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Response of onion plants to arbuscular mycorrhizae

2. Effects of nitrogen fertilization on biomass and bulb firmness

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Abstract The effects of N fertilization on growth and root colonization of preinoculated onion (*Allium cepa* L. cv. Improved Autumn Spice) were studied. Onion transplants, inoculated with either *Glomus intraradices*, *G. versiforme* or nothing at sowing, were grown under three levels of N in soils which had either been irradiated, irradiated and amended with nonmycorrhizal microflora, or not irradiated. Interactions between inoculation and soil treatment had a significant effect on dry biomass and final bulb diameter. Control plants cultivated in non-irradiated natural soil grew normally because of the presence of indigenous arbuscular mycorrhizae, but control plants in irradiated soils were stunted. There was no such difference among inoculated plants. In non-irradiated natural soil, bulbs of onions inoculated with *G. intraradices* or *G. versiforme* were significantly firmer than bulbs of control plants. Bulb firmness decreased as N fertilization level increased. In non-irradiated natural soil, tissue P concentration of onion plants preinoculated with either fungus was significantly higher than that of control plants. In all soil types, N, P, and Zn concentrations were higher in onion plants colonized by *G. versiforme* than in those colonized by *G. intraradices*. The opposite was true of Mn tissue concentration.

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Introduction

Arbuscular mycorrhizal (AM) fungi increase the P intake of inoculated plants and improve their nutrition (Harley and Smith 1983). However, the influence of N fertilization on root colonization and growth stimulation by arbuscular mycorrhizae of onion (*Allium cepa*) has received little attention.

Wang and Hayman (1982) noted that NH_4NO_3 did not affect the colonization of alfalfa by AM fungi, but reduced that of onion. Onions receiving high levels of N fertilization (384 µmol week^{-1}) combined with P and/or AM fungus treatments grew rapidly, while the growth rate of onion plants receiving low N fertilization (120 µmol week^{-1}) decreased steadily over time (Smith et al. 1986). Hepper (1983) obtained similar results with lettuce.

Bååth and Spokes (1989) studied the effect of combined P and N fertilization on chives. In AM plants, N amendments stimulated plant growth irrespective of P levels. Both the source of N used (NH_4 vs NO_3 ions) and the quantity available to the host plant determined the type of response.

Furlan and Bernier-Cardou (1989) studied the effects of N, P, and K fertilization on the formation of arbuscular mycorrhizae, growth, and mineral concentration of onion. N fertilization stimulated root colonization, and the yield increases because of P fertilization were larger when plants had not been fertilized with N (191%) than when they had been (103%). Like Hepper (1983), Furlan and Bernier-Cardou (1989) insisted on the necessity of having an optimal ratio of N, P, and K, as well as other essential minerals available in the soil for a given host plant-AM fungus combination in order to stimulate the symbiosis and maximize yield.

The present study was performed to evaluate the influence of N fertilization on the growth of preinoculated

onion plants in natural soils that had been irradiated, irradiated and amended with a non-mycorrhizal microflora, or non-irradiated. The non-irradiated soil treatment was designed to assess the influence of indigenous AM fungi and non-mycorrhizal microflora on plant growth.

Materials and methods

Soil used in this experiment was a mineral soil (sombric brunisol) sterilized by gamma irradiation (^{60}Co, 15 kGy, 22°C), except for the portion used in the natural soil treatments. It was mixed with silica no. 10 in a 3:1 soil:silica ratio, to avoid compaction. Before dilution with silica, the major characteristics of the soil were as follows: pH (soil:water ratio 1:2) 6.3, 26 g kg^{-1} organic matter (wet oxidation), 1.9 g kg^{-1} total N, 1,083 µg g^{-1} total P, 43 µg g^{-1} available P, 172 µg g^{-1} K, 1,780 µg g^{-1} Ca, and 130 µg g^{-1} Mg. This soil was amended with either 310, 465, or 620 mg N kg^{-1} of dry soil – according to treatment – applied as $Ca(NO_3)_2.4H_2O$, 65 mg P kg^{-1} applied as $Ca(H_2PO_4)_2.H_2O$, and 110 mg K kg^{-1} applied as K_2SO_4.

