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Effect of salinity on mycorrhizal onion and tomato in soil with and without additional phosphate

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Summary Vesicular-arbuscular mycorrhizal fungi (VAM) are known to increase plant growth in saline soils. Previous studies, however, have not distinguished whether this growth response is due to enhanced P uptake or a direct mechanism of increased plant salt tolerance by VAM. In a glasshouse experiment onions (*Allium cepa* L.) were grown in sterilized, low-P sandy loam soil amended with 0, 0.8, 1.6 mmol P kg^{-1} soil with and without mycorrhizal inoculum. Pots were irrigated with saline waters having conductivities of 1.0, 2.8, 4.3, and 5.9 dS m^{-1}. Onion colonized with *Glomus deserticola* (Trappe, Bloss, and Menge) increased growth from 394% to 100% over non-inoculated control plants when soil P was low ($\leq$ 0.2 mmol kg^{-1} $NaHCO_3$-extractable P) at soil saturation extract salinities from 1.1 dS m^{-1} to 8.8 dS m^{-1}. When 0.8 and 1.6 m*M* P was added no dry weight differences due to VAM were observed, however, K and P concentrations were higher in VAM plants in saline treatments. *Glomus fasciculatum* (Gerdeman and Trappe) and *Glomus mosseae* (Nicol. and Gerd.) isolates increased growth of VAM tomato 44% to 193% in non-sterilized, saline soils (10 dS m^{-1} saturation extract) despite having little effect on growth in less saline conditions when soil P was low. Higher tomato water potentials, along with improved K nutrition by VAM in onion, indicate mechanisms other than increased P nutrition may be important for VAM plants growing under saline stress. These effects appear to be secondary to the effects of VAM on P uptake.

Introduction

Recent investigations have shown that certain plants such as lavender (*Lavandula spica* L.), tomato (*Lycopersicon esculentum* Mill.), onion (*Allium cepa* L.), and bell pepper (*Capsicum annuum* L.) have increased growth under saline conditions when their roots are colonized by vesicular-arbuscular mycorrhizal (VAM) fungi[3,10,18]. All of these studies have been carried out under low soil P conditions.

The control of salinity in these studies was insufficient to precisely examine the relative salt tolerance of VAM and non-inoculated plants. However, in another study, salinity was precisely controlled and a significiant VAM-salinity interaction was found[16].

In the study of a VAM-salinity interaction, it is essential to determine if the well-known influence of VAM on P uptake is the primary mechanism by which the fungus is able to increase salt tolerance. This is especially true when considering onion and tomato, two plants demonstrated to have increased yields under saline conditions when P applications were increased[5,7].

The influence of salinity on plant P concentration is especially important in the context of VAM response. In many important crops, as salinity increases plant P concentrations decrease[7], and in these plants it may be most beneficial to inoculate with efficient strains of VAM that are tolerant of soil salinity.

The effects of VAM fungi on salt-stressed plants may not be limited to improved P nutrition. VAM could influence plant hormones[4,15] or they may improve water uptake[2]. Either of these factors could affect salt tolerance in plants.

The objective of this study was to distinguish between enhancement of phosphate nutrition by VAM and any other effects VAM may have on onion and tomato growth and elemental composition in saline soils.

Materials and methods

Onion experiment

This experiment was conducted using Delhi sandy loam with neutral pH (6.8), low electrical conductivity of the saturation extract (EC_{se}), and deficient phosphate ($\leq$ 0.12 mmol kg^{-1} $NaHCO_3$-extractable P). The unamended soil contained 2.0, 17.6, 2.1 and 0.87 mmol kg^{-1} K, Ca, Mg and Na respectively in the saturation extract, and 3.1, 46.6, 10.7, and 8.9 μmol kg^{-1} DTPA-extractable Cu, Fe, Zn, and Mn respectively. Total soil N was 0.5 g kg^{-1}.

The experimental design was a randomized complete block factorial with three factors: four salinities and three soil P concentrations at each salinity, either inoculated or not inoculated with the VAM fungus *Glomus deserticola* (Trappe, Bloss and Menge), formerly *G. fasciculatum* isolate 0–1. The 24 treatments were replicated eight times for a total of 192 containers.

