilizers (Table 2), where enhancement was nil except for the Scotts N+ product (Fig. 2). Enhancement of root biomass was especially greater with OR fertilizers and mycorrhizae, compared to less root biomass enhancement with most CRI fertilizers, except for the Ap14 and

N+ treatments. Presence of mycorrhizae in CRI fertilizer treatments significantly increased shoot ($P < 0.003$) and root ($P < 0.001$) growth over nonmycorrhizal equivalents, although individual treatments were variable. Similar levels of statistical significance were obtained with OR fertilizer treatments (Table 2). Mycorrhiza formation ranged from 31% to 59% of root length colonized over all fertilizer treatments at the 1 \times rates.

Contrast comparisons (Table 2) confirmed the suppression of AM fungal colonization by CRI fertilizers as a group over OR fertilizers (including the hybrid Regain), exclusive of LANS. Both CRI and OR fertilizers suppressed root colonization more than LANS alone.

EXPERIMENT 3. In this study, miniature rose was grown in sandy loam medium or a soilless potting mix and fertilized with an expanded number of fertilizers at 1 \times label rates. In the sandy loam medium, mycorrhiza formation

was good with all the OR fertilizers used (52% to 86% root length colonized), and growth enhancement was significant, (Table 2), although it was absent with Bandini (Fig. 3). Little or no growth enhancement occurred in inoculated OR fertilizer treatments compared to Plant Marvel. Plant growth was greater overall with the higher P formulations of Woodace, Osmocote, and Apex. However, these latter fertilizers totally suppressed mycorrhiza formation. When Osmocote and Apex formulations with lower P formulations (OS18 and API6) were used (compared to the higher P formulations), mycorrhiza colonization was greater than in high P formulations, although shoot growth was reduced (Fig. 3). Curiously, fertilization with Apex 21 resulted in poor plant growth and low mycorrhiza colonization in spite of its low P formulation. This particular formulation is designed to slowly release nutrients to established landscape perennials over a 4 to 5 month period, which proved to be unsatisfactory for young plants with rapidly developing roots.

Experiment 3 also included miniature rose plants grown in a soilless medium with no starter fertilizer charge (Mix B). Again, growth was significantly less with OR fertilizers in this medium than with the CRI fertilizers ($P < 0.001$), and there was little to no mycorrhiza growth enhancement (Fig. 4). AM root colonization with the OR fertilizers was more variable than in sandy loam, with a large increase for Bandini (52% in sandy loam; 86% in Mix B) and a large decrease for BioSol (86% in sandy loam; 41% in mix B).

Overall growth for miniature roses treated with CRI fertilizers was also less in Mix B (Fig. 4) than sandy loam (Fig. 3). Again, high P formulations strongly suppressed mycorrhiza development compared to those with lower P, but interestingly there was more mycorrhiza-induced growth enhancement of both shoots and roots in this soilless mix than with the sandy loam.

Also notable is the greater mycorrhiza-induced growth enhancement of miniature roses fertilized with PM 13-2-13 fertilizer in the soilless mix compared to sandy loam, even though mycorrhiza formation was reduced (Figs. 3 and 4).

Contrast analyses confirmed that in both sandy loam and soilless mix, CRI fertilizers as a group were more suppressive to AM root colonization