Onion plants preinoculated with either *Glomus intraradices* or *G. versiforme*, and non-mycorrhizal controls were produced as described in Charron et al. (2001). At transplanting, 8 weeks after sowing, root colonization in seedlings inoculated with *G. intraradices* or *G. versiforme* had reached >50%. Transplants were placed into 15-cm pots containing the various combinations of N and soil treatments. Over a 24-h period, half of the pots containing irradiated soil received 2×50 ml pot^{-1} of a non-mycorrhizal microflora liquid suspension free of AM fungi. This microbial suspension was obtained from 15 l of natural soil mixed with 15 l of distilled water. This mix was blended for 10 min in a disinfected concrete mixer. The liquid part was then filtered over two layers of triple thickness cheese-cloth separated by a 2-cm layer of cotton. The filtrate was passed through a 38-µm sieve to eliminate all propagules of AM fungi. Samples of the filtrate were observed under a stereoscopic microscope to ascertain the absence of AM fungus propagules.

Plants were kept in a growth chamber under a 16-h photoperiod, 24/18°C (day/night temperature, SD 1°C), 280 µmol m^{-2} s^{-1} light intensity, and 65% relative humidity. All onion transplants were grown individually in pots according to N fertilization, soil treatment, inoculum type, and replicate, and harvested 12 weeks after transplanting. Starting at the end of the third week after transplanting, until harvest, "cross-diameters" of all bulbs were measured every 3 weeks as described in Charron et al. (2001).

Bulb firmness (texture, N mm^{-1}) was measured 12 h after harvest with an Instron Computerized Compression Testing System [model 4201; see Charron et al. (2001) for details].

Plant tissue of each plant was analyzed for N, P, K, Ca, Mg, and micronutrients as in Charron et al. (2001), except for control plants cultivated in either of the two irradiated soils. These plants did not provide enough tissue for chemical analyses.

The experiment was designed as seven complete randomized block replicates of a 3^3 factorial arrangement of inoculum (*G. intraradices*, *G. versiforme* or nothing), soil treatment (irradiated, irradiated and amended with non-mycorrhizal microflora, and non-irradiated natural soil), and N fertilization level (310, 465, and 620 mg N kg^{-1} of dry soil). Blocks and pots within blocks were randomly rotated every 3 weeks. There were 3^3×7=189 pots, each with one plant. The variances of dry biomass, final bulb diameter (average of two cross-diameters), percent root colonization, bulb firmness (three-point average), and the tissue concentration of nine macro- and micronutrients were analyzed according to the experimental design and treatment structure. Main effects and interaction sums of squares were partitioned with appropriate contrasts. To be declared significant at the α=0.05 level, the *P* values of contrasts had to be smaller than α'=0.05/13=0.0038. This Bonferroni procedure allows for the number of tests of the contrast being performed, i.e., the number of variables analyzed, which was 13.

Because of their lack of growth at all N levels, non-inoculated plants grown in irradiated soil or in soil irradiated and amended with non-mycorrhizal microflora were excluded from the statistical analyses of bulb firmness, root colonization and plant tissue concentrations of nutrients. This leaves a total of 21 treatments defined by available combinations of the three inocula, the three soil types, and the three N levels for these 11 variables.

Dry biomass and final bulb diameter required a square-root transformation to achieve variance homogeneity (Steel and Torrie 1980). Means were computed on the square-root scale and back-transformed for presentation in the text or in tables. Differences between these means and SEs of these differences are given on the square-root scale.

The square roots of average cross-diameters measured every 3 weeks were analyzed as a separate set of repeated measures. The analysis accounts for the correlation between successive measures on the same plants (Crowder and Hand 1990).

All analyses were performed with the GLM procedure of SAS/STAT software (SAS Institute 1989, 1997).

