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Seasonal dynamics of the association between sweet potato and vesicular-arbuscular mycorrhizal fungi

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Abstract. To better understand the behavior of selected vesicular-arbuscular mycorrhizal (VAM) isolates in the field, we documented the growth of roots, root hairs, and VAM colonization of inoculated and noninoculated sweet potato plants (*Ipomea batatas* (L.) Lam. cv White Star) over a growing season. We also determined the seasonal dynamics of P and Zn uptake, and shoot and storage-root growth. Shoot cuttings were inoculated with an isolate of either *Glomus etunicatum* Becker and Gerdemann or *Acaulospora rugosa* Mortan, or were not inoculated, and were harvested 2, 4, 8, 13, 20, and 27 weeks after planting (WAP). At each harvest, roots were sampled at 0 to 30, 30 to 60, and 60 to 90 cm depths and at 0, 23, 83, and 116 cm from the base of the shoot. At the end of the study, the roots of three noninoculated plants were sampled by soil horizon. Inoculation had no affect on shoot growth or total shoot uptake of P and Zn; shoot dry mass and P and Z content increased rapidly up to 20 WAP, while shoot length continued to increase through 27 WAP. Shoot-P concentration of plants inoculated with *A. rugosa* at 2 and 8 WAP were higher than the noninoculated plants, while shoot-Zn concentration was not affected by inoculation. Storage-root yields of inoculated plants were higher than yields for noninoculated plants. Root length density, and percentage of root length with root hairs and VAM colonization were highest and most dynamic near the base of the plant. Percentage of root length colonization by VAM fungi was highest in the E2 horizon, intermediate in the Bh horizon, and lowest in the Ap horizon. Percentage of root length with root hairs had the opposite pattern. Intensive measurements of root characteristics close to the base of the plant, and shoot P-content and concentration during the period of rapid yield production, provided the most useful data for evaluating the activity of effective isolates.

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Introduction

To better understand the function of vesicular-arbuscular mycorrhizal (VAM) fungi in promoting plant growth it is important to view the symbiosis temporally – over the life of the plant – and spatially – throughout the full extent of the root system. Plant nutrient and water demand, allocation of carbohydrates and mineral nutrients, as well as benefits attributed to VAM fungi can vary considerably through a growing season (Douds and Chaney 1986; Fitter 1986; Dunne and Fitter 1989). Root and mycorrhiza function also varies with soil water content, soil horizon, and proximity to the point of inoculum placement. In addition, root hairs, which may be functionally analogous to external hyphae of VAM fungi in terms of water and P uptake, may be suppressed by mycorrhiza (O'Keefe 1989), and are sensitive to soil water content and P level (Mackay and Barber 1984).

Yield increases after inoculation with VAM fungi are attributed generally to colonization by the introduced fungus followed by increased uptake of P or other diffusion-limited nutrients such as Zn (Abbott and Robson 1984). O'Keefe and Sylvia (1992) documented the chronology of mycorrhiza-mediated P uptake for glasshouse-grown sweet potato. The relationship between inoculation and growth response is often obscured in field experiments, however, because there may be little difference in root colonization between plants incoculated with VAM fungi and noninoculated controls due to the presence of indigenous VAM fungi (Mosse 1977; Medina et al. 1988). This would be true particularly in nonfumigated soils, late in the growing season, and at points distant from the inoculum. Furthermore, the P concentrations of plants among various inoculation treatments may be different only during a portion of the growing season (Fitter 1986; Dunne and Fitter 1989). As plant-growth rate increases, dilution effects may obscure

treatment differences in initial-P concentrations, while differences in total-P content may be carry over effects of early growth. Plant partitioning of P may also change during different plant-growth stages (Dunne and Fitter 1989).

The fungal isolates used in this study were shown previously to be effective at promoting the growth of glasshouse-grown sweet potato under P-deficient conditions (Hung et al. 1990). To better understand the behaviour of these isolates in the field, we documented VAM development in relation to that of the plant. Our specific objectives were to (1) determine the distribution of roots, root hairs, and VAM colonization of sweet potato over a growing season and (2) evaluate the relationships among seasonal variation in root length density, root hairs, VAM colonization, P and Zn uptake, shoot growth, and storage-root yield.