The soil was autoclaved twice over a three day period, then mixed with 0, 0.8, and 1.6 mmol P kg^{-1} as $Ca(H_2PO_4)_2$. Soil was placed in 2.2 l plastic containers lined with perforated polyethylene bags. One three-week-old onion seedling (*Allium cepa* L. cv. Burpee Yellow Globe Hybrid 5276) was transplanted into each pot over a bed of 5 g of VAM inoculum. The inoculum consisted of chopped roots and soil from a 3.5 month old pot culture of *G. deserticola* on sudan grass. The uninoculated treatments received 5 ml of an inoculum filtrate which was sieved through a 45 μm filter to assure similar microbial populations in all treatments (excluding VAM fungi).

The plants were established for two weeks prior to salinization. Irrigations were applied through a mini-sprinkler system with flow rates of 300 ml min^{-1}. Four levels of saline irrigation water (1.0, 2.8, 4.3, and 5.6 dS m^{-1}) were produced by appropriate dilutions of a 2 *M* NaCl:1 *M* $CaCl_2$ stock solution. Soil NO_3-N concentrations were maintained at approximately 3.0 m*M* with KNO_3. Salinization began 36 days after seeding (DAS). Irrigations were scheduled using small tensiometers along with visual observations. A leaching fraction of about 60% (drainage volume/irrigation volume) was maintained throughout the experiment. During each irrigation, leachates from one-half the replications were collected and measured for P concentration, electrical conductivity, and pH. Leachate volumes were estimated during each irrigation to help predict the total amount of P lost due to leaching through the course of the experiment.

At 95 DAS the plants were harvested. The bulbs and shoots were rinsed in deionized water, separated, and oven-dried at 60°C. From each pot four soil cores (2.5 cm diameter by 20 cm deep) were removed for EC_{se} measurements. The roots were collected by washing the remaining soil volume and decanting the water-soil-root mixture through a 1 mm sieve. Several randomly selected root lengths were stored in FAA (formalin acetal alcohol) solution for later quantification of VAM colonization, while the remaining root mass was dried. The FAA-treated roots were cleared in KOH and stained using Trypan blue in lactophenol[17]. Percentage colonization was evaluated by presence or absence of hyphae, spores, vesicles, or arbuscules in a randomly distributed root sample in each 1 mm^2 of a 100 mm^2 grid.

Potassium, Na, Ca, Mg, Cu and Zn concentrations in plant shoot and bulb tissues were determined in an acid digest (2:1 ratio of nitric to 70% perchloric acid) using a Perkin-Elmer 370A atomic absorption spectrophotometer[9]. Tissue P concentrations were determined in the acid digest with a Technicon autoanalyzer. Potassium, Na, Ca and Mg concentrations in saturation extracts were determined using atomic absorption. Soil Cu, Zn, Fe and Mn were determined similarly on a DTPA extract.

Tomato experiment

This experiment was a randomized block with three salinities, six VAM treatments (five isolates and one control), and non-inoculated controls with and without P. The five VAM isolates were collected from saline soils. These isolates were previously screened for growth response with tomato[18]. Isolate S-33 was *Glomus deserticola*. Isolates S-30 and S-47 were *G. fasciculatum* (Gerdeman and Trappe) types, and S-29 and S-50 were *Glomus mosseae* (Nicol. and Gerd). The non-inoculated control treatments were given no P or 1 mmol kg^{-1} P as $Ca(H_2PO_4)_2$. The VAM treatments were given no P. The soil used was a Rositas fine sand with neutral pH (7.2) and low electrical conductivity (0.8 dS/m) having $NaHCO_3$-extractable P of 0.11 mmol kg^{-1}. The soil was sterilized as in the onion experiment. Soil Na, K, Ca, and Mg were 4, 1, 29, 6, mmol kg^{-1}, respectively, in saturation extract. DTPA-extractable Zn, Fe, Mn, Cu were 0.1, 0.1, 0.06, and 0.01 mmol kg^{-1} respectively. Two-week-old tomato seedlings (*Lycopersicon esculentum* Mill. Heinz 1350) were transplanted and after two weeks thinned to one plant per 0.5 l clay pot. The irrigation schedule was based on tensiometer readings (< -0.03 MPa tension) to achieve a leaching fraction of about 60%, similar to that in the onion experiment. Electrical conductivities of the three salinity treatments were 1.0, 5.0 and 10.0 dS m^{-1} achieved by adding NaCl, $CaCl_2$ and $MgCl_2$ in a 5:3.5:1.5 ratio by weight of Na:Ca:Mg. Electrical conductivities and pH were monitored from leachate samples.