Results

Dry biomass and final bulb diameter

Twelve weeks after transplanting, the interaction between inoculation and soil treatment had a significant effect on dry biomass and final bulb diameter ($P \leq 0.0001$, Tables 1, 2). It was caused by the poor growth of control plants cultivated in irradiated soil and irradiated soil amended with a non-mycorrhizal microflora (means, 0.13 g for dry biomass, 5.48 mm for final bulb diameter, Table 2) as compared to their normal growth in natural soil [means, 7.95 g for dry biomass, 43.03 mm for final bulb diameter; differences (square-root scale), –2.46± 0.06 g$^{1/2}$ for dry biomass (±SE), –4.22±0.08 mm$^{1/2}$ for final bulb diameter]. Inoculated plants were not affected by soil irradiation [means, 7.90 g for dry biomass, and 43.65 mm for final bulb diameter of inoculated plants in irradiated soils, 7.51 g for dry biomass, and 42.90 mm for final bulb diameter of inoculated plants in natural soil; differences (square-root scale), 0.07±0.04 g$^{1/2}$ for dry biomass, 0.05±0.06 mm$^{1/2}$ for final bulb diameter, Table 2]. There was little or no difference between the dry biomass or final bulb diameter of control plants cultivated in non-irradiated natural soil and those of inoculated ones in any soil type (Table 2). N fertilization had no apparent effect on dry biomass or final bulb diameter (P>0.04, Table 1), nor was there any evidence of interactions between N fertilization and the other factors (P>0.06).

Over the 12-week period, the diameter of inoculated onions was almost constantly larger than that of the controls ($P \leq 0.0001$ for both intercept and shape of the growth curves, results not shown). It was also larger in natural soil than in irradiated soil ($P \leq 0.0001$ for both intercept and shape). These effects were mainly because of the strong interaction between soil type and inoculation ($P \leq 0.0001$ for both intercept and shape): control onions grown in irradiated soil were stunted throughout the experiment while onions in other inoculum-soil type combinations grew normally and at similar rates. On average

Table 1 ANOVA (*P*-values) of the square roots of dry biomass (g) and final bulb diameter (mm), of bulb firmness (N mm^{-1}), and of root colonization (%) of onion plants. *G. int. Glomus intraradices*, *G. ver. G. versiforme*, *Inoc.* inoculted, *IRR* irradiated soil, *IRRM* irradiated soil amended with non-mycorrhizal microflora, *NAT* non-irradiated natural soil

Sources of variation and contrasts	*df*	Dry biomass	Final bulb diameter	*df*	Bulb firmness	*df*	Root colonization
Inoculum (I)	2			2		2	
Inoc. vs control (I1)	(1)	**0.0001**	**0.0001**	(1)	**0.0001**[a]	(1)	0.8897[a]
G. int. vs *G. ver.* (I2)	(1)	0.1474	0.4786	(1)	0.2226	(1)	**0.0001**
Soil (S)	2			2		2	
(IRR+IRRM) vs NAT (S1)	(1)	**0.0001**	**0.0001**	(1)	0.1411[b]	(1)	**0.0003**[b]
IRR vs IRRM (S2)	(1)	0.4962	0.2293	(1)	0.7515[b]	(1)	0.0074[b]
I×S	4			2		2	
I1×S1	(1)	**0.0001**	**0.0001**	–	–	–	–
I1×S2	(1)	0.6387	0.0280	–	–	–	–
I2×S1	(1)	0.2071	0.5862	(1)	0.1280	(1)	0.1186
I2×S2	(1)	0.0743	0.0507	(1)	0.4193	(1)	0.7342
N	2			2		2	
Linear (N1)	(1)	0.0441	0.7101	(1)	**0.0004**	(1)	0.7342
Quadratic (N2)	(1)	0.0452	0.6694	(1)	0.8651	(1)	0.0326
I×N	4			4		4	
I1×N1	(1)	0.0719	0.1369	(1)	0.8306[a]	(1)	0.4974[a]
I1×N2	(1)	0.0857	0.0632	(1)	0.5514[a]	(1)	0.3278[a]
I2×N1	(1)	0.8336	0.8600	(1)	0.3425	(1)	0.3093
I2×N2	(1)	0.2301	0.9727	(1)	0.8680	(1)	0.8446
S×N	4			4		4	
S1×N1	(1)	0.1255	0.1285	(1)	0.8003[b]	(1)	0.0566[b]
S1×N2	(1)	0.9479	0.7429	(1)	0.6399[b]	(1)	0.4886[b]
S2×N1	(1)	0.8664	0.1078	(1)	0.3353	(1)	0.6775
S2×N2	(1)	0.9262	0.5726	(1)	0.7395	(1)	0.3377
I×S×N	8			4		4	
I1×S1×N1	(1)	0.3197	0.6029	–	–	–	–
I1×S1×N2	(1)	0.3562	0.1101	–	–	–	–
I1×S2×N1	(1)	0.6908	0.7117	–	–	–	–
I1×S2×N2	(1)	0.8706	0.4670	–	–	–	–
I2×S1×N1	(1)	0.0896	0.2883	(1)	0.4499	(1)	0.1514
I2×S1×N2	(1)	0.6660	0.6659	(1)	0.6599	(1)	0.1291
I2×S2×N1	(1)	0.5732	0.3219	(1)	0.1090	(1)	0.6775
I2×S2×N2	(1)	0.6877	0.8798	(1)	0.4736	(1)	0.3377
Error mean square[c]	156	0.0475	0.0989	119	0.0046	120	0.4111

