20% leaf surface infected, 30% of the leaf surface infected, 40% of the leaf surface infected, and 50% infection or greater. Friedman's nonparametric test for significance was applied to determine significant difference. Tukey's least square difference (LSD) test was applied to separate means.

Results and discussion

Oil application significantly reduced mildew severity in vegetative growth as compared with that of the unsprayed control ($P = 0.05$) (Fig. 1). Under Corvallis conditions, the extent of mildew following 4- or 2-week oil applications was not significantly different (Fig. 1). The mildew severity between the untreated control and the 4- or 2-week treatments for Boskoop Giant, Consort, and Crusader, the highly- and medium-susceptible cultivars, was reduced by about 20%; that for Polar and Rovada, the least-susceptible cultivars, was reduced by about 6% (Fig. 1).

In conclusion, the application of mineral oil at either a 4- or 2-week interval reduced mildew severity on black or red currant shoots and leaves. An equivalent level of control was achieved with either 4- or 2-week spray under study conditions. In other areas of high inoculum, a 2-week application (label recommendation) may be needed. Reduction of the mildew was greatest on the most susceptible types. This study was conducted on 2-year old plants which had not reached full fruiting capacity. Further study is needed to determine if oil application affects yield in currants.

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Vesicular-Arbuscular Mycorrhiza and Plant Growth Response to Soil Amendment with Composted Grape Pomace or Its Water Extract

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ADDITIONAL INDEX WORDS. *Allium cepa*, endomycorrhizae, humic substances, onion, phosphorus, soil pasteurization

SUMMARY. Composted materials with high humic and microbial content, and their water extracts, are increasingly used in the nursery industry as potting mix components or as liquid amendments for the purposes of enhancing plant growth. Common speculation is that such materials either contain beneficial microbes or stimulate those in or added to the medium, such as vesicular-arbuscular mycorrhizal (VAM) fungi, known to have growth-stimulating effects on plants. Experiments were conducted to determine if one such compost enhanced plant growth by stimulating VAM fungi or other growth-enhancing microbes, by simply providing limiting nutrients [phosphorus (P)], or a combination of the two. Highly mycorrhiza-responsive onion (*Allium cepa*) 'White Lisbon' was used to evaluate the interactions of composted grape pomace (CGP), the VAM

fungus *Glomus intraradices*, and preplant soil heat treatment on onion growth under P-limiting conditions. CGP and its water extract stimulated onion growth under P-limiting conditions in the absence of VAM; the extract was more effective than the granular CGP. Growth was enhanced further by addition of *G. intraradices*, and the extract enhanced its colonization of roots. Heat pretreatment of the soil inconsistently affected growth-enhancement by CGP or its extract. Thus, inoculating plant roots with mycorrhizal fungi in combination with this composted organic amendment or its extract was beneficial. The effect could have been due to the CGP providing a source of P to overcome the P-limiting conditions, and to the mycorrhizal fungus enhancing P uptake by its extraradical hyphae and thereby increasing nutrient-use efficiency.

The application of organic amendments with high humic content in horticultural and agricultural practices has numerous benefits, some of which include improved soil structure and increased fertility (Vaughan and Malcolm, 1985), which consequently stimulate plant growth through diverse complex mechanisms. Guttay (1982, 1983) reported mixed growth responses to humic substances depending upon the bioassay host, compost substrate, and presence or absence of mycorrhizal fungal propagules. Organic materials with high humic content resulting from composting, or humic extracts from soil have been shown to influence microflora populations and activity. Visser reported that humic acid increased populations of diverse soil bacteria (1985a), possibly through changes in their metabolic processes (1985b). Root disease caused by *Fusarium* or *Pythium* on douglas fir (*Pseudotsuga menziesii*) was suppressed by soil amendment with organic substances high in humic content (Schisler and Linderman, 1989). A hypothesis explaining these effects on plant growth is that the humic substances stimulate beneficial soil microbes that in turn stimulate plant growth or suppress disease.