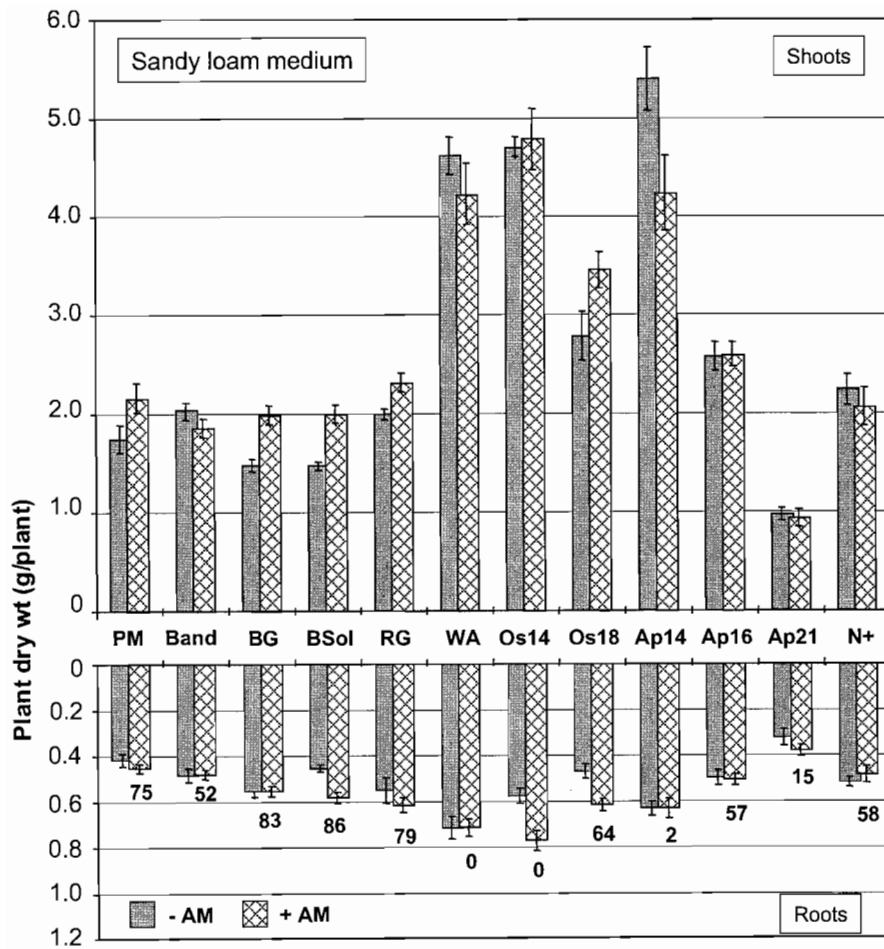


Fig. 3. Fertilizer and inoculation effects on miniature roses grown in a sandy loam-peat-perlite mix and root colonization by the arbuscular mycorrhizal (AM) fungus *Glomus intraradices* (Expt. 3). Numbers under +AM columns are percentages of root length with AM colonization. Fertilizer treatments: PM = Plant Marvel 13-2-13; Band = Bandini; BG = BioGro; BSol = BioSol; RG = Regain; WA = WoodAcc; Os14 = Osmocote 14-14-14; Os18 = Osmocote 18-6-12; Ap 14 = Apex 14-14-14; Ap 16 = Apex 16-5-9; Ap 21 = Apex 21-2-11; N+ = Scotts 21-4-7. Standard error bars indicated for each treatment (n = 8); 28.35 g = 1.0 oz.

than OR fertilizers (which included the hybrid Regain), exclusive of PM 13-2-13 (Table 2). In sandy loam, PM affected fungal activity no differently than the OR fertilizers ($P < 0.373$), but in soilless mix B, suppressed colonization significantly compared to the OR fertilizers ($P < 0.001$) as well as the CRI fertilizers ($P < 0.001$).

These results are not readily explainable given the extremely complex nature of both the physicochemical

properties and microbial constituents of soilless media. The low N-P-K formulations of the OR fertilizers were relatively ineffective in stimulating plant growth in this medium, even when mycorrhiza formation was substantial. However, we did not evaluate production of extraradical hyphae, only intraradical colonization. It is possible that extraradical hypha production was inhibited in the soilless medium. Furthermore, the nutrient concentration in the OR fertilizers generally was lower than in the CRI fertilizers, except in the experiment where up to 4x rates were used.

P availability generally is the focal point amongst nutrients when considering AM activity, and our own studies demonstrate better root colonization with low-P formulated CRI fertilizers and OR fertilizers (Expt. 3; Figs. 3 and 4). However, there are scattered studies in the literature that have examined effects of nitrogen level and form on AM function (Hepper, 1983; Johnson, et al., 1984; Ortas, et al., 1996; Sylvia and Neal, 1990; Valentine, et al., 2001, 2002). Chambers et al. (1980) showed

that adding ammonium (NH_4^+)-based inorganic salts tended to reduce AM colonization, while Davis and Young (1983) found that nitrate (NO_3^-)-based salts were more inhibitory to colonization of wheat roots, but also that AM fungal isolates were affected differently. Sylvia and Neal (1990) showed that under N-limiting conditions, additional P had no effect or increased AM root colonization, depending on the AM fungal species. However, under N-sufficient conditions, adding P suppressed AM colonization, indicating that plant N stress affected the resistance of the host root to AM colonization.

Villegas and Fortin (2001, 2002) reported that insoluble P sources became more soluble in the presence of either NH_4^+ or NO_3^- fertilizers, as long as AM fungi and phosphate-solubilizing microbes were present together in the *in vitro* system. Depending upon the nitrogen form, however, the amount of chemically- versus microbially-mediated activity may differ in affecting media pH.

Expanding these concepts to mineral soil or soilless systems is complex and beyond the purpose of our study. Most, if not all, of our tested CRI fertilizers are predominantly NO_3^- -N, designed to accommodate horticulture industry protocol for soilless mixes and plant production. Mineralization and solubilization dynamics will differ from those in a mineral soil system, even if plant type, fungal isolate, and other variables were the same, which may be indicated by our results in Expt. 3 (Figs. 3 and 4).