[a] Natural soil only; [b] Inoculated plants only; [c] Actual mean square, not a *P* value

Table 2 Means (n=21) over all N levels of dry biomass (g), final bulb diameter (mm), and N, P and Zn tissue concentrations (%) of onion plants, by soil type, by AM fungal species and control. *SE(diff.)* SE of the difference between any two of the above means; for other abbreviations, see Table 1

Soil	AM fungal species		Control	AM fungal species		Control
	G. int.	*G. ver.*		*G. int.*	*G. ver.*	
	Dry biomass (g)			Final bulb diameter (mm)		
IRR	8.24	7.24	0.13	43.82	41.22	5.66
IRRM	8.01	7.95	0.13	44.09	45.02	5.06
NAT	7.45	7.56	7.95	42.90	42.90	43.03
SE(diff.)	0.07			0.10		
	N tissue concentration (%)			P tissue concentration (%)		
IRR	1.09	1.45	–	0.127	0.200	–
IRRM	1.26	1.30	–	0.128	0.189	–
NAT	1.04	1.17	0.98	0.174	0.195	0.149
SE(diff.)	0.07			0.011		
	Zn tissue concentration (%)					
IRR	0.0017	0.0026	–			
IRRM	0.0017	0.0019	–			
NAT	0.0014	0.0017	0.0015			
SE(diff.)	0.0002					

Table 3 Means of bulb firmness (N mm^{-1}), and N and Ca tissue concentrations (%) over all AM fungal and soil treatments, by N level; means of Mg tissue concentrations (%) over all soil types by N level by AM fungal species. *Lin.* Slope of the straight line of best-fit; for other abbreviations, see Table 1

N (mg kg^{-1})	Bulb firmness (*n*=49)	Mg		N (*n*=49)	Ca (*n*=49)
		G. int. (*n*=21)	*G. ver.* (*n*=21)		
310	0.319	0.172	0.167	0.997	0.902
465	0.296	0.167	0.182	1.120	1.010
620	0.269	0.165	0.208	1.430	1.080
Lin.	-0.00016	-0.2227×10^{-4}	1.3164×10^{-4}	0.2165	0.0890
SE(Lin.)	0.00002	0.3665×10^{-4}	0.3665×10^{-4}	0.0095	0.0110

over the 12-week period, bulb diameter increased with N fertilization level (P=0.0027 for the intercept of the growth curves).

