Endomycorrhizae and Growth of ‘Sweetheart’ Strawberry Seedlings

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Abstract. Growth of strawberry (*Fragaria ×ananassa* Duch. ‘Sweetheart’) seedlings inoculated with six spore levels ranging from 0 to 12,000 spores/plant of the mycorrhizal fungi *Glomus intraradices* Schenck and Smith was studied in the greenhouse and with greenhouse plants subsequently moved to the field. Plant height, leaf area, and number of leaves increased significantly with inoculum spore densities ranging from 750 to 12,000 spores/plant in relation to control plants in the greenhouse and field. In the greenhouse, there was a linear relationship between percent infection and spore density, although the relationship was cubic in the field. In the field study, control plants were infected with indigenous mycorrhizae, but inoculated plants produced more runners than the control plants, and foliar Cu and Ca increased linearly with increased spore density. Inoculated plants contained significantly more dry matter than the controls. For inoculated plants, root dry weight increased linearly with increased spore density. We conclude that a minimum spore density of 750 spores/plant is sufficient for a positive growth response.

Strawberry parent selection for breeding programs focuses on traits such as fruit size, flesh firmness, color, disease resistance, and yield. The breeder selects promising parents, conducts controlled crosses, and achenes are germinated in greenhouses and subsequently planted in the field. Some plants may not be selected due to seedling death or poor growth, which may be related to soilborne diseases, insufficient nutrients, nematodes, and poor root growth in seedling establishment (Maas, 1984).

Vesicular–arbuscular mycorrhizae (VAM) improve plant growth through increased uptake of P, reduction of soilborne diseases (Maronek et al., 1981), increased plant vigor and survival (Solbrig, 1981), and reduced transplant injury (Menge, 1982). Inoculation of seedlings with mycorrhizal fungi resulted in increased plant growth of tomato (*Lycopersicon esculentum* Mill.) (Daft and Nicolson, 1969), increased runner formation (Holevas, 1966), or more flowers and fruit (Daft and Okusanya, 1973) in strawberry. Although soils may naturally contain VAM (Khan, 1972), stimulation of growth by indigenous mycorrhizae may not be sufficient for significant growth response (Powell, 1981). Daft and Nicolson (1966) noted that initially low spore-count concentration stimulated the host less than more concentrated inoculum. Although other studies have shown growth stimulation by inoculation with mycorrhizal

fungi (Diem et al., 1981; Robertson et al., 1988; Ross and Harper, 1970), inoculum levels of 10,000 spores of *G. mosseae* (Nicol. & Gerd.) Gerdmann & Trappe per plant are unnecessary for maximum plant growth in citrus (Nemec, 1983). In a strawberry breeding program, the increased growth obtained by inoculating transplants with mycorrhizae could be useful since low vegetative vigor has been observed during plantation establishment in nonfumigated soils (Larson and Shaw, 1995). Moreover, breeders select varieties for enhanced fruit production, and at the reproductive stage, a high P demand exceeds the capacity of the root system (Dunne and Fitter, 1989). Furthermore, effect of mycorrhizal infection on parent plants may be carried to offspring (Koide and Lu, 1992). The present study was done to 1) evaluate the effect of mycorrhizal infection on strawberry seedling growth and physiology and 2) determine the minimum inoculum density needed to obtain a positive growth response in the field.

Materials and Methods

Production of pot-cultured inoculum. The endophyte *Glomus intraradices* was used as the fungal inoculum. Plastic pots (3000 cm³) were filled with sterilized masonry sand and mixed with 0.2 g of Osmocote 17N–9P–13K (3 to 4 months release rate) fertilizer/L (Grace-Sierra, Houston). Each container was inoculated with 4 g of inoculum of *glomus* (1000 spores/g), and 50 sorghum (*Sorghum vulgare* L.) seeds were planted in each container. The pots were kept in the greenhouse at 25 to 32 °C and water was applied as needed. The sorghum was grown for 6 months and application of water was reduced in the final 3 weeks to maximize spore production (Menge, 1982). After 6 months, plants were cut near the base

and one-half of the sand–spore mixture was mixed with sterilized sand (1:1), and a new set of pots was filled with this mixture. As earlier, sorghum seeds were grown for 6 months in a manner to ensure maximum spore production.