Materials and methods

Experiment design and sampling strategy

The experiment was a three (inoculations) by six (harvest times) factorial with a randomized complete block design and three replications per treatment. Sweet potato plants were inoculated with an isolate of *Glomus etunicatum* Becker and Gerdemann (INVAM FL906) or *Acaulospora rugosa* Mortan (INVAM FL981), or were not inoculated. Plants were harvested 2, 4, 8, 13, 20, and 27 weeks after planting (WAP). At each harvest, roots were sampled at 0 to 30, 30 to 60, and 60 to 90 cm depths and at 0, 23, 83, and 116 cm from the base of the shoot.

Cultural practices

The field soil was a Pomona sand (sandy, siliceous, hyperthermic, Ultic Haplaquod) that was intensively managed for vegetable production. Initial soil characteristics are presented in Table 1. A 15-0-14 analysis fertilizer was incorporated at a rate of 224 kg ha^{-1} prior to bed preparation. Additional fertilizer applications were side dressed at 36 kg ha^{-1} at planting, and 8 and 12 WAP.

The field was fumigated with Telone II (1,3-dichloropropene) at the rate of 118 l active ingredient (a.i.) ha^{-1}, 9 weeks before planting to control soil-borne pathogens. For weed control, Poast (2[1-(ethoxyimino)butyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen-1-one) was applied at the rate of 0.43 kg a.i. ha^{-1} at four and five WAP. For insect control, Ambush ((3-phenoxyphenyl)methyl(I)*cis*,*trans*-ethenyl-2,2-dimethcyclopropane-carboxylate) was applied at the rate of 1.72 l a.i. ha^{-1} at 1 WAP and Thiodan (6,7,8,9,10,10-hexachloro-1,5,5a,6,9,9a-hexahydro 6,9,-methano-2,4,3-benzodioxatheipin-3-oxide) was applied at the rate of 0.45 kg a.i. ha^{-1}, at 4 WAP. The fungicide Bravo (tetrachloroisophthalonitrile) was applied at the rate of 0.95 l a.i. ha^{-1}, at 4 WAP.

Shoot cuttings were planted 1.5 m apart on 1.5 m centers directly into the bed, in the case of noninoculated plants, or over a 5-g (fresh weight) pad of inoculum buried 5 cm deep, from pot cultures of either *G. etunicatum* or *A. rugosa*. A slurry consisting of 20 g (fresh weight) of pot culture material from both isolates suspended in 2 l of H_2O was sieved three times through a 1-mm-mesh screen and five times through a 22.0-μm-mesh screen. This was placed in the planting hole at a rate of 10 ml per plant to all plants in an attempt to standardize introduced bacterial populations among treatments. The propagule densities of the inocula and of the indigenous VAM fungi at planting were estimated by most probable number (MPN) assays (Daniels and Skipper 1982).

Table 1. Soil characteristics at three depths prior to fertilization. Values represent the means of three samples, and each sample was a composite of two borings 3 m apart

Depth (cm)	K[a] (mg kg^{-1})	P[a] (mg kg^{-1})	Zn[a] (mg kg^{-1})	pH[b] (mg kg^{-1})	Organic matter (mg g^{-1})
0–30	12 (3)	24 (9)	2.8 (0.3)	5.5 (0.2)	13 (3)
30–60	13 (4)	159 (70)	1.5 (0.8)	5.3 (0.01)	16 (4)
60–90	12 (9)	60 (11)	0.2 (0.04)	5.5 (0.01)	5 (1)

[a] Melich I extractable, standard deviation in parentheses
[b] In 1:2 soil:H_2O suspension

Plant sampling and tissue analysis

At each harvest, shoot length, shoot dry mass, P and Zn concentration of the shoot, and storage-root yield were determined. Dry mass and mineral concentrations were determined for entire shoots at the first three harvests. For the last three harvests, fresh mass was determined in the field and shoot subsamples (approximately 1 kg) were taken randomly for determination of dry mass and nutrient content and these values were adjusted to a whole-plant basis. Tissue samples were dried at 70° C to constant weight and ground to pass through a 2-mm sieve. Subsamples (0.2 g) were dry-ashed at 500° C for 3 h, digested in 10 ml of 1.0 N HCl on a warm hotplate, evaporated to dryness, resuspended in 5 ml of concentrated HCl, and digested a second time. The resulting digest was taken to dryness and the resuspended in 20 ml of 0.1 N HCl. The final solution was analyzed using atomic adsorption spectrophotometry for Zn and colorimetrically for P (Murphy and Riley 1962).

