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Effect of two vesicular-arbuscular mycorrhizal fungi on the growth of micropropagated potato plantlets and on the extent of disease caused by *Rhizoctonia solani*

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Abstract Two micropropagated potato cultivars, Goldrush and LP89221, were inoculated into sowing trays with either *Glomus etunicatum* or *G. intraradices* in a greenhouse. After 2 weeks, plantlets were transplanted into pots and roots were challenged 7 days later with *Rhizoctonia solani*. At different times after *R. solani* infection, disease severity, mortality rate, root colonization levels, various growth parameters, and shoot mineral content were evaluated. In Goldrush, only inoculation with *G. etunicatum* led to a significant reduction in disease severity, ranging between 60.2% and 71.2%, on both shoot and crown. This decrease was not observed in LP89221. Compared with the control plantlets, inoculation of Goldrush with *G. etunicatum* or *G. intraradices* reduced significantly the mortality rate by 77% and 26%, respectively, whereas vesicular-arbuscular mycorrhizal (VAM) fungi did not significantly influence the mortality rate in LP89221. In Goldrush, inoculation with *G. etunicatum* significantly increased shoot fresh weight, root dry weight and the number of tubers produced per plant, whereas *G. intraradices* only significantly increased the number of tubers. Tuber and root fresh weights of both potato cultivars were significantly reduced by *R. solani* infection. However, *R. solani*-infected plantlets of both Goldrush and LP89221, inoculated with *G. etunicatum*, produced significantly greater tuber fresh weight than non-VAM plantlets. In *R. solani*-infected plantlets of Goldrush but not LP89221, *G. etunicatum* and *G. intraradices* increased root fresh weight by approximately 140.3% and 76.5%, respectively, compared with non-VAM plants. The potato cultivars Goldrush and LP89221 responded differently to VAM fungal inoculation and to *R. solani* infection in terms of shoot mineral content.

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Introduction

Rhizoctonia solani Kühn (AG-3) is an important soilborne plant pathogen affecting potato (*Solanum tuberosum* L.) (Banville et al. 1996). *R. solani*-infected plantlets may develop crown rot, root rot, or stem canker, which often leads to wilting and to plant death in severe cases. The *Rhizoctonia* disease of potato is a problem occurring throughout the world. It is widespread in North America and endemic to many regions of Canada, including the province of Quebec (Banville 1989). Control of *Rhizoctonia* disease has commonly relied on cultural practices and on the use of chemicals. However, cultural practices alone are not always efficient and, at the present time, no effective fungicides are available, although some chemicals are recommended. In recent years, efforts have concentrated on the biocontrol of this pathogen using antagonistic microorganisms (Homma 1996; Lewis and Kulik 1996) or hypovirulent isolates of *R. solani* (Sneh 1996; Bandy and Tavantzis 1990) as potential alternatives to chemicals.

Vesicular-arbuscular mycorrhizal (VAM) fungi, the most widespread symbionts in plants, have long been associated with increased plant mineral nutrition. The mycorrhizal symbiosis results in improved plant growth in many crops and in enhanced resistance to various abiotic stresses, including water stress (Sylvia and Williams 1992; Jeffries 1987), transplant injury (Menge et al. 1978), and toxic-metal effects (Weissenhorn et al. 1994; Sylvia and Williams 1992; Dehn and Schüepp 1990). Over the last few years, the use of VAM fungi as potential biological control agents of soilborne plant pathogens has received increased attention (Azcón-Aguilar and Barea 1996; St-Arnaud et al. 1995; Hooker et al. 1994; Linderman 1994; Sharma et al. 1992; Jalali and Jalali 1991; Jeffries 1987; Schenck 1987; Dehne 1982).

For example, mycorrhizal symbionts were shown to improve resistance against *Phytophthora parasitica* in citrus (Davis and Menge 1981), *Sclerotium cepivorum* Berk. in onion (Torres-Barragán et al. 1996), *Fusarium* in tomato (Caron et al. 1986) and alfalfa (Hwang et al. 1992), and *Verticillium* in cotton (Liu 1995). Consequently, the use of VAM fungi, through inoculation of crops or stimulation of naturally occurring populations, could be a promising approach to control development of potato diseases. Although promising results show that the VAM fungus *Glomus intraradices* can suppress development of potato dry rot, a post-harvest disease caused by the fungus *Fusarium sambucinum* (Niemira et al. 1996), to our knowledge no extensive study has been undertaken to evaluate the influence of VAM fungi on fungal diseases affecting potato plants.