Bulb firmness

None of the interactions between inoculum, soil treatments, and N fertilization had any effect on bulb firmness (P>0.10, Table 1). N fertilization had a negative linear effect on bulb firmness (P=0.0004, Table 3). In non-irradiated natural soil, onion plants inoculated with *G. intraradices* or *G. versiforme* were significantly firmer than control plants (means, 0.328 N mm^{-1} and 0.256 N mm^{-1} for inoculated and control plants, respectively; difference, 0.073±0.018 N mm^{-1}, P≤0.0001). Bulbs of plants inoculated with either AM fungal species were apparently equally firm in all soil types (P=0.2226 for the contrast between *G. intraradices* and *G. versiforme*). Soil treatments had no apparent effect on bulb firmness (P>0.14).

Root colonization

On average over soil treatments, root colonization of onion plants inoculated with *G. intraradices* was more abundant than that of plants colonized by *G. versiforme* (P≤0.0001, Table 1; means, 72% and 50%, respectively; difference, 21±2.3%). It was also higher on inoculated plants grown in irradiated soil, amended or not, than on inoculated plants grown in natural soil (P=0.0003, Table 1; means, 65% and 56%, respectively; difference, 9±3.0%). The main indigenous fungi were *Glomus rubiforme* (Gerd. and Trappe) Almeida and Schenck and *G. fasciculatum* (Thaxter) Gerd. and Trappe emend. Walker and Koske. Indigenous fungal species were identified by Dr Y. Dalpé (Agriculture and Agri-Food Canada, Ottawa).

Plant tissue mineral concentration

Interactions involving N fertilization generally had little effect on the concentration of nutrients in plant tissue (Table 4). Mg tissue concentration increased with increasing N fertilization when plants were inoculated with *G. versiforme*, but remained stable over N fertilization levels when they were inoculated with *G. intraradices* (P=0.0036, Tables 3 and 4): the slope of the linear regression of mean Mg tissue concentration on N fertilization level was smaller than its SE when plants were inoculated with *G. intraradices*, but it was more than 3.5 times the size of its SE and positive when they were inoculated with *G. versiforme*.

Soil irradiation apparently had no effect on the P uptake of plants inoculated with *G. versiforme* but decreased that of plants inoculated with *G. intraradices* [P≤0.0001 for the interaction between fungal species and the contrast between irradiated and natural soils (I2×S1), Tables 2 and 4]. In the two irradiated soils, plants inoculated with *G. versiforme* had a higher P tissue concentration than plants inoculated with *G. intraradices*. The corresponding difference in natural soil did not seem substantial. On average over all soil types, plants inoculated with *G. versiforme* took up more P than plants inoculated with *G. intraradices (P*≤0.0001 for the contrast between the two fungal species, Tables 2 and 4).

The addition of microflora to irradiated soil increased the N tissue concentration of plants inoculated with *G. intraradices* but decreased that of plants inoculated with *G. versiforme* [P=0.0020 for the interaction between fungal species and the presence of microflora in irradiated soils (I2×S2), Tables 2 and 4]. In irradiated soil amended with soil microflora, the N uptake of plants was approximately the same whether they had been inoculated with *G. versiforme* or with *G. intraradices*. In unamended irradiated soil, *G. versiforme* produced a higher N uptake than *G. intraradices.*

The addition of microflora to irradiated soil did not affect the Zn tissue concentration in the presence of *G. intraradices*, but decreased it when plants were inoculated with *G. versiforme* (P=0.0033 for I2×S2, Tables 2 and 4). As for N uptake, the two fungal species were similarly efficient at Zn uptake in amended irradiated soil, but *G. versiforme* was more efficient than *G. intraradices* in unamended irradiated soil.

On average over soil types and N fertilization levels, inoculation with *G. versiforme* yielded higher N, P, and Zn tissue concentrations than inoculation with *G. intraradices*; the reverse was true for the Mn tissue concentration (means for Mn, 0.0055% for *G. versiforme*, 0.0058% for *G. intraradices*; difference for Mn, 0.0003±0.0001%, P≤0.0001 for I2 of N, P, Mn and Zn, Tables 2 and 4). In natural soil, the P uptake of inoculated plants was higher than that of control plants (P=0.0003, Tables 2 and 4).