Root sampling

Complete root systems were excavated at 2 and 4 WAP. For the remainder of the harvests, root systems were sampled with a sharp, 7-cm-diameter bucket corer to a depth of 90 cm. Two cores were taken from each distance-depth combination and the data averaged, except for the samples taken directly over the base of the main shoot where the sample consisted of one core. Roots were removed from the cores in the field by wet sieving and decanting onto 2.0- and 0.199-mm mesh screens. Total root length, percentage of the root with root hairs, and percentage of the root length colonized by VAM fungi were determined by the gridline-intersect method (Giovannetti and Mosse 1980).

Samples by soil horizon

At the end of the study, roots of three noninoculated plants were sampled in the Ap, Bh, and E2 horizons. Average depths for the respective horizons were 0–41, 41–60, and 60–276 cm. Pits were dug (3 m long × 1 m deep × 1 m wide), longitudinal to the hill and centered on a plant. A sample of roots (approximately 25 g) was removed from each horizon and VAM colonization and root hairs were quantified as described above.

Statistical analysis

Data were subjected to analysis of variance using the general linear models procedure (SAS 1985). The variables were analyzed

further when $P \leq 0.10$. The effects of harvest time, depth, and distance from the base of the shoot were analyzed by regression. The effect of VAM inoculation was tested by single-degree-of-freedom contrasts comparing each of the two inoculated treatments to the control. Means of root length density, percentage of root length colonized by VAM fungi, and percentage of root length with root hairs were positively correlated with their variances and these data were power transformed, following the method of Glenn et al. (1987), before statistical analysis. Response-surfaces were generated for quantitative root variables from untransformed data using the minimum curvature method of grid interpolation (Golden Software 1989).

Results and discussion

VAM propagule numbers

The MPNs of the inocula were 42 propagules/10 g soil for *G. etunicatum* and 44 for *A. rugosa*. At planting, the MPNs of the indigenous VAM population were 0, 13, and 4.5 propagules/10 g at the 0- to 30-, 30- to 60- and 60- to 90-cm depths, respectively.

Shoot growth and nutrient content

Inoculation with VAM fungi had no affect on shoot growth, total shoot uptake of P and Zn, and shoot-Zn concentration. Maximum shoot dry mass was reached by 20 WAP (Fig. 1A) while shoot length continued to increase through 27 WAP (Fig. 1B). The total P and Zn contents of the shoots reached maximum levels by 20 WAP (Fig. 1C, D). Shoot-Zn concentration increased up to 8 WAP and the decreased, except for a slight increase in the last few weeks as shoots senesced (Fig. 1E).

The shoot-P concentrations of plants inoculated with *A. rugosa* at 2 and 8 WAP were significantly higher than the control (Fig. 2). A decrease in shoot-P concentration occurred across all inoculation treatments during the period of rapid shoot elongation (8 to 20 WAP) and was likely caused by a growth dilution effect. The drop in shoot-P concentration late in the growing season, when shoot mass was decreasing, suggests that there was a net movement of P out of the shoot, most likely to the fibrous or storage roots. Dunne and Fitter (1989) found that strawberry rhizomes are "recharged" with P towards the end of the growing season. Sweet potato may have a similiar strategy for storing P until the next season through reallocation of P from the shoots to the roots.