Organic matter and humic substances influence endomycorrhizal fungi (Giovannetti and Avio, 1985; Hepper and Warner, 1983; Sreenivasa, 1994; Soedarjo and Habte, 1993;

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Vallini et al., 1993), and ectomycorrhizae (Schisler and Linderman, 1989; Tan and Nopamombordi, 1979). Not surprisingly, fungal response depended on the organic substance and soil characteristics. St. John et al. (1983) reported increased proliferation of external hyphae of VAM fungi around organic material. However, Vallini et al. (1993) found increased concentrations of humic acids reduced hyphal growth, but stimulated growth of the host plant and populations of rhizosphere bacteria. Joner and Jakobsen (1995) found that both quality and quantity of organic matter affected VAM fungal activity, with higher organic matter rates increasing hyphal length.

It is difficult to distinguish direct effects of humus on plant growth from those mediated via humic effects on the soil microflora. Our preliminary studies on the influence of organic amendments with high humic content, or their extracts, on VAM fungal activity and plant growth suggested at least partial mediation by other soil microbes. However, this mediation did not seem to result from organisms present in the nonsterile extracts, but instead from organisms in the soil. The study presented in this paper examined the influence of CGP, a humic-rich organic material with high P content, or a water extract of it, on VAM colonization of roots and subsequent growth enhancement of onions grown in P-limited soil. Soils were treated at different temperatures before planting to selectively reduce components of the microflora and thereby assess the role of microorganisms in mediating any plant growth responses.

Materials and methods

EXPERIMENTAL DESIGN. This greenhouse study consisted of a factorial combination of three soil pasteuriza-

tion temperature (T) treatments [20 °C (68 °F) nontreated control, 50 and 100 °C (122 and 220 °F)], three soil amendment treatments of CGP (2% granular, a water extract of CGP, and a nonamended soil control), and two VAM fungal treatments (with and without). All treatments were replicated eight times and arranged on the greenhouse bench in a randomized block design.

Shoot and root dry weights were square-root transformed, and percentage root colonizations were arcsin transformed to correct for unequal variance and best model fit. Transformed data were subjected to standard statistical procedures for factorial experiments, including analysis of variance (Systat; SPSS, Inc., Chicago), orthogonal contrasts, and Fisher's protected Least Significance Difference tests to separate treatment means (Petersen, 1985). Actual data are shown in this paper.

BIOLOGICAL MATERIALS AND SOIL. The base soil medium was a 1:1 (v:v) mixture of a Willamette Valley alluvial silt loam and river sand, which contained 11 mg·L⁻¹ (ppm) available (Bray) P and had a pH of 6.3 (2 water : 1 soil, supernatant).

Our preliminary studies indicated that microbial-mediated activity was not intrinsic to the actual organic material, but that soil organisms might be involved and that pasteurization to reduce soil microbial populations might be a means of documenting their involvement in the compost-induced plant growth effect. Thus, we tested several temperatures (resulting from treatment with air-steam mixtures) at which different microbial populations, and thus their activity, would be affected. The soil was treated with aerated steam for 30 min at 50 and 100 °C to achieve temperatures that would at least temporarily, but selectively, reduce populations of Gram (-) bacteria (50 °C) or actinomycetes and spore-forming bacteria (100 °C).

Unheated soil served as the control with an ambient storage temperature of 20 °C.

Glomus intraradices fungal inoculum was obtained as the commercial product Nutri-Link (NPI, Salt Lake City). Before mixing, the inoculum was lightly ground into smaller particles for better distribution in the soil-sand medium. Once the steamed medium had cooled, inoculum was incorporated at the suggested rate of 2.2 g·L⁻¹ (2200 ppm) in one-half of each pasteurization temperature treatment using a twin-shell dry blender. The other nonmycorrhizal half received no inoculum.

CGP treatments were applied after soils cooled. In one-third of all VAM × T combinations, granular CGP was mixed with soils at 2% by volume using a twin-shell dry blender. Another one-third of all VAM × T combinations remained unamended with any CGP. An extract of CGP was added to the final one-third of all VAM × T combinations. To prepare the extract, 4 L (1.06 gal) of distilled water were added to 1.0 kg (2.2 lb) of air-dried, sieved [2-mm (0.08-inch)] CGP, and stirred intermittently for 24 h. The solution was filtered through cheesecloth to remove the largest particles, then centrifuged at 13,000 g_n for 20 min. The liquid was decanted and suction-filtered through Whatman 1 filter paper, autoclaved to sterility [115 °C (207 °F), 0.104 MPa (15 lb/inch²), 15 min], and stored at 5 to 6 °C (41 to 43 °F). This liquid served as the stock solution for subsequent applications. Twenty-four hours before and after sowing onion seeds, designated soils were drenched with the CGP extract (diluted 1:1 with distilled water) at 20 mL (0.68 fl oz) per tube. Further applications (4:1 dilution) were given at biweekly intervals [10 mL (0.34 fl oz)] per plant).