In natural conditions as well as through inoculation, most species or isolates of VAM fungi can establish symbiosis with a very wide host range, including potato plants (Bhattarai and Mishra 1984). However, many studies have demonstrated that the VAM fungus-plant cultivar combination influences plant responses. Among six VAM fungi tested, including *Gigaspora margarita*, *Glomus clarum*, *G. intraradices*, *Glomus mosseae*, *Glomus versiforme*, and *Glomus vesiculiferum* on three onion cultivars, Yao (1996) reported that the combination *G. versiforme* and the cultivar Golden Mosque 224A was the most effective in terms of growth and yield enhancement, while the combination *G. clarum* and the cultivar Early Harvest 210 appeared less efficient. Other work has shown that the effect of VAM fungi varies with the cultivar in cotton (Liu 1995), soybean (Khalil et al. 1994), maize (Khalil et al. 1994; Toth et al. 1990), millet (Tewari et al. 1993), trifoliate orange (Viyanak and Bagyaraj 1990), rice (Secilia and Bagyaraj 1994) in terms of plant growth, yield, and mineral nutrition, as well as plant responses against pathogen agents (Liu 1995; Matsubara et al. 1995). Such differences justify the need to identify the best combinations of VAM fungal species or strains and host plant in order to make better use of VAM fungal inoculation in crops improvement and disease management.

As a part of ongoing research on the effect of VAM fungi on potato plantlets, the aim of the present study was to determine the effect of the VAM fungi *G. etunicatum* and *G. intraradices* on the growth of micropropagated potato plantlets and on disease development of potato plantlets challenged with *R. solani*.

Materials and methods

Plantlet micropropagation

Two potato cultivars (Goldrush and LP89221) obtained from the Station de Recherche Agriculture et Agroalimentaire Canada (La Pocatière, Quebec) were multiplied in vitro by shoot cuttings. Plantlets were grown under sterile conditions on a basal salt mixture and vitamin medium (Murashige and Skoog 1962) supplemented with 8 g/l of bacto agar (Difco, Becton Dickinson, Md.) and sucrose (30 g/l). The pH of the medium was adjusted to 5.7. Plantlets were maintained in a growth chamber at 23°C under cool-white fluorescent lights with an irradiance of 25 μE/m^2/s and a photoperiod of 16 h/day. They were subcultured on fresh medium every 4 weeks until a sufficient number of plantlets was obtained.

Inoculum of *R. solani*

The virulent strain of *R. solani* (AG-3) isolated from a potato tuber, kindly provided by Service de Recherche en Défense des Cultures (MAPAQ, Quebec, Canada), was maintained on bacto agar at 4°C. The inoculum was prepared according to McDonald and Rovira (1985) with slight modifications. Oats (*Avena sativa* L.) were placed in Erlenmeyer flasks containing water (1 g of oats/ml of water), soaked for 20 h, drained off water, and autoclaved (121°C; 30 min) on each of 3 successive days. The oats were then inoculated with agar plugs covered with actively growing *R. solani* mycelium (Cartwright and Benson 1995) or with sterile bacto agar plugs (control), incubated under laboratory conditions for 3 weeks and shaken every 4–5 days to prevent packing of the seeds. Seeds were air-dried (24 h) under sterile conditions before use.