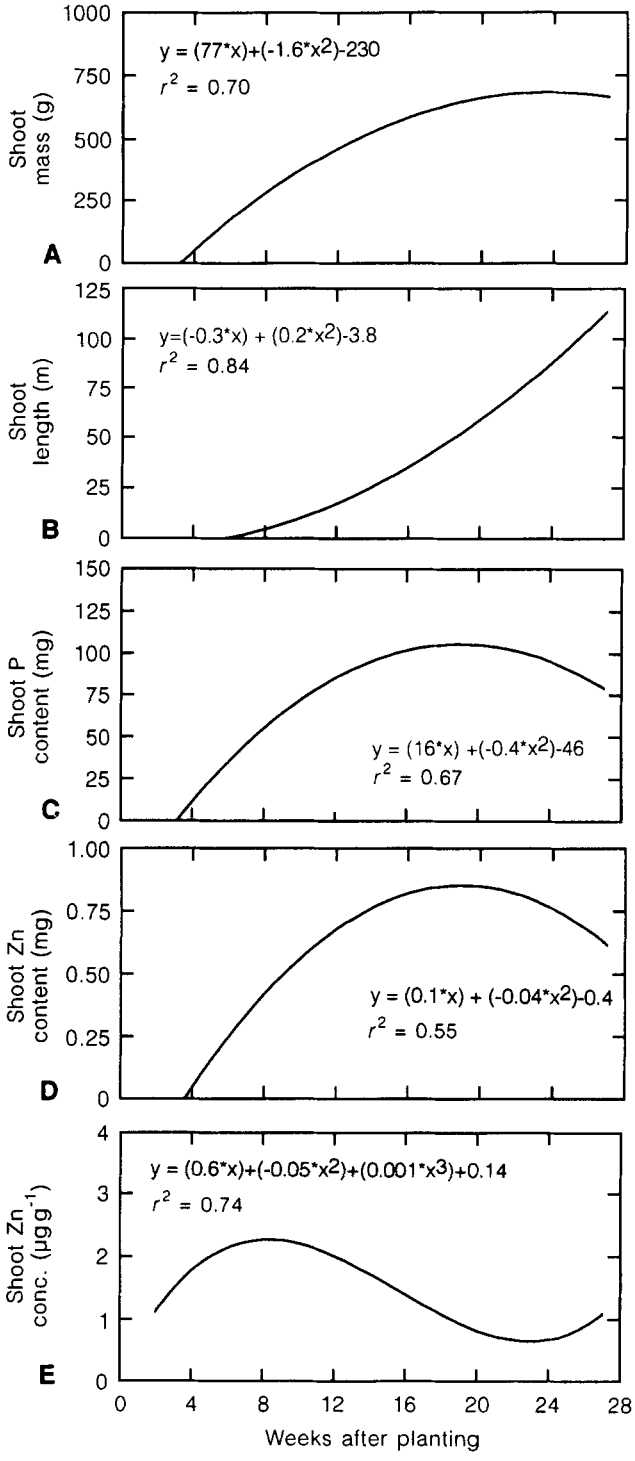

Fig. 1. **A** Shoot dry mass, **B** shoot length, **C** total shoot-P, **D** shoot-Zn content, and **E** shoot-Zn concentration of sweet potato over the 27-week growing season

Storage-root yield

At 20 WAP, storage-root yields of plants inoculated with *G. etunicatum* (2.3 kg/plant, $P \leq 0.05$) and *A. rugosa* (1.7 kg/plant, $P \leq 0.10$) were higher than yields for noninoculated plants (0.2 kg/plant). At 27 WAP, only plants inoculated with *A. rugosa* (2.9 kg/plant, $P \leq 0.10$) had higher yields than the noninoculated plants (1.2 kg/plant). Yields for *G. etunicatum*-inoculated plants were 1.7 kg/plant.

Root growth

Few roots were found in the 60- to 90-cm depth and this depth was excluded from the analysis. There were signif-

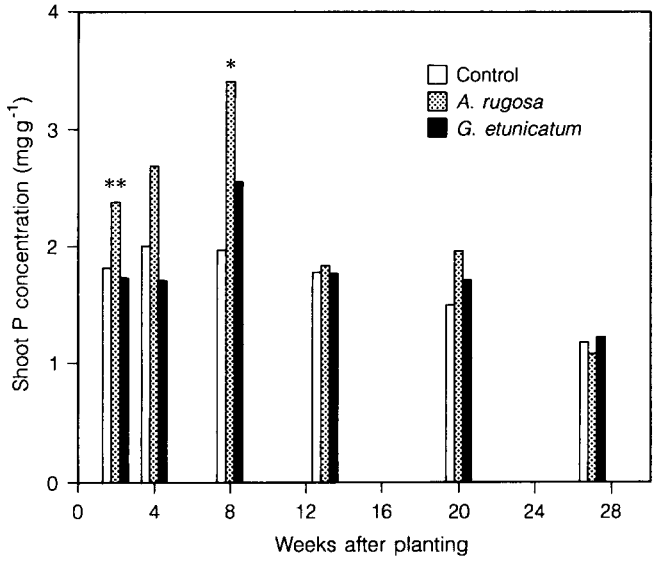

Fig. 2. Shoot-P concentration of sweet potato over the 27-week growing season. *Bars* represent the mean of three replicates. *Asterisks* (* = $P \leq 0.10$, ** = $P \leq 0.05$) indicate differences within a harvest date between the control and the inoculated treatments using single-degree-of-freedom contrasts