Determination of spore concentration. Random samples of the spore–sand mixture were taken from seven pots mixed thoroughly and bulked to ensure uniformity. A 50-g sample was subjected to wet-sieving and decanting (Gerdemann and Nicolson, 1963) to separate spores from root pieces. The volume of the sand–water mixture was recorded and 5 mL of this mixture was placed in a petri dish marked with 1-cm grids and the number of spores per 10 squares was counted. From this, the number of spores per original volume was calculated. An average of three samples was taken to determine the spore concentration in the sand inoculum.

Treatments. The experiment was conducted in the greenhouse and in the field using six treatments and four replications in a randomized complete-block design. The treatments consisted of inoculum mixture consisting of spores, sand, and root pieces placed into 25 × 25 × 5-cm flats. On the basis of 50 seedlings/flat, inoculum mixtures were adjusted to produce six spore densities (SD): 0, 750 ± 36, 1500 ± 72, 3000 ± 145, 7500 ± 362, and 12,000 ± 579 spores/seedling. For each flat, the remaining volume was filled and mixed with Sunshine No. 2 peat (Fissions Horticulture, Mississauga, Ont., Canada) for a sand : peat ratio of 1:2, 1:1, 2.5:1, 9:1, and 25:1 for each treatment. The control treatment consisted of no spores, but had the same proportion of sand : peat mix corresponding to each treatment. For all treatments, Osmocote (17N–9P–13K) slow-release fertilizer was added at 0.2 g·L⁻¹.

Seeds (100) of the homozygous strawberry ‘Sweetheart’ (Park Seed, Greenwood, S.C.) were planted in trays on 30 June 1992 and were subsequently thinned to 50 seedlings/tray. Ten plants from each treatment were randomly selected and planted in the field at the Univ. of Arkansas Fruit Substation, Clarksville, on 3 Oct. 1992. The soil was a Linker sandy loam (Typic Hapludults) with pH 6.1 and 0.8% organic matter. All plants were planted at 20 × 20-cm spacing. Urea, at 43 kg·ha⁻¹, was applied on 1 Nov. 1992. The SAS general linear model procedure was used to analyze the data and perform the regression analysis (SAS Inst., Cary, N.C.).

Infection determination. The roots were cleared by boiling them in 10% potassium hydroxide solution. Trypan blue (0.25 g) was mixed with 250 mL of lactophenol (Phillips and Hayman, 1970). Roots were submerged in this 0.1% solution, autoclaved at 101 °C and 1 MPa for 3 min, and then washed with water and autoclaved in an additional lactophenol solution for 3 min. The roots were washed and spread out evenly in petri dishes marked with 2.5-cm grids. The percent infection was determined using the gridline intersect method (Giovannetti and Mosse, 1980).

Plant measurements. In the greenhouse, the number of plants having four, five, six, or seven leaves was counted on all seedlings at

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24, 34, 44, and 54 days after planting (DAP), respectively (i.e., having four leaves at 24 days, five leaves at 34 days, etc.). Plant height was determined on 15 randomly selected plants for each treatment at 34, 51, and 68 days DAP. On day 90, plants from all treatments were harvested, and 15 randomly selected plants were oven-dried at 80 °C for 4 days and total dry weight was determined.

In the field, percent stand was determined for all treatments on 11 Apr. 1993, and for six randomly selected plants per treatment, the number of leaves per plant was counted on 26 May 1993. Leaf area (mother plant plus runner), measured with a leaf area meter (Lambda Instrument Corp., Lincoln, Neb.), and the number of runner plants per mother plant were determined on 5 June 1993 on five randomly selected plants in each treatment. Four randomly selected plants (mother plant plus runner) were destructively harvested on 5 June, oven-dried at 80 °C for 4 days, and dry weights recorded.

Incidence of root infection was determined on 1 Oct. 1992 and 5 June 1993 by random sampling of five and 10 plants, respectively, from each noninoculated (control) treatment replication and pooling the roots within a replication. For each inoculated treatment, four root samples per replication were pooled and incidence of infection determined. Foliar nutrient analyses were conducted on nonsenescent, fully expanded leaves for four randomly sampled plants from each inoculated treatment and for five plant samples pooled for each control treatment replication. Leaf samples were oven-dried at 80 °C for 3 days, then ground using a Wiley mill (Arthur Thomas, Philadelphia) to pass through a 16-mesh (1.02-mm pores) screen. Total N was determined with the combustion method using a Leco FP228 (Leco, St. Joseph, Mich.) N determinator. All other elements were determined by inductively coupled plasma spectrometry following HNO₃ digestion. Samples were analyzed at the Agricultural Services Laboratory, Dept. of Agronomy, Univ. of Arkansas, Fayetteville.