Table 4 ANOVA (*P*-values) of plant tissue macro- and micronutrient concentrations (%) in onion grown under three levels of applied N in IRR, IRRM, and in NAT. For abbreviations, see Table 1

Sources of variation and contrasts	*df*	N	P	K	Ca	Mg	Fe	Cu	Mn	Zn
Inoculum (I)	2									
Inoc. vs control[a] (I1)	(1)	0.0393	**0.0003**	0.5689	0.8673	0.1667	0.7819	0.0232	0.3162	0.4476
G. int. vs *G. ver.*[b] (I2)	(1)	**0.0001**	**0.0001**	0.0111	0.9075	0.0063	0.2514	0.0093	**0.0001**	**0.0001**
Soil (S)	2									
(IRR+IRRM) vs NAT (S1)	(1)	**0.0001**	0.0345	0.0355	0.1293	0.2074	0.1019	**0.0001**	**0.0001**	**0.0001**
IRR vs IRRM (S2)	(1)	0.8760	0.6776	0.1871	0.2164	0.5427	0.1029	0.8883	**0.0018**	**0.0016**
I×S	2									
I2×S1	(1)	0.1133	**0.0001**	0.0624	0.5534	0.1198	0.8193	0.0628	0.0337	0.0225
I2×S2	(1)	**0.0020**	0.6412	0.3331	0.1491	0.6575	0.0542	0.7787	0.6165	**0.0033**
N	2									
N linear (N1)	(1)	**0.0001**	0.3742	0.0212	**0.0018**	0.0068	0.6016	0.0243	0.1156	0.4359
N quadratic (N2)	(1)	0.0311	0.6984	0.2020	0.7027	0.5525	0.6800	0.8511	0.0518	0.4347
I×N	4									
I1×N1[a]	(1)	0.8741	0.5134	0.1970	0.7462	0.2537	0.5703	0.8883	0.6653	0.7395
I1×N2[a]	(1)	0.6830	0.6649	0.3587	0.8433	0.9932	0.0918	0.9353	0.2539	0.5142
I2×N1[b]	(1)	0.6941	0.1090	0.0197	0.7450	**0.0036**	0.0640	0.2337	0.0468	0.0939
I2×N2[b]	(1)	0.9241	0.4379	0.9645	0.3413	0.7508	0.1099	0.2408	0.4007	0.8377
S×N	4									
S1×N1	(1)	0.9665	0.5778	0.1192	0.2756	0.7453	0.0497	0.1500	0.0045	0.4243
S1×N2	(1)	0.6627	0.7184	0.9006	0.3841	0.5659	0.2297	0.0689	0.2695	0.6443
S2×N1	(1)	0.0974	0.3810	0.6952	0.8938	0.4583	0.8940	0.4393	0.4191	0.0257
S2×N2	(1)	0.5082	0.5799	0.9759	0.7592	0.5883	0.0356	0.1515	0.7843	0.2537
I×S×N	4									
I2×S1×N1	(1)	0.1222	0.6307	0.3978	0.9682	0.3687	0.2591	0.9169	0.8233	0.7271
I2×S1×N2	(1)	0.5343	0.8157	0.3609	0.1943	0.5495	0.0046	0.7089	0.5767	0.2236
I2×S2×N1	(1)	0.6989	0.8204	0.5672	0.8281	0.5408	0.1729	0.6672	0.0808	0.5687
I2×S2×N2	(1)	0.7223	0.7768	0.9844	0.5604	0.7301	0.3181	0.7281	0.2164	0.9625
Error mean square[c]	120	0.0549	0.001258	0.131022	0.071669	0.001355	7.57×10^{-5}	2.40×10^{-8}	2.28×10^{-7}	2.41×10^{-7}

[a] Natural soil only; [b] All soil types; [c] Actual mean square, not a *P* value

Plant tissue concentrations of N, Cu, Mn, and Zn were higher in irradiated soils than in natural soil ($P \leq 0.0001$ for S1 of N, Cu, Mn and Zn, Tables 2 and 4). Mean Cu and Mn tissue concentrations of onion plants grown in irradiated soil were 0.00109% and 0.0061%, respectively, compared to 0.00097% for Cu and 0.0049% for Mn of onion plants grown in natural soil (differences, 0.00011±0.00003% for Cu, and 0.0012±0.0001% for Mn). Tissue concentrations of Mn and Zn were also higher when plants were grown in unamended irradiated soil than when the irradiated soil was amended with microflora (means for Mn, 0.0062% in unamended irradiated soil, 0.0059% in amended irradiated soil, $P \leq 0.0018$, Tables 2 and 4).