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Table 1. Chemical analyses of composted grape pomace (CGP) treatments.

Compost treatment ^a	pH	P ^b (mg·kg ⁻¹) ^x	K (mg·kg ⁻¹) ^x	Ca	Mg (cmol·kg ⁻¹) ^x	Na	CEC	EC (S·m ⁻¹) ^x	Fe	Mn	Cu	Zn (mg·kg ⁻¹) ^x	NH ₄ -N	NO ₃ -N	TC (g·kg ⁻¹) ^x	TN
Control	6.3	11	74	7.6	3.5	0.2	13.2	0.11	110.0	19.6	1.4	0.5	5.0	32.5	0.8	0.03
CGP	6.7	901	25350	9.4	12.7	0.7	100.4	0.86	37.8	54.8	5.1	906.0	14.1	1.3	43.3	2.50
2% CGP	6.4	20	273	8.4	3.9	0.2	14.1	0.14	84.0	18.0	1.3	1.0	4.3	42.1	0.7	0.05
CGPex	7.1	227	1230	7.0	10.6	17.5	18.0	0.34	0.9	2.1	0.2	1.5	7.6	0.3	0.2	0.02

^aControl = 1 sand : 1 loam with no compost; CGP = granular composted grape pomace; 2% CGP = composted grape pomace mixed 2% (vol) in 1 sand : 1 loam; CGPex = water extract of granular composted grape pomace.

^bP = plant available phosphorus (Bray); K = potassium; Ca = calcium; Mg = magnesium; Na = sodium; CEC = cation exchange capacity; EC = exchangeable salts; Fe = iron; Mn = manganese; Cu = copper; Zn = zinc; NH₄-N = ammonium form of nitrogen; NO₃-N = nitrate-nitrogen; TC = total carbon; TN = total nitrogen.

^x1.0 mg·kg⁻¹ = 1.0 ppm; 1.0 cmol·kg⁻¹ = 1 meq/100g; 1.0 S·m⁻¹ = 10.0 mmhos/cm; 1.0 g·kg⁻¹ = 1.0%.

Table 2. Analysis of variance and orthogonal contrast probability values describing effects of heat treatment (T), composted grape pomace (CGP) and mycorrhiza (VAM) on onion biomass and percentage of roots with *Glomus intraradices* colonization.

Analyses	Probability values (P) ^z		
	Biomass		% VAM colonization
	Root	Shoot	
CGP	0.001	0.001	0.001
T	0.077	0.002	0.268
VAM	0.001	0.001	n/a ^y
CGP × T	0.033	0.057	0.072
CGP × VAM	0.003	0.001	n/a
T × VAM	0.016	0.343	n/a
CGP × T × VAM	0.355	0.510	n/a
Mean square error	0.003	0.012	0.005
Orthogonal contrasts of CGP treatments			
None vs. (CGP and CGPex) ^x	0.001	0.001	0.001
CGP vs. CGPex	0.026	0.001	0.001

^zAnalyses of transformed data.

^yn/a = not applicable.

^xCGP = granular composted grape pomace mixed 2% (vol) in 1 sand : 1 loam; CGPex = water extract of granular composted grape pomace.

tainers [160 cm³ (10.2 inch³)] total volume; Stuewe and Sons, Inc., Corvallis, Ore.) were filled with 125 cm³ (8 inch³) of a given treatment (T × CGP × VAM) soil, then topped by a 10 cm³ (0.64 inch³) layer of corresponding T × CGP, noninoculated soil. Three bunching onion seeds (*Allium cepa* L. 'White Lisbon') were sown per tube and then covered by another 20 cm³ (1.3 inch³) of noninoculated soil that had been treated at the corresponding temperature. The seed and soil profiles of all treatments were misted heavily with water.