Results

Greenhouse studies

Leaf growth. Some mycorrhizal plants had more leaves per plant than nonmycorrhizal plants at each examination (DAP) (Fig. 1). At 24 DAP, inoculation with 1500 or 3000 spores resulted in more plants that had four leaves compared to SD of 0, 7500, or 12,000. At 34 DAP, the 1500 SD resulted in more plants with five leaves than 0 or 12,000 SD. The 750 and 3000 SD also were superior to the control. At 44 DAP, the 1500 SD was superior to 0, 7500, and 12,000 SD. The 3000 SD was associated with more plants with six leaves than the control at this date. On the final measurement date (54 DAP), plants with seven leaves were more common with 750, 1500, and 3000 SD than with the control. There was a significant quadratic relationship between SD and the number of plants that had four, five, six, or

Fig 1. Influence of spore density on leaf production by 'Sweetheart' strawberry seedlings. Plants with four, five, six, and seven leaves determined at 24, 34, 44, and 54 days, respectively (i.e., four leaves at 24 days, five leaves at 34 days, etc.). Quadratic regression 24 DAP, $Y = 6.35 + 8.6X - 1.4X^2$; 34 DAP, $Y = 7.94 + 14.1X - 2.19X^2$; 44 DAP, $Y = 10.47 + 8.43X - 1.40X^2$; 54 DAP, $Y = 16.59 + 6.41X - 0.88X^2$; significant at $P \leq 0.01$; $n = 4$ with 50 subsamples.

seven leaves at 24, 34, 44, and 54 DAP ($P \leq 0.01$).

Seedling height. At 51 and 68 days, inoculated plants were taller than control plants (Table 1), but there was no effect of inoculum SD on plant height ($P > 0.05$), and there was a significant interaction between mycorrhizal inoculation and measurement dates for seedling height ($P < 0.01$) (Table 1).

Drymatter production. Mycorrhizal strawberry seedlings produced significantly more total dry weight than the controls ($P < 0.01$), and there was a linear positive relationship between total dry weight of inoculated seedlings and SD ($P \leq 0.0001$) (Table 2). However, the nonlinear components were nonsignificant for the mycorrhizal seedlings ($P > 0.05$).

Field studies

At the time of removal from the greenhouse, the two highest SD (7500 and 12,000) resulted in the highest infection incidences (Table 3). At the time of removal from the field, these same treatments resulted in infection rates of $\approx 60\%$, while the infection was slightly higher, and equal, with 750 and 1500 spores/plant. One-third of the control plants were infected with indigenous mycorrhiza. There was a linear relationship between SD and percent infection at the time of removal from the greenhouse; however, at removal from the field, there was a cubic relationship between SD and percent infection ($P = 0.02$).

Mycorrhizal infection had no effect on

plant survival ($P > 0.05$), which ranged from 80% to 95%, but inoculated strawberry plants had significantly more leaves, larger leaf area, and more runners per plant than the controls ($P < 0.01$) (Table 4).

The concentrations of major and most of the minor nutrients in leaves were similar for inoculated and the control plants. However, there was a linear relationship between spore density and Ca and Cu concentrations; but the nonlinear components were nonsignificant ($P > 0.05$) (Table 5). Root dry weights decreased linearly with increasing SD ($P = 0.03$). The

Table 1. Analysis of variance of greenhouse-grown mycorrhizal and nonmycorrhizal strawberry seedling height at 34, 51, and 68 days.

Treatment	Mean seedling ht (cm)	
	Inoculated	Control
Days		
34	1.07 $\pm$ 0.54 ^z	0.80 $\pm$ 0.42 ^z
51	2.31 $\pm$ 0.92	1.56 $\pm$ 0.71
68	3.70 $\pm$ 0.94	2.44 $\pm$ 0.88
Mean	2.36 $\pm$ 0.06	1.60 $\pm$ 0.06
Significance		
Treatment (Trt)		
(Inoculated $\times$ noninoculated)	0.0001***	
Spore density	0.66 ^{NS}	
Trt $\times$ spore density	0.54 ^{NS}	
Trt $\times$ day	0.0001***	
Spore density $\times$ day	0.63 ^{NS}	

^zMeans $\pm$ SE.