Plant tissue concentrations of N and Ca increased proportionally with N fertilization level ($P \leq 0.0018$, Tables 3 and 4).

Discussion

Stunted growth of control plants grown in irradiated soils without AM fungal inoculation has been reported previously (Sasa et al. 1987). In the absence of AM fungi, lack of P limited growth. The addition of a non-mycorrhizal soil extract did not overcome the stunting of growth. It is our interpretation that the ecological equilibrium of the microflora could not be re-established in the short course of the experiment. Smith and Smith (1981) mentioned that, despite the addition of a microbial filtrate from a natural soil to a sterilized soil, the microbial flora of broccoli was not re-established in a 28- or 40-day period.

If soil nutrients are unbalanced, firmness may be affected. In this experiment, increasing N fertilization decreased bulb firmness. Smock and Neubert (1950) observed a decrease in apple firmness under high N levels. Indeed, excessive N fertilization may depress the uptake of Ca which is of fundamental importance for membrane permeability and the maintenance of cell integrity (Mengel and Kirkby 1982).

Jarstfer et al. (1998) reported that Mg application reduced the tissue Ca concentration. In this experiment, N, Ca, and Mg increased proportionally with fertilization level when plants were inoculated with *G. versiforme*, while Mg concentration remained stable in the presence

of *G. intraradices*. These results suggest that soil mineral contents of these elements were likely close to equilibrium because no interaction was observed between Ca and Mg.

All onion plants that grew in non-irradiated natural soil formed arbuscular mycorrhizae with native fungi. In this soil, onion plants preinoculated by *G. intraradices* or *G. versiforme* produced firmer bulbs than those colonized by the native species. Even if our results show an advantage of preinoculating seedlings with the selected AM fungal species, it is possible that similar bulb firmness could have been achieved by preinoculation with native AM fungal species.

The greater N, Cu, Mn, and Zn tissue concentrations of onions grown in irradiated soils, compared to those of plants grown in non-irradiated natural soil, may be explained by soil irradiation leading to increased nutrient availability (Cawse 1975; Jakobsen and Andersen 1982). Even if irradiation increases the availability of a macronutrient in the soil, growth of the host plant cannot improve unless a proper microflora including AM fungi is established.

The comparison of *G. versiforme* to *G. intraradices* in all soil treatments shows the greater efficiency of *G. versiforme* in supplying, in particular, N, P and Zn to the host plant. Yet, root colonization of onion plants by *G. versiforme* was lower than that by *G. intraradices*. Hence, a high root colonization level does not necessarily lead to better nutrient uptake or plant growth. This was also observed by De Silva et al. (1996) and Williams et al. (1992) for strawberry plants grown in the field. Sanders et al. (1977) attributed small differences among fungi to different rates of root colonization. Abbott and Robson (1982) argued that differences among AM fungi in their effectiveness at increasing plant growth were directly correlated with their ability to colonize roots and form an extensive network of hyphae in the surrounding soil. It is likely that *G. versiforme* spread faster through the root system than *G. intraradices*. In future experiments, measurement of extraradical hyphae might help to explain differences in efficiency among AM fungal species.

In non-irradiated natural soil, the use of onion plants preinoculated by selected AM fungal species significantly improved P uptake compared to native species. Of the two fungal species tested, *G. versiforme* was the most efficient at nutrient uptake. This study provides no evidence that colonization by indigenous mycorrhizal fungi increased the dry biomass of onion plants relative to controls, as observed by De Silva et al. (1996).

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