icant ($P \leq 0.10$) interactions of depth with the other variables, so separate analyses of variance were done on the other two depths (Table 2). In the 0- to 30-cm depth, root-length density was higher near the base of the shoot at all harvests except the last two (Fig. 3A, Table 3). At the last two harvests there was a decrease in root density around the base of the plant due to the appearance of storage roots. In the 30- to 60-cm depth, the only significant difference occurred 4 WAP (Fig. 3D, Table 3). The only effects due to inoculation were at 20 WAP and the 30- to 60-cm depth, where *G. etunicatum* (2.49 cm cm^{-3}) and *A. rugosa* (2.35 cm cm^{-3}) had higher ($P \leq 0.05$) root-length densities than the control (1.05 cm cm^{-3}).

It is surprising that inoculation effects on root-length density appeared only at 20 and 27 WAP. An environmental stress during the growing season may have accentuated the benefit of the introduced isolates (Sylvia and Williams 1992). During the latter part of the growing season, plants exhibited symptoms of water stress and rainfall was infrequent. An intermittent benefit of VAM corresponding to water stress has been reported by Fitter (1986) in grasslands. In addition, this was also the period with the most pronounced increase in storage-root yield, VAM colonization, and root hair formation in the inoculated plants compared to the controls.

Colonization by VAM fungi

At the 0- to 30-cm depth, colonization was more evenly distributed throughout the root zone than root-length density (Fig. 3B). There was a negative, linear relationship between distance and percent colonization at 8, 13, and 20 WAP, while at 2, 4, and 27 WAP the relationship was cubic (Table 3). At all harvests, r^2 values were low as colonization tended to occur in patches with many root samples having no colonization.

At the 30- to 60-cm depth, colonization appeared to be distributed throughout the root zone over the entire growing season, similar to that found in the 0- to 30-cm depth (Fig. 3E). However, there was no significant interaction between harvest time and distance from the base of the plant, and no significant effect of distance on colonization. The effect of harvest time at this depth was

Table 2. *P* values from analysis of variance by depth for root measurements during a 27-week field experiment. CV, Coefficient of variation

Source of variation	Root length density	Percentage of root length colonized	Percentage of root length with root hairs
0 to 30 cm			
Block (B)	0.7013	0.1055	0.3859
Inoculation (I)	0.3952	0.1519	0.8854
B*I	0.1657	0.1711	0.1059
Horizontal distance (Z)	0.0001	0.0001	0.0001
Harvest (H)	0.0001	0.0001	0.0001
H*Z	0.0001	0.0333	0.0001
I*H	0.2002	0.0001	0.0486
I*Z	0.9489	0.9459	0.8771
I*Z*H	0.5111	0.8526	0.9186
CV (%)	20	31	42
30 to 60 cm			
Block (B)	0.8702	0.8331	0.4786
Inoculation (I)	0.2350	0.2167	0.3469
B*I	0.4468	0.0279	0.0058
Horizontal distance (Z)	0.0001	0.0228	0.0001
Harvest (H)	0.0001	0.0001	0.0001
H*Z	0.0174	0.6052	0.2474
I*H	0.0292	0.0001	0.0782
I*Z	0.7473	0.7758	0.3570
I*Z*H	0.7958	0.7771	0.0060
CV (%)	26	36	65