^{NS}, ***Nonsignificant or significant at $P \leq 0.001$, respectively; $n = 4$, with 15 subsamples per replication.

Table 2. Effect of mycorrhizal spore density on total dry matter of greenhouse-grown 'Sweetheart' strawberry seedlings 90 days after planting.

Spore density (no./plant)	Total dry wt (g) ^z
0	1.45
750	2.01
1,500	2.10
3,000	2.33
7,500	2.50
12,000	3.50
Significance	
Inoculated vs. noninoculated	**
Spore density	
Linear	0.0001
Quadratic	0.08
Cubic	0.16

^zn = 4, with 15 subsamples per replication.

**Significant at $P \leq 0.01$.

Table 3. Infection percentage of 'Sweetheart' strawberry seedlings inoculated with *Glomus intraradices*.^z

Spore density (no./plant)	Infection (%) at removal from	
	Greenhouse ^y	Field ^x
0	0	33
750	45	65
1,500	50	65
3,000	59	59
7,500	62	56
12,000	72	60
Significance		
Linear	0.001	0.28
Quadratic	0.302	0.16
Cubic	0.114	0.02

^zFour subsamples from each replication were taken for infection measurement for inoculated treatments.

^yPercent infection was estimated on greenhouse-grown seedlings on 1 Oct. 1992, 90 days after planting. Control treatments were pooled with five root samples per replication.

^xPercent infection was estimated on field-grown plants 1 day after removal from the field. Control treatments were pooled with 10 root samples per replication.

most dry matter per plant was obtained with the 750 spores per plant (Table 6), and inoculated plants produced significantly higher shoot and root dry matter than noninoculated controls ($P < 0.01$). Inoculated strawberry plants had significantly higher root : shoot ratios than the controls ($P < 0.01$); moreover, a significant quadratic relationship existed between SD and the root : shoot ratio (Table 6).

Discussion

The mycorrhizal fungus *G. intraradices* increased strawberry plant growth in the greenhouse and in the field compared to noninoculated plants. These results corroborate other findings with strawberries (Holevas, 1966; Kiernan et al., 1984; Robertson et al., 1988). In the greenhouse, infection of *G. intraradices* increased linearly with increasing inoculum density. Although it has been reported that 100 spores of *Glomus* E3 per strawberry plant resulted in a 70% infection rate (Koomen et al., 1987), we found that 12,000 spores per plant resulted in a similar infection rate. However, after field-planting, the infection rates for all

Table 4. Growth response of field-grown 'Sweetheart' strawberry seedlings infected with various spore densities.

Spore density (no./plant)	Leaf count ^z	Leaf area ^y (cm ²)	Runners (no.) ^x
0	4.2	136	6.1
750	5.4	168	6.1
1,500	5.1	197	7.2
3,000	5.3	196	7.1
7,500	5.1	194	6.8
12,000	5.1	158	6.6
Significance			
Inoculated vs. noninoculated	**	**	**
Spore density			
Linear	0.38	0.25	0.92
Quadratic	0.81	0.06	0.43
Cubic	0.83	0.54	0.27

^zSix subsamples per replication counted on 26 May.

^yTwo subsamples per replication counted on 5 June.

^xFive subsamples per replication counted on 5 June.

**Significant at $P \leq 0.01$.

Table 5. Concentration of Ca and Cu in leaves of field-grown 'Sweetheart' strawberry seedlings.

Spore density (no./plant)	Foliar elements (dry wt basis) ^z	
	Ca (%)	Cu (mg·kg ⁻¹)
0	1.0	4.2
750	1.0	3.7
1,500	1.0	4.2
3,000	1.2	5.0
7,500	1.2	4.0
12,000	1.5	7.5
Significance		
Spore density		
Linear	0.02	0.02
Quadratic	0.90	0.20
Cubic	0.44	0.16

^zFoliar samples collected from four subsamples per replication. Five plant subsamples from each control treatment were pooled per replication.

treatments were similar. This agrees with findings reported on infection of strawberry by *G. intraradix* V18 and *G. intraradix* V20 (Vestberg, 1992a).