Mycorrhization of acclimatizing potato plantlets

Three-week-old potato plantlets of both cultivars were excised to obtain uniform size. They were individually rooted and grown in sowing trays (72 cells/tray). Each cell (diameter: 3 cm, volume: 50 ml) was half-filled with low phosphorus peat-based growing substrate (Pro-Mix BX; Premier Tech., Rivière-du-Loup, Quebec, Canada) amended with 5 ml of either uninoculated (control) or inoculated substrate (approximately 2.7 propagules/ml) with *G. etunicatum* Becker & Gerd or *G. intraradices* Schenck & Smith (Premier Tech). Plantlets were transferred to the glasshouse where they were acclimatized for 2 weeks under a plastic tunnel and sprayed with tap water for 10 s every 16 min. The rooted plantlets were then individually transplanted with their cell content into 18-cm-diameter pots containing a mixture of soil, peat-based growing substrate (Pro-Mix BX) and turface (Turface MVP; Lake Cook Road, Buffalo Grove, Ill.) (3/1/1; v/v/v) previously sterilized by gamma irradiation (Co-60, 15 kGy, 22°C). Plants were grown in a glasshouse under natural daylight supplemented with high-pressure sodium lamps (100 μE/m^2 per second PAR) to maintain a minimal photoperiod of 16 h/day. Each pot was weekly supplied with a nutrient solution (200 ml) containing per litre (1 ml) Fe-EDTA, (150 mg) KNO_3, (190 mg) $Ca(NO_3)_2.4H_2O$, (50 mg) $NaH_2PO_4.H_2O$, (100 mg) $MgSO_4.7H_2O$, (0.34 mg) $MnSO_4.H_2O$, (0.05 mg) $CuSO_4.5H_2O$, (0.1 mg) $ZnSO_4.7H_2O$, (0.6 mg) H_3BO_3, (1 mg) NaCl, (400 mg) $(NH_4)_4Mo_7O_{24}.4H_2O$. Plants were watered as needed.

Infection of mycorrhizal and non-mycorrhizal potato plantlets with *R. solani*

At 7 days after transplantation, soil at the base of potato plantlets was gently pushed aside to expose portions of the root system. Non-infected (χ control) or *R. solani*-infected oats (5 seeds per pot) were then placed directly in contact with uncovered roots at five points equidistant from the stem. Roots were covered with soil immediately after inoculum application.

Disease assessment

Disease severity (crown rot, shoot rot) was rated weekly on both infected and non-infected plantlets. Disease assessment was performed 2, 3, 4, and 5 weeks after *R. solani* inoculation. An arbitrary scale (0–5) was established to assess disease severity where 0 = no symptom and 5 = plant death. Presence of *R. solani* on each infected-plant was confirmed by re-isolation of the fungus.

Harvest, plant growth, root colonization, and plant mineral contents

Six plants were harvested for each treatment (2 plants/block × 3 blocks) at the 5th, 7th, and 9th week after *R. solani* infection. At each harvest time, tuber, root and shoot fresh weights as well as the number of tubers produced and the root dry weights were recorded. At each harvest time, a small sample of fine roots (2–3 g fresh wt.) randomly selected from each plant was cleared and stained with Trypan blue according to Phillips and Hayman (1970). Root colonization by VAM fungi was then estimated using the grid-line intersect method (Giovannetti and Mosse 1980). Total shoot material from two replicate plants in each treatment was ground and analysed for total P, K, Ca, Zn, Mn, and Fe concentrations. Wet-acid digestion was used for P, K, and Ca contents, while dry-ashed was used for Zn, Mn, and Fe analyses. P concentration was determined by the vanadate-molybdate method (Tandon et al. 1968), whereas other elements were analysed using atomic absorption spectrophotometer (Perkin-Elmer Atomic Absorption Spectrometer 3300, Veberlingen, Germany).

Experimental design and statistical analysis

Experiments were performed using a factorial arrangement 2 (cultivar) × 3 (2 VAM fungi + control) × 2 (*R. solani*-infected + non-infected) in a randomized complete block design with three replicates. Each experimental unit consisted of six plants randomly distributed in each block. The entire experiment was set up twice, successively from March 1997 to June 1997, and from March 1998 to June 1998. Analysis of variance (ANOVA) was carried out with the GLM (General Linear Models) procedure of SAS Institute Inc. (1999). When significant (P<0.05), treatment means were compared using Fisher's protected LSD. For mortality and disease severity, healthy plantlets were excluded from statistical analyses due to their lack of infection by *R. solani* in order to obtain an homogenous variance. Except for disease severity, which was different according to the time of disease assessment, all other data presented are means of the three times of harvest. For all parameters measured, values are means of the two experiments of recorded data as there was no significant difference between the two experiments.