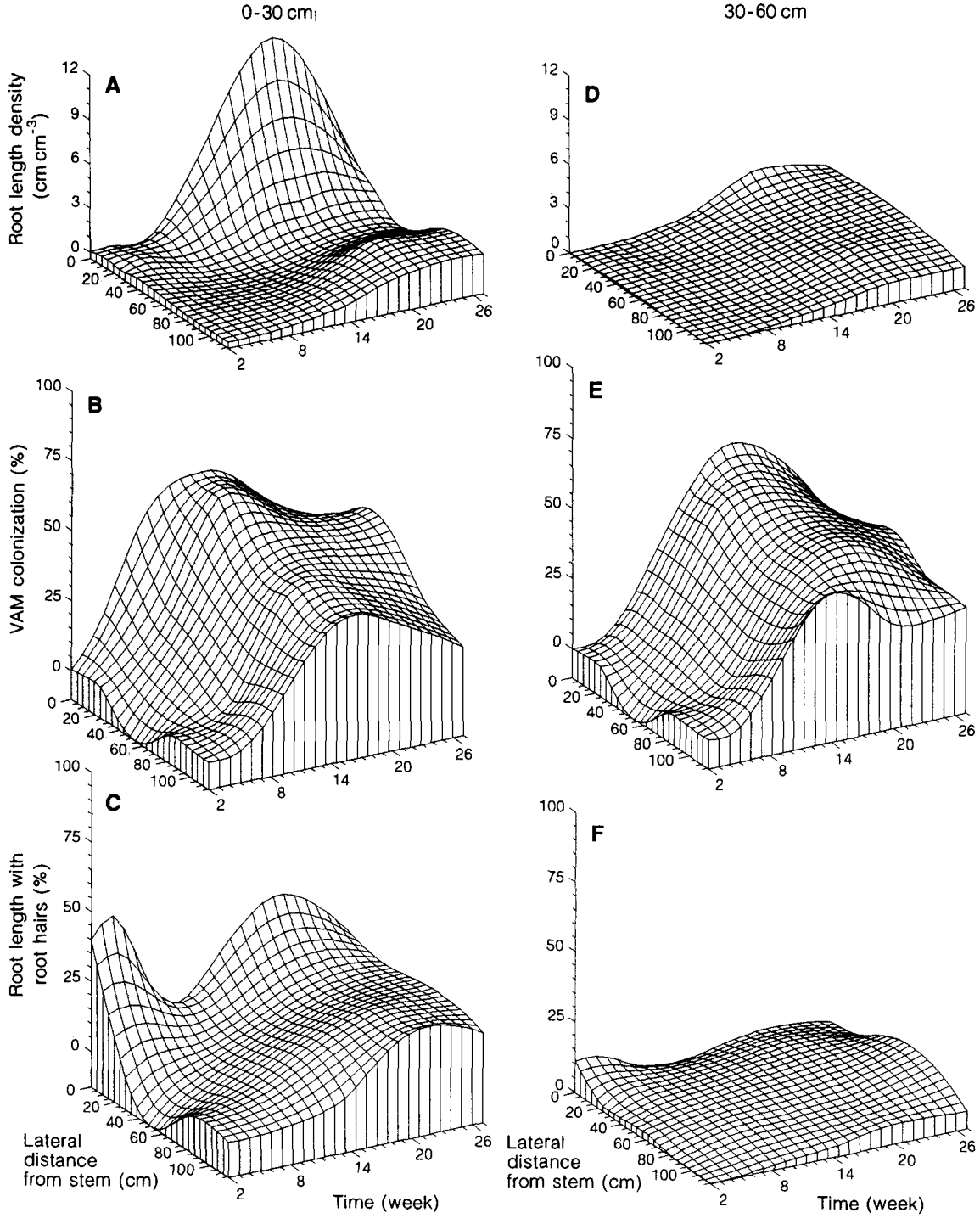

Fig. 3. The lateral distribution at depths of 0–30 cm and 30–60 cm, respectively, of sweet potato roots (**A, D**), percentage of the root length colonized with VAM fungi (**B, E**) and percentage of the root-length containing root hairs (**C, F**) over the course of a growing season. Each graph represents an interpolation of 354 data points and combines all inoculation treatments

quadratic, meaning the colonization was lowest at the beginning and the end of the growing season (Table 3).

There was no effect of inoculation on VAM colonization of roots until 13 WAP when plants inoculated with *A. rugosa* has less ($P \leq 0.0001$) colonization (24% at 0- to 30-cm depth and 22%–60 cm) than the noninoculated plants (64 and 55% at the respective depths). At 20 WAP, colonization was higher ($P \leq 0.01$) in the 0- to 30-cm depth in both *G. etunicatum* (48%) and *A. rugosa* (59%) plants than in the noninoculated plants (33%). The low level of colonization of plants inoculated with *A. rugosa* at 13 WAP was unexpected, particularly as colonization in this treatment increased dramatically by 20 WAP. A possible explanation is that this *A. rugosa* isolate was sensitive to the fungicide applied. While Bravo has been shown to suppress VAM fungi, and isolates