To standardize the initial microflora, a water-wash of Nutri-Link inoculum was passed through a 45-mm sieve (Tyler equivalent 325-mesh) and Whatman 1 filter paper. Each nonmycorrhizal tube received 15 mL (0.44 fl oz) of that filtrate 48 h after seeding.

GROWTH AND HARVEST CONDITIONS.

Two-week-old onions were thinned to one plant per tube, and were watered as needed, except for designated CGP extract applications and fertilization. All plants were fertilized weekly with Long Ashton nutrient solution (Hewitt, 1966) modified to supply limited phosphorus at 11 mg·L⁻¹. Greenhouse controls were set to maintain 23/15 °C (74/58 °F) average day/night temperatures. Supplemental lighting with high-pressure sodium vapor lamps supplied seedlings with an average of 600 mmol·m⁻²·s⁻¹ at canopy level for 16-h daylengths during the months of mid-October to mid-December.

Plants were harvested 10 weeks after emergence. Roots were washed

and cut from shoots below the bulb, weighed, and sub-sampled for subsequent microscopic evaluation of VAM colonization. Remaining roots and all shoots were then oven-dried at 65 °C (149 °F) for 48 h and weighed. Total root dry weight was adjusted for weight of the subsample used for VAM assessment. VAM colonization of onion roots was assessed on 1-cm (0.4-inch) sections after clearing and staining by modified procedures of Phillips and Hayman (1970), replacing lacto-phenol with lacto-glycerin. Percentage of root length with signs of VAM colonization was estimated by the method of Biermann and Linderman (1980).

The Soil Testing Laboratory at Oregon State University analyzed soil subsamples for residual nutrient content (Table 1). Extractable P was analyzed by the Bray dilute acid-fluoride method. Extractable potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na), and cation exchange capacity were determined with atomic absorption spectrophotometry following extraction with ammonium acetate. Other extractable nutrient levels were determined by routine methods of the Laboratory (Berg and Gardner, 1978).

Results and discussion

The addition of CGP, either in a granular form or a water extract, substantially enhanced onion shoot and root biomass compared to nonamended soil without VAM fungal inoculation (Table 2, Figs. 1 and 2). Temperature and VAM treatment factors alone also significantly influenced plant growth,

although their interactions were not always significant (Table 2). Pretreatment of the soil at 50 or 100 °C inconsistently reduced the growth enhancement by CGP or its extract in both nonmycorrhizal and mycorrhizal onions.

All noninoculated onion roots at the 50 and 100 °C temperature treatments remained free of colonization by VAM fungi. However, after 6 weeks of growth, it became visually evident there was an indigenous endophyte present in the nonpasteurized (20 °C) treatments, particularly in the nonamended soil. Microscopic observation revealed a small amount of internal root colonization (5% to 7%), mainly as intraradical hyphae and infrequent vesicles; extraradical hyphae were abundant. This indigenous endophyte was less detectable in the inoculated 20 °C treatments, given the more dense colonization habit of *G. intraradices*. Colonization by this endophyte complicated the root colonization results for this particular T × VAM treatment, but analyses indicated no significant differences in colonization between the 20 and 50 °C treatments in any CGP treatment (Table 2).

Root colonization by *G. intraradices* ranged from 20% to 39%, and was significantly greater in the presence of 2% CGP or CGP extract compared to the nonamended control (Table 3). Differences in colonization were significantly influenced by CGP alone, and not by temperature.

Our results partially confirm the hypothesis that organic soil amendments with high humic content stimulate plant

Fig. 1. Influence of composted grape pomace (CGP), its water extract (CPGex), and soil temperature treatments (20 [unheated], 50 or 100 °C) (68, 122, or 220 °F) on shoot biomass of nonmycorrhizal (-VAM) and mycorrhizal (+VAM) (*Glomus intraradices*) onions. Bars with the same letter within a VAM treatment (-VAM = lower case; +VAM = upper case) are not significantly different at $P \leq 0.05$ (28.35g = 1.0 oz).