Results

Mycorrhizal colonization

For both potato cultivars, mean values of root colonization by *G. etunicatum* were 5.2%, 7.4%, and 6.5%, and by *G. intraradices* values were 4.7%, 7.2%, and 5.0% at the 8th, 10th and 12th week, respectively, after mycorrhizal inoculation. Root colonization by VAM fungi was not significantly affected by the presence of *R. solani* (data not shown).

Disease development

Effect of VAM fungi on *R. solani* disease severity was evaluated only in infected-plants of the potato cultivars Goldrush (Fig. 1) and LP89221 (Fig. 2). For Goldrush, *R. solani* disease severity on shoots was significantly lower in VAM plantlets than the controls after 2 weeks of infection. However, 3, 4, and 5 weeks after inoculation with the pathogen, only *G. etunicatum* significantly reduced disease severity on both shoot and crown. Decrease in disease severity was in the range of 60.2–71.2%. VAM fungi did not significantly influence disease severity evaluated on shoot and crown in the cultivar LP89221. Plantlets of Goldrush, inoculated or not with VAM fungi, were more susceptible to *R. solani* attacks than corresponding plantlets of LP89221 (Figs. 1, 2).

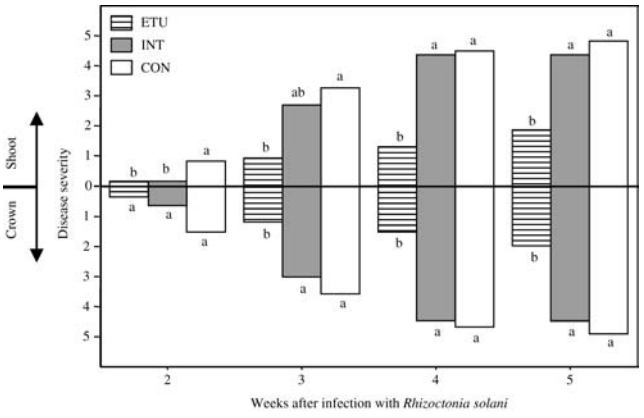

Fig. 1 Effect of mycorrhizal fungi (*ETU Glomus etunicatum*, *INT G. intraradices*, *Con* Control) on disease severity on potato cultivar Goldrush infected with *Rhizoctonia solani*. Values (for each week) for disease severity rating in shoot or crown followed by the same letter are not significantly different according to an LSD test (P <0.05)

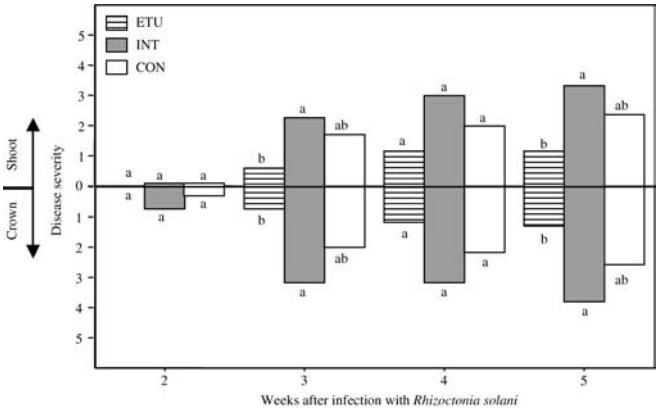

Fig. 2 Effect of mycorrhizal fungi (*ETU Glomus etunicatum*, *INT G. intraradices*, *Con* Control) on disease severity on potato cultivar LP89221 infected with *Rhizoctonia solani*. Values (for each week) for disease severity rating in shoot or crown followed by the same letter are not significantly different according to an LSD test (P <0.05)

Mortality of plants

In both cultivars, *R. solani* caused mortality in non-VAM and VAM plantlets. For each treatment, mortality was higher for Goldrush than for LP89221 (Table 1). In comparison with non-VAM control plantlets (mortality: 43.75%), inoculation of Goldrush with *G. etunicatum* or