Table 3. The effect of distance from the shoot base and depth on power-transformed root length density, percentage root length colonized by VAM fungi and root length with root hairs. Exponents for transformations were 0.225, 0.40, and 0.35 for root length density, VAM colonization and root hairs, respectively

Harvest week[a]	Regression equation	*P* value	r^2
Root length density, 0–30 cm			
2	$y=(0.0054*x)+(-0.0004*x^2)+(2.39E\text{-}06*x^3)+(0.5057)$	0.0001	0.78
4	$y=(0.0278*x)+(-0.0007*x^2)+(3.40E\text{-}06*x^3)+(0.5473)$	0.0001	0.94
8	$y=(-0.0130*x)+(0.0001*x^2)+(0.7416)$	0.0031	0.38
13	$y=(-0.0322*x)+(0.0005*x^2)+(-2.0E\text{-}06*x^3)+(1.46)$	0.0001	0.66
20	$y=(-0.0370*x)+(0.0007*x^2)+(-3.5E\text{-}06*x^3)+(1.70)$	0.0001	0.65
Root length density, 30–60 cm			
4	$y=(0.0409*x)+(-0.0008*x^2)+(4.23E\text{-}06*x^3)+(0.0506)$	0.0010	0.55
Percentage of root length colonized, 0–30 cm			
2	$y=(0.0458*x)+(-0.0012*x^2)+(6.87E\text{-}06*x^3)+(0.2115)$	0.0058	0.32
4	$y=(0.0356*x)+(-0.0013*x^2)+(7.92E\text{-}06*x^3)+(1.52)$	0.0390	0.34
8	$y=(-0.0400*x)+(4.08)$	0.0015	0.34
13	$y=(-0.0123*x)+(5.07)$	0.0241	0.14
20	$y=(-0.0082*x)+(4.89)$	0.0265	0.14
27	$y=(0.0619*x)+(-0.0015*x^2)+(7.80E\text{-}06*x^3)+(3.81)$	0.0016	0.38
Percentage root length colonized, 30–60 cm			
2 to 27[b]	$y=(0.6*x)+(-0.02*x^2)-1.4$	0.0001	0.80
Percentage of root length with root hairs, 0–30 cm			
2	$y=(-0.09*x)+(0.001*x^2)+(3.48)$	0.0001	0.92
4	$y=(-0.07*x)+(0.0003*x^2)+(3.71)$	0.0001	0.90
Percentage of the root length with root hairs, 30–60 cm			
13	$y=(0.029*x)+(-0.0002*x^2)+(1.12)$	0.0223	0.21
20	$y=(0.08*x)+(-0.001*x^2)+(6.9E\text{-}06*x^3)+(1.12)$	0.0811	0.19
27	$y=(0.03*x)+(-0.0003*x^2)+(1.33)$	0.0238	0.20

[a] Excluded weeks did not have a significant ($P<0.10$) distance response
[b] There was no significant harvest effect

vary in sensitivity to pesticides (Trappe et al. 1984), this explanation assumes that a majority of the root system was colonized by the introduced fungus. Alternatively, this isolate may have been sensitive to the side-dressed fertilizer applications.

Percentage of root length colonized began to decline at the same time as yield began to increase, suggesting a shift in carbohydrate allocation from the symbiont to the storage root. There is evidence that seasonal variation in root carbohydrates is related to VAM colonization (Douds and Chaney 1986).

Root hairs

At the 0- to 30-cm depth, the percentage of root length with root hairs decreased with increased distance from the stem at the first two harvests (Fig. 3C). The low density of root hairs at 8 WAP may have been due to the rapid increase in growth of the root system which outpaced root-hair formation. Except for the first two harvests at the 0- to 30-cm depth, distribution of root hairs was not significantly affected by harvest, or had low r^2 values (Table 3). This was due to isolated patches of high root-hair density, interspersed with areas of roots with no root hairs. At the 30- to 60-cm depth and at 12, 20 and 27 WAP, the percentage of the root length with root hairs was highest at the two middle distances, but overall root hairs were few (Fig. 3F, Table 3). Inoculation had no effect ($P<0.01$) on percentage of the root length with root hairs at either depth. Coefficients of variation (cv) percentage for the root with root hairs were higher than for either root density or VAM colonization (Table 2), suggesting that for this parameter sampling may have been inadequate.