Plants were harvested at 2 months from planting. Immediately prior to harvesting, water potential readings from stem ends cut 15 cm from the top node of 3 replicates of each treatment were determined using a Scholander pressure bomb (PMS Instrument Co., Corvallis, OR). Dry weights of root and shoot tissue, percent VAM colonization of roots, plant height, and concentrations of P, K, Na and Ca in shoot tissue were determined as in the onion experiment. Data were analyzed using two-way analysis of variance and Duncan's Multiple range test.

Results

Onion experiment

VAM onion dry weights were greater than non-inoculated plants at all salinities in the treatments without P (Table 1). Where 0.8 and 1.6 mmol P kg^{-1} were added initially, plants did not respond toVAM. In the 1.0 dS m^{-1} salinity, high and intermediate P treatments, non-inoculated plants had significantly higher shoot dry weights than their colonized VAM counterparts.

Table 1. VAM colonization, total shoot (shoot + bulb) and root dry weights of onion at specified saturation extract electrical conductivities (EC_{se})

Treatment				Dry weight		EC_{se}
P (mmol kg^{-1})	EC_{iw} [2] dS m^{-1}	VAM +/– [1]	VAM colonization (%)	Shoots (g/plant)	Roots (g/plant)	(dS m^{-1})
0	1.0	+	54.4	0.79*	0.30*	1.1
		–	0.0	0.16	0.08	1.2
	2.8	+	38.1	0.55*	0.23*	3.3
		–	0.0	0.10	0.06	3.3
	4.3	+	43.1	0.32*	0.13	6.9
		–	0.0	0.08	0.04	6.6
	5.9	+	52.0	0.14	0.05	8.8
		–	0.0	0.07	0.03	8.3
0.8	1.0	+	27.9	2.09	0.71	1.0
		–	0.0	2.48*	0.65	1.0
	2.8	+	16.5	1.36	0.38	3.2
		–	0.0	1.28	0.35	2.9
	4.3	+	37.6	0.98	0.32	6.5
		–	0.0	0.86	0.29	6.5
	5.9	+	33.8	0.46	0.15	8.6
		–	0.0	0.60	0.20	9.2
1.6	1.0	+	5.0	2.83	0.74	1.0
		–	0.0	3.33*	0.82	1.0
	2.8	+	11.1	1.67	0.45	3.2
		–	0.0	1.84	0.44	3.1
	4.3	+	19.1	0.93	0.25	7.0
		–	0.0	1.13	0.32	7.4
	5.9	+	7.4	0.62	0.18	8.7
		–	0.0	0.67	0.11	9.3

[1] +/– Corresponds to inoculated and non-inoculated with VAM *G. deserticola*.
[2] EC_{iw} is irrigation water electrical conductivity.
* Adjacent +/– VAM pairs significantly different ($P \leq 0.05$) using students t-test.

Analysis of variance on total shoot dry matter production indicated highly significant main effects due to salinity, added P, and a highly significant P-VAM interaction. However, since VAM did not affect shoot growth at the higher P level, there was no overall significant main effect of VAM.

Relative reductions in yield due to salinity were approximately 12% per dS m^{-1} increase above a salinity of 1.3 dS m^{-1}. This observation is in good agreement with salt tolerance data previously reported[13]. This relation was constant for plants with tissue P levels above 77 mmol kg^{-1}. Analysis of covariance on relative dry weights as a function of salinity showed no significant effects of either P or VAM except in the low-P, non-inoculated plants which had significantly

Table 2. VAM onion concentration of P, K, Mg, Ca, Na, Cu, Zn as influenced by salinity and phosphorus