Although Niemi and Vestberg (1992) obtained no differences in total shoot and root biomass between controls and mycorrhizal plants in micropropagated seedling strawberries, enhanced dry matter production has been reported with *Glomus* spp. CPH-23 on micropropagated strawberry (Chavez and Ferrera-Cerrato, 1990). In our greenhouse study, mycorrhizal plants at the highest inoculum level produced 70% more total dry matter than the controls. In a field study, Robinson (1984) observed no growth differences between inoculated and noninoculated strawberry plants. The findings of our field study corroborate findings of Vestberg (1992a) and Niemi and Vestberg (1992) in which mycorrhizal strawberry transplants that were growing in the field grew better than the control plants.

Foliar nutrient concentration in shoots of mycorrhizal plants showed a linear relationship for Ca and Cu with increasing spore density. However, control plants and mycorrhizal plants had similar amounts of other elements, possibly as a result of infection by indigenous mycorrhiza in the controls. In-

creased growth of inoculated plants could have been due to increased speed of regrowth (Barrows and Roncadori, 1977) or reduced disease incidence from soilborne pathogens (Schenck and Kellam, 1978). As in other studies (Hrselova et al., 1989; Niemi and Vestberg, 1992; Vestberg, 1992b), mycorrhizal plants produced more runner plants than the controls.

In our study, higher root : shoot ratios for mycorrhizal plants could be due to higher root dry weight of mycorrhizal than nonmycorrhizal plants, although this is contrary to the results of Kiernan et al. (1984), who found a higher root : shoot ratio in nonmycorrhizal than in mycorrhizal strawberry plants. Control plants, although colonized with indigenous mycorrhiza, did not have more root dry matter than mycorrhizal strawberry plants. Although infected with indigenous mycorrhiza, control plants had less root infection than the inoculated plants, which agrees with a study by Vestberg (1992a), also on strawberry. There was no correlation between percent infection and growth. Similar findings have been reported by Williams et al. (1992) and Koomen et al. (1987). Indigenous mycorrhiza may have influenced the growth of strawberry plants in the control (Powell, 1981). However, inoculated plants may have had an advantage over the indigenous infected plants since they were already colonized before planting (Lopez-Aguillon and Mosse, 1987). Contrary to findings by Vestberg (1992a), overwintering did not decrease the ability of introduced fungus to increase growth of the plants in our studies.

Biermann and Linderman (1983) reported that pretransplant inoculation could permit selection and establishment of more efficient strains of mycorrhiza that could colonize new roots after plant establishment. Exposing seedlings in seedling flats to VAM infection would tend to equalize VAM infection before field planting. Thus, in the field all seedlings would be more nearly equal in VAM, whereas indigenous VAM infection in nonfumigated soils would be variable. In a nonfumigated soil, pathogenic fungi or low seedling vigor in plants after seedling establishment may result in these plants being discarded at selection, thus leading to the loss of a superior genotype (J.N. Moore, personal communication). Seedling diseases caused by plant pathogenic fungi could be overcome by VAM, which could thus increase the chances of selecting a desired genotype in a breeding program. Our study demonstrates that it is possible to introduce a mycorrhizal fungus into strawberry roots via seed bed application. A spore density of 750 spores/plant was sufficient for a positive growth response in nonsterilized preinoculated soil.

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Table 6. Effect of mycorrhizal spore density on strawberry plant dry weight and root : shoot ratio of field-grown 'Sweetheart' strawberry plants.

Spore density (no./plant)	Dry wt (g) ²			Root : shoot
	Shoot	Root	Total	
0	15.5	1.2	16.7	0.009
750	28.1	2.5	30.6	0.014
1,500	26.6	2.9	29.5	0.015
3,000	28.0	2.4	30.4	0.012
7,500	22.1	1.5	23.6	0.008
12,000	22.6	2.1	24.7	0.014
Significance				
Inoculated vs. noninoculated	**	**	**	*
Spore density				
Linear	0.10	0.03	0.08	0.43
Quadratic	0.66	0.09	0.56	0.02
Cubic	0.55	0.26	0.49	0.48

²Four subsamples per replication measured on 5 June.

*,**Significant at $P \leq 0.05$ or 0.01 , respectively.

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