Fig. 2. Influence of composted grape pomace (CGP), its water extract (CPGex), and soil temperature treatments (20 [unheated], 50 or 100 °C) (68, 122, or 220 °F) on root biomass of nonmycorrhizal (-VAM) and mycorrhizal (+VAM) (*Glomus intraradices*) onions. Bars with the same letter within a VAM treatment within each CGP treatment are not significantly different at $P \leq 0.05$ (-VAM = lower case; +VAM = upper case) (28.35g = 1.0 oz).

growth by stimulating beneficial soil microorganisms such as mycorrhizal fungi. Since the experiment was conducted in P deficient soil, the effect could have been that the amendments simply provided a source of P to the plants. When combined with VAM fungi, however, CGP stimulated greater root biomass, and this in concert with extraradical VAM fungal hyphae probably provided improved nutrient uptake for the plants. The interaction was strongest when the water extract of CGP was used, suggesting that nutrients, especially P, were already in an available form for uptake. VAM colonization is normally suppressed or eliminated by high concentrations of inorganic P (Biermann and Linderman, 1983), but that appears not to be the case with organic forms of P. VAM fungi may be more stimulated by organically bound P (Jayachandran et al., 1992), and are not inhibited by high concentrations (Tarafdar and Marschner, 1994). Whether or not the CGP extract stimulated greater amounts of extraradical VAM fungal hyphae was not measured, but if that had been the case, then they would have provided increased absorptive capacity that would have contributed to the increased plant growth. We assume improved P uptake in this P-deficient soil, although P content in the tissues was not measured.

In this experiment we used differential temperature treatments to selectively eliminate segments of the soil microflora (Baker and Roistacher, 1957). Our results show that temperature treatments inconsistently decreased granular CGP-stimulated shoot growth in both nonmycorrhizal and mycorrhizal onions (Figs. 1 and 2), but not with the extract. The decrease was more distinct in nonmycorrhizal onions, probably because of the enhanced growth stimulated by the indigenous endophyte present in the unheated (20 °C) controls. Effects of heat treatments on root growth were inconsistent, and there was generally no reduction in root growth response due to temperature treatments. These results suggest that soil microbes might have had an influence on the growth response from CGP amendment, but their role is not clear.

Our results indicate that VA mycorrhizae and organic substances with high humic content interact synergistically, enhancing plant growth more in combination than separately.

Table 3. Influence of composted grape pomace (CGP), its water extract, and soil temperature treatments on root colonization of onions.

CGP treatment ^z	VAM treatment ^y [°C (°F)]	Soil temp (%) ^x	Root colonization
Control/ None	-VAM	20 (68)	7.0
		50 (122)	---
		100 (220)	---
	+VAM	20 (68)	23.1 ab
		50 (122)	20.1 a
		100 (220)	21.9 a
2% CGP	-VAM	20 (68)	6.9
		50 (122)	---
		100 (220)	---
	+VAM	20 (68)	29.6 cd
		50 (122)	28.1 bc
		100 (220)	39.0 e
CGPex	-VAM	20 (68)	4.8
		50 (122)	---
		100 (220)	---
	+VAM	20 (68)	35.9 c
		50 (122)	35.3 de
		100 (220)	33.4 cde

^zCGP = granular composted grape pomace mixed 2% (vol) in 1 sand : 1 loam; CGPex = water extract of granular composted grape pomace.

^yVAM = not inoculated (-VAM) or inoculated with *Glomus intraradices* (+VAM).

^xMeans with the same letter are not significantly different at $P \leq 0.05$; untransformed data.

Since evaluation of the microbial shifts induced by both the humic substances and the VAM fungi was not done, it is not possible to draw conclusions about the involvement of soil microbes that participate in the mycorrhizal growth enhancement effect. However, the results indicate that their removal by heat treatments may alter the growth-enhancing effects attributed to mycorrhizae. In addition, our results indicate that such microbes might have been stimulated by the addition of the 2% CGP, CGP extract, or by the presence of mycorrhizal fungi in the mycorrhizosphere (Linderman, 1988). The selective increase in diversity of bacteria resulting from nutrient enrichment by VAM fungal hyphae (Andrade et al., 1997) in the hyphosphere could result in microbes with growth-stimulating properties. Those same microbes could be further stimulated by the presence of humic substances in the CGP, as suggested by Visser (1985a).

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