Treatment			Concentration						
			P	K	Mg	Ca	Na	Cu	Zn
P (mmol kg^{-1})	EC_{iw} dS m^{-1}	VAM +/–[1]	(mmol kg^{-1})					(μmol kg^{-1})	
0	1.0	+	96*	474	91	453	152	189*	506
		–	48	746	78	473	105	120	561
	2.8	+	98*	465	73	494	358	162	613
		–	40	987*	81	518	379	158	506
	4.3	+	96*	782	66	539	480	150	619
		–	42	755	82	679*	421	185	815
	5.9	+	106*	1030*	68	688	843	188	838*
		–	41	767	86	878*	876	188	602
0.8	1.0	+	121	624	184*	457	190	158	423
		–	100	637	92	481	252	147	728*
	2.8	+	101	642	73	521	340	142	736
		–	88	718	67	533	366	100	636
	4.3	+	94	552	56	580	443	130	692
		–	83	654	57	560	393	110	707
	5.9	+	89	1021*	53	694	629	132	725
		–	77	724	57	788	633	96	747
1.6	1.0	+	130	130	91	488	252	142	514
		–	134	134	87	420	252	120	608
	2.8	+	118	118	72	487	347	101	517
		–	121	121	74	507	339	108	681
	4.3	+	106	106	58	622	492	140	584
		–	114	114	66	622	469	123	602
	5.9	+	96	96	58	682	598	114	605
		–	100	100	59	643	613	111	610

[1] +/– Corresponds to inoculated and non-inoculated with VAM *G. deserticola.*
* Adjacent +/– VAM pairs significantly different ($P \leqslant 0.05$) using students t-test.

($P \leqslant 0.05$) lower slope values. The low-P, non-inoculated plants had mean P concentrations below 50 mmol kg^{-1} (Table 2).

The fraction of root segments infected with VAM was not related to the salinity of either the irrigation water or the saturation paste extracts. Increasing soil P significantly decreased VAM colonization (Table 1).

Mean shoot P concentrations were greater in VAM plants at all salinities at both low and intermediate soil P levels, but not at high soil P. Phosphorus concentrations and total accumulation increased with increasing soil P. The concentration of P decreased as salinity increased at all P fertility levels. Analysis of variance indicated significant salinity-P and VAM-P interactions ($P \leqslant 0.05$). VAM increased

P concentration but not total accumulation significantly.

There was a significant salinity-VAM ($P \leqslant 0.01$) interaction with K concentration. Potassium concentrations in VAM onion shoot tissue were greater than in non-inoculated plants at high salinity when soil P was low and intermediate (Table 2). Greater concentrations of K in VAM plants at high salinities indicate this interaction is, like P concentration, predominantly expressed at low soil P.

As salinity increased, the concentrations of Na and Ca in the shoot increased (Table 2). Sodium and Ca concentrations in plants grown with low soil P at high salinity were slightly higher than at similar salinities when P was added to the soil. These ions decreased in concentration when growth increases due to P addition were large. Sodium concentrations increased with increasing salinity in all plants. Low P mycorrhizal plants, due to significant growth increases, accumulated significantly more Na.

Calcium concentrations were higher in the non-inoculated plants than in VAM plants in the 4.3 and 5.9 dS m^{-1} salinity in the P-deficient condition. Magnesium concentrations were significantly higher in the 1.0 dS m^{-1} intermediate soil P VAM plants and in the 5.9 dS m^{-1} non-inoculated plants. Magnesium concentrations significantly decreased with increasing salinity.

Copper concentrations were greater in VAM plants in the 1.0 dS m^{-1} treatment at low soil P. As soil P increased, the differences decreased; yet concentrations remained higher in VAM plants. Little effect of VAM on Zn concentration was found. Total accumulation of P, Mg, Na, Cu and Zn was greater in VAM onion shoots in the P-deficient condition compared with non-inoculated plants (Table 3). As soil P was increased, however, this trend was reversed. Relative nutrient concentrations of bulb tissue were similar to those found in shoots.

The estimates of P leached (Table 4) indicate little effect of VAM on P solubilization. These data do indicate a reduction in the amount of P leached in the 1.6 mmol kg^{-1} soil P addition with increasing salinity, however. The amounts of P lost due to leaching during the experiment were 17%, 31%, and 43% of the initial amount for the low, intermediate, and high P additions, respectively.

Tomato experiment

Dry weights of VAM tomato plants, compared to non-inoculated P-deficient plants, were significantly greater only at the highest salinity for isolates *G. mosseae* S-50 and *G. fasciculatum* S-30. Plants with added P were significantly larger than both VAM and non-inoculated, P-deficient plants at all three salinities (Table 5).