Table 1 Effect of *Glomus etunicatum* and *G. intraradices* on shoot fresh weight, root dry weight, number of tubers per plant and on the mortality of potato cultivars Goldrush and LP89221 either non-infected (healthy plants) or infected with *Rhizoctonia solani*. Means in each row followed by the same letter are not significantly different according to an LSD test ($P<0.05$). For mortality, only *R. solani*-infected plantlets were included in the statistical analyses. Non-infected (healthy plants) and *R. solani*-infected plantlets were included in statistical analyses for growth parameters

Parameter	Cultivar	Treatment		
		G. etunicatum	*G. intraradices*	Control
Mortality (%)	Goldrush	9.90c	32.31b	43.75a
	LP89221	7.12b	19.97a	14.97ab
Shoot fresh wt. (g)	Goldrush	10.90a	8.46b	7.86b
	LP89221	10.05a	10.17a	10.16a
Root dry wt. (g)	Goldrush	0.30a	0.26b	0.24b
	LP89221	0.28ab	0.27b	0.32a
Number of tubers	Goldrush	6a	6a	4b
	LP89221	3a	3a	3a

Table 2 Effect of *Glomus etunicatum* and *G. intraradices* on tuber and root fresh weight of the potato cultivars Goldrush and LP89221, either non-infected (healthy plants) or infected with *Rhizoctonia solani*. Means in each column followed by the same letter are not significantly different according to an LSD test ($P<0.05$). Differences between means of non-infected (healthy plants) and *R. solani*-infected plants are significant ($P<0.001$)

Treatment	Goldrush				LP89221			
	Tuber fresh wt. (g)		Root fresh wt. (g)		Tuber fresh wt. (g)		Root fresh wt. (g)	
	Healthy	Infected	Healthy	Infected	Healthy	Infected	Healthy	Infected
G. etunicatum	48.17a	37.10a	13.90a	10.86a	45.23a	30.68a	11.21a	7.07a
G. intraradices	47.76a	13.13b	13.01a	7.98b	35.68c	17.54b	11.20a	7.19a
Control	46.84a	8.65c	14.00a	4.52c	40.23b	21.95b	12.86a	7.65a
Means	47.59	19.62	13.64	7.79	40.38	23.39	11.76	7.30

G. intraradices significantly reduced mortality by 77% (mortality: 9.90%) and 26% (mortality: 32.31%), respectively. VAM fungi did not significantly influence mortality in LP89221.

Effect of VAM fungi on growth parameters of healthy and *R. solani* infected-plantlets

Means of shoot fresh weight, root dry weight, and number of tubers produced in both cultivars Goldrush and LP89221 (inoculated or not with VAM fungi) were not influenced by *R. solani* infection (data not shown). Significant interactions between cultivars and VAM fungi were observed for shoot fresh weight ($P=0.0076$), root dry weight ($P=0.0010$), and number of tubers ($P=0.0001$). Effects of *G. etunicatum* and *G. intraradices* on these parameters are presented in Table 1. In Goldrush, inoculation with *G. etunicatum* significantly increased shoot fresh weight, root dry weight and number of tubers produced per plant, whereas *G. intraradices* only significantly increased tuber number (Table 1). In LP89221, VAM fungi did not significantly increase plant shoot fresh weight, root dry weight, or production of tubers (Table 1).

Interactions between potato cultivars, VAM fungi, and *R. solani* were significant for tuber fresh weight ($P=0.0001$) and root fresh weight ($P=0.0005$). Tuber fresh weight of both Goldrush and LP89221 was significantly reduced by *R. solani* infection (Table 2). Tuber fresh weight in healthy-plantlets of Goldrush was not affected by VAM fungi (Table 2). Mycorrhizal plants of Goldrush infected by *R. solani* produced significantly greater tuber fresh weight than non-VAM plants. Inoculation of healthy and *R. solani*-infected plantlets of LP89221 with *G. etunicatum* significantly increased tuber fresh weight, while *G. intraradices* decreased significantly tuber fresh weight in healthy plants, compared with non-VAM plants (Table 2). Root fresh weights