The strong positive interaction between mycorrhizae and the OR fertilizers is unexplained. In addition to the fact that all the OR fertilizers had low P formulations, one possibility, as mentioned above, is that mycorrhizae encourage more substrate-degrading microbes than in their absence (Linderman, 1992; Villegas and Fortin 2001, 2002), so that without mycorrhizae nutrients are limiting to plant growth. Another possibility is that the extraradical hyphae of AM fungi more effectively absorb nutrients, released by substrate degradation, that were slow to move in the soil solution to nonmycorrhizal roots, possibly because they are bound in microbial biomass. Still another possibility is that mycorrhizae + OR fertilizers stimulate greater root growth, thus enhancing direct nutrient uptake by roots.

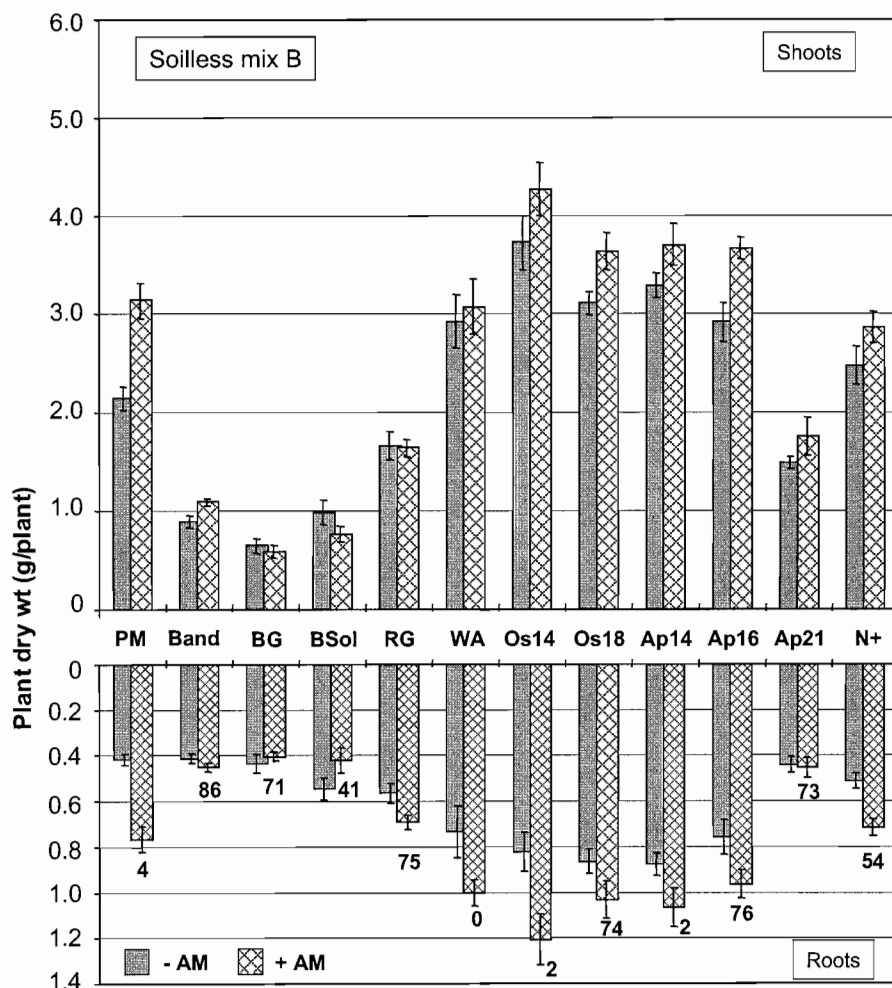


Fig. 4. Fertilizer and inoculation effects on miniature rose grown in soilless potting mix (Grower's Gold B) and root colonization by the arbuscular mycorrhizal (AM) fungus *Glomus intraradices* (Expt. 3). Numbers under +AM columns are percentages of root length with AM colonization. Fertilizer treatments: PM = Plant Marvel 13-2-13; Band = Bandini; BG = BioGro; BSol = BioSol; RG = Regain; WA = WoodAce; Os14 = Osmocote 14-14-14; Os18 = Osmocote 18-6-12; Ap14 = Apex 14-14-14; Ap16 = Apex 16-5-9; Ap21 = Apex 21-2-11; N+ = Scott 21-4-7. Standard error bars indicated for each treatment (n = 8); 28.35 g = 1.0 oz.

In this study using commercially available fertilizers, we have documented the greater compatibility of OR fertilizers with AM by *G. intraradices* than CRI fertilizers with high P formulation. However, using CRI fertilizer formulations with lower P also allowed substantial mycorrhizae formation, although growth was minimally enhanced over the nonmycorrhizal treatments. The striking relationship between OR

fertilizers and mycorrhizae remains an open question requiring further research. From a grower's point of view, OR fertilizers are slower to provide the nutrition needed for optimal growth, but could provide long-term benefit in enhancing fertilizer-use efficiency over a plant's whole growth cycle, and favoring mycorrhiza formation and subsequent plant health benefits.

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