Table 3. VAM onion total accumulation (in μmol plant^{-1}) of P, K, Mg, Ca, Na, Cu, Zn as influenced by salinity and phosphorus

Treatment			Total accumulation (μmol plant^{-1})						
P (mmol kg^{-1})	EC_{iw} dS m^{-1}	VAM +/–[1]	P	K	Mg	Ca	Na	Cu	Zn
0	1.0	+	64.1*	303	54.2*	298*	94*	1.16*	3.40
		–	6.0	109	10.1	66	14	0.17	0.64
	2.8	+	48.2*	240	34.7*	237*	169*	0.81*	2.89
		–	3.6	69	6.1	39	28	0.12	0.42
	4.3	+	26.4	173	18.4	140*	137*	0.41	1.68
		–	3.1	40	4.2	38	31	0.11	0.40
	5.9	+	11.0	104	7.5	75	86	0.29	0.85
		–	3.1	130	3.3	41	40	0.10	0.24
0.8	1.0	+	203	1070	144	309	320	2.76	7.22
		–	211	1235	198*	749*	538*	3.79	15.21*
	2.8	+	116	788	85.2	602	393	1.69*	8.49
		–	91.6	754	69.6	546	359	0.97	6.56
	4.3	+	78.2	415	41.2	461	379	1.05	5.95
		–	58.5	464	40.0	398	277	0.77	4.71
	5.9	+	30.3	364	19.0	270	260	0.44	2.43
		–	30.3	337	293	389	302	0.47	3.81
1.6	1.0	+	306	1873	210	1134	575	3.22	12.0
		–	384	1895	251*	1260	725	3.60	17.6*
	2.8	+	165	933	104	633	474	1.35	7.22
		–	194	808	132*	875	591	1.92	12.1*
	4.3	+	81	477	44	480	367	1.00	4.34
		–	109	643	60	573	440	1.11	5.73
	5.9	+	49	259	31	319	302	0.50	3.36
		–	59	314	34	390	358	0.66	3.07

[1] +/– Corresponds to inoculated and non-inoculated with VAM *G. deserticola*.
* Adjacent +/– VAM pairs significantly different ($P \leqslant 0.05$) using students t-test.

Table 4. Estimate of P leached (μmol P pot^{-1}) from 2.2 l pots during onion experiment each value is an average of four replications

Treatment		Soil P level*		
EC_{iw} dS m^{-1}	VAM +/–	P_0	P_1	P_2
1.0	+	32	388	773
	–	34	413	807
2.8	+	39	398	737
	–	27	293	723
4.3	+	27	432	642
	–	32	362	664
5.9	+	25	421	650
	–	25	350	540

* P_0, P_1, and P_2 refer to initial soil P additions of 0, 0.8, and 1.6 mmol kg^{-1}.

Table 5. Tomato shoot dry weights and mycorrhizal dependency ratio as influenced by salinity when inoculated with five VAM isolates

Treatment		Dry wt		Xylem
EC_{iw} dS m^{-1}	VAM species	shoots (g/plant)	MDR[1] (%)	potential (– MPa)
1.0	G.m. S29	3.10	91	0.60
	G.m. S50	2.83	85	0.50
	G.f. S30	4.14	131	0.54
	G.f. S47	4.12	117	0.48
	G.d. S33	2.62	75	0.50
	Non-inoculated	3.47	–	0.53
	Non-inoculated + P	17.32+	–	0.54
5.0	G.m. S29	3.13	129	0.61
	G.m. S50	3.19	131	0.61
	G.f. S30	3.88	155	0.63
	G.f. S47	3.33	129	0.63
	G.d. S33	2.00	76	0.65
	Non-inoculated	2.67	–	0.74
	Non-inoculated + P	12.69+	–	0.70
10.0	G.m. S29	2.44	245*	0.72
	G.m. S50	3.22+	329*	0.62
	G.f. S30	3.12+	312*	0.60
	G.f. S47	2.08	210*	0.72
	G.d. S33	1.58	145	0.76
	Non-inoculated	1.10	–	0.89
	Non-inoculated + P	14.01+	–	0.57

[1] Mycorrhizal dependency ratio is dry weight of VAM plants as a percentage of non-inoculated control plants without P.

+ Significantly different ($P \leqslant 0.05$) than non-inoculated controls without P at one given salinity level according to DMR test.

* Significantly different ($P \leqslant 0.05$) than non-inoculated controls without P at all salinity levels according to DMR test.