Soil horizon study

Soil horizon had a significant ($P\leq 0.10$) effect on the percentage of root length colonized by VAM fungi and formation of root hairs. Soil horizons that had high root hair formation had low VAM colonization. Mean colonization was highest in the E2 horizon (74%), followed by the Bh horizon (56%), and lowest in the Ap horizon (32%). Conversely, root hairs were highest in the Ap horizon (29%), followed by the Bh horizon (18%), and lowest in the E2 horizon (3%). High Al concentrations are diagnostic of the Bh horizons and Al is known to suppress root-hair formation in some plants while many VAM fungi have a degree of Al tolerance (Barkdoll 1987). Root hairs were fewest in the E2 horizon, which certainly has lower total amounts of Al than the Bh horizon. However, the soil-solution concentration of Al may be higher in this horizon than in the Bh horizon because of the lack of buffering capacity in the Eh hori-

zon and the leaching of Al from the Bh horizon into the E2 horizon. If VAM hyphae and root hairs are functionally analogous, then compensation for Al-induced root-hair inhibition by VAM fungi may be important. It is intriguing to consider that sweet potato can obtain P from a P-rich, but chemically hostile environment, through reliance on Al-tolerant VAM fungi.

Conclusions

The VAM isolates used in this study increased storage-root yield in the field. However, over the growing season there was no variable that could consistently explain the response. The only measurable difference between inoculated and noninoculated sweet potato shoots early in the growing season was a greater P concentration in *A. rugosa*-inoculated plants. Had harvests been done only at crop maturity, we would not have been able to speculate that the increase in yield due to VAM inoculation was related to an early increase in P concentration. However, since total P uptake was not effected by inoculation, and root-P content was not measured, we cannot say for certain that the introduced VAM fungi afforded the plants an advantage early in the growing season.

The effects of VAM inoculation were most evident when the plants were producing storage roots. Early and rapid colonization has been a good predictor of effectiveness (Abbott et al. 1983; Medina et al. 1988). However, another component of effectiveness may be the long-term relationship between the symbionts. For instance, the ability of a VAM isolate to maintain a hyphal network under temperature or water-supply extremes may be important for symbiotic effectiveness in promoting plant growth. Symptoms of water stress were evident during storage-root formation. This may have accentuated the advantage of introduced VAM isolates.

Introduced isolates compete with indigenous VAM populations (Abbott and Robson 1984; Menge et al. 1982); however, they may not need to compete throughout the root zone, but only within a zone of sufficient magnitude to influence plant growth. This would likely be the zone of highest root density. Within this zone the introduced fungi have advantages over the indigenous fungi, including higher inoculum density and closer proximity to young roots. We found that roots were most dynamic, and colonized root density was highest, near the inoculum. Therefore, the introduced VAM isolates could influence plant growth even in the presence of an indigenous population that may have dominated the root system further from the point of inoculation. It follows that sampling roots close to the base of the plant should be more instructive than sampling further away. Furthermore, differences in the response of root hairs and mycorrhiza to edaphic conditions found in specific soil horizons emphasizes the need to consider root function in terms of the collective contributions of individual horizons, not average properties for the entire profile. The optimal strategy for future studies would be to sample by soil horizon.

The root-sampling approach was sufficient to obtain representative samples for root density and VAM colonization as coefficients of variation (CVs) were reasonably low. Root-hair data, on the other and, was more variable and may need to be sampled more intensively in the future. Nonetheless, an analysis of root data at each sampling distance revealed no discernable trend in the magnitude of the CVs with increasing distance from the base of the plant (data not presented).

By delineating the chronology of the VAM association over a growing season, we have confirmed that values obtained at the final harvest will not be indicative of values for other times in the growing season (Abbott and Robson 1984; Fitter 1986). For example, shoot-P content and VAM colonization were higher when the plants first began to produce storage roots than at the final harvest. The production of storage roots lagged behind the period of most rapid root growth by 4 weeks and storage-root yield continued to increase after both VAM colonization and root-length density began to decrease. We believe that intensive measurements of root characteristics and total (root and shoot) P content and concentration during the period of yield formation would be the most useful strategy for determining the mechanisms of isolate effectivity. To generalize beyond this study, measurements of root characteristics and plant nutrient uptake should focus on times when P and water demand are rate limiting, such as during periods of water stress, exponential growth, and yield development.

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