Tomato dry weights were reduced approximately 50% by salinity in the non-inoculated control plants without P. Growth reductions due to salinity were smaller with four of the VAM isolates; one isolate, *G. mosseae* S-50, induced a slight growth increase at 10 dS m^{-1}. Addition of 1.0 mmol P kg^{-1} reduced sensitivity of yield to salinity.

As with onion, VAM colonization was not related to salinity and differences between isolates were not significant. There was no VAM colonization in the non-inoculated treatments. Water stress at the highest salinity with plants colonized by S-30, S-50 VAM isolates, and for plants amended with 1.0 mmol kg^{-1} P, was significantly ($P \leqslant 0.05$) less (higher water potential) than for the non-inoculated plants (Table 5).

Table 6. Concentrations of P, K, Na and Ca in tomato shoots as influenced by salinity when inoculated with five VAM isolates

Treatment		Concentration (mmol kg^{-1})			
EC_{iw} dS m^{-1}	VAM species	P	K	Na	Ca
1.0	G.m. S29	30.6	922	61.7	63.1
	G.m. S50	28.4	538	66.5	69.2
	G.f. S30	29.0	727	57.4	62.6
	G.f. S47	35.5	529	64.8	75.1
	G.d. S33	31.6	887	56.6	72.9
	Non-inoculated	37.9	937	76.5	64.6
	Non-inoculated + P	37.4	794	67.8	91.2
5.0	G.m. S29	30.0	569	144	71.7
	G.m. S50	17.7	694	147	75.2
	G.f. S30	30.6	764	150	77.4
	G.f. S47	30.6	456	152	82.8
	G.d. S33	34.2	750	148	85.0
	Non-inoculated	30.3	731	163	92.4
	Non-inoculated + P	34.0	735	210	77.4
10.0	G.m. S29	28.4	510	281	81.9
	G.m. S50	24.8	520	274	86.6
	G.f. S30	33.2	570	281	94.5
	G.f. S47	30.3	406	283	93.5
	G.d. S33	42.3	452	295	91.0
	Non-inoculated	30.6	504	226	114.3
	Non-inoculated + P	34.8	641	339	86.0

Assessment of mycorrhizal dependency ratio (MDR), the dry weight of VAM plants as a percent of non-inoculated plants without P, was determined in this study where P concentration was similar at all three salinities. A significant VAM effect on MDR with four isolates was seen at the highest salinity only (Table 5).

As soil salinity increased, the concentration of Ca in shoots increased slightly while Na increased noticeably (Table 6). At the highest salinity, plants not colonized with VAM or not given additional soil P had a lower concentration of Na but a greater concentration of Ca. As with onion, the total accumulation of both ions was greatest in plants with added soil P (Table 7).

There was no effect of salinity or added soil P on P concentration of tomato leaves and shoots, and there was no VAM effect on P uptake. Total accumulation increased as soil P was increased. Increased salinity did not decrease P accumulation as it did in onion. Total accumulation and concentration of K was not affected by increasing P or salinity. Added soil P increased total accumulation of K, but VAM colonization

Table 7. Total accumulations of P, K, Na and Ca in tomato shoots as influenced by salinity when inoculated with five VAM isolates

Treatment		Total accumulation (mmol plant^{-1})			
EC_{iw} dS m^{-1}	VAM species	P	K	Na	Ca
1.0	G.m. S29	74.2	2330	133	1464
	G.m. S50	57.4	1115	143	1472
	G.f. S30	95.5	2348	290	2101
	G.f. S47	52.1	1712	205	2382
	G.d. S33	66.8	1903	122	1628
	Non-inoculated	91.9	2571	213	2721
	Non-inoculated + P	50.3	10786	907	8901
5.0	G.m. S29	71.3	1347	342	1715
	G.m. S50	69.0	1571	367	1877
	G.f. S30	96.8	2301	467	2360
	G.f. S47	79.0	1209	378	2093
	G.d. S33	54.2	1218	253	1400
	Non-inoculated	69.4	1678	344	2008
	Non-inoculated + P	345.0	7308	2187	7873
10.0	G.m. S29	52.2	961	502	1580
	G.m. S50	42.9	1275	659	2133
	G.f. S30	50.3	1412	674	2254
	G.f. S47	50.0	671	447	1482
	G.d. S33	50.0	613	400	1111
	Non-inoculated	29.0	492	232	1054
	Non-inoculated + P	42.1	7564	3955	10143

did not. As salinity increased, total accumulation of K decreased slightly (Table 7).

Discussion

Onions inoculated with VAM and grown under saline P-deficient conditions showed increased growth and enhanced nutrient concentration and total ion uptake when compared to non-inoculated plants. These findings are supported by others who have reported similar results with salt grass, lavender, onion and bell pepper[1,3,10,16].

Analysis of variance on total onion dry weights indicate highly significant ($P \leqslant 0.001$) decreases in growth due to salinity and growth increases due to P. Additions of P increased onion growth under saline stress. Inoculation of onion with VAM increased tissue P concentrations when soil P was low. When soil P was increased, there was no increase in P by VAM. The lack of response of VAM plants to increased P has been discussed by others[6,8,14].

The results of this study do not support one important aspect of the findings by Ojala *et al.*[16]. Their conclusion that onion growth under saline conditions was dependent on the presence of VAM was based on an experimental design that would not separate P effects from VAM effects on plant growth. Evidence from the present study indicates increased onion growth under saline conditions depends primarily on P nutrition regardless of the presence of VAM. Since P levels provided by VAM were still limiting onion growth, it was difficult to identify any direct contribution by VAM to onion salt tolerance.

The main role of the VAM fungus *Glomus deserticola* in improving growth of onion in saline soil appeared to be increasing P accumulation and concentrations when soil P was low. When sufficient P is added to the soil a parasitic relationship may exist in that fungal respiration represents a carbon drain on the host plant[6].

Significant quantities of P were leached from the P-amended soils. At the higher soil P concentrations the total amount of P leached was reduced as salinity increased. Lower P concentrations in the leachate may be a result of some form of calcium phosphate precipitation. This fixation of P at high salinities may stimulate or inhibit VAM depending on how this difference in soil P availability affects the host plant.

Salinity, fertility and VAM all influence the concentration of essential plant nutrients[5,12,19]. For example, by reducing plant biomass, while not affecting the uptake of certain ions, salinity can cause a 'concentration effect'[12]. Similarly when an essential plant nutrient that is deficient is added, as was the case in this study for P, then other elements can be diluted. Because of the large differences in vegetative production among treatments, nutrient data are presented both on basis of concentration and as total accumulation (the product of dry matter and concentration).

A 'concentration effect' occurred under the P-deficient condition in the non-inoculated plants. As soil P was increased, shoot growth increased and diluted the concentration of Ca. A similar dilution occurred with VAM plants at low soil P where the endophyte improved the P status of the plant. The similar response of onion to VAM and to inorganic P supports the hypothesis that VAM enhance plant growth under saline conditions primarily by increasing P concentration in plant tissues.

Growth in salinized soil due to VAM colonization was limited by P availability primarily, although other elements (*e.g.*, K) may be important. The generally higher K concentrations in VAM onion plants as salinity increased suggests an added benefit. Addition of

P eliminated this trend, although infection was likewise decreased.

With tomato when P was added, growth increased dramatically and obscured salinity effects. In this experiment VAM fungi did not greatly increase P uptake, and their effects on growth and nutrient uptake under saline conditions were small. Nevertheless, colonization by some isolates significantly increased relative dry weight at high salinities even though they were unable to overcome P-deficiency symptoms.

Improved plant water relations and growth caused by VAM in saline conditions may indicate that mechanisms other than P uptake may be involved, although their effects may be small. Reports of cytokinin production in ectomycorrhizal fungi *in vitro*[15] and a decrease in cytokinin in roots of sunflower and tobacco with increased salinity[11] indicate that hormonal production in VAM may be a possible mechanism for salt tolerance in associated plants. Higher VAM tomato water potential under saline stress conditions suggests VAM may improve water uptake. This was supported by data presented here.

Although S-30 was collected from what appeared to be low saline soil conditions[18], and S-50 was collected from a saline soil, tomatoes inoculated with *G. mosseae* S-50 and *G. fasciculatum* S-30 under low P grew as well at high salinity as they did under low salinity. This suggests that increased plant growth caused by VAM in salinized soil is not necessarily related to environmental salinity in the natural habitat of these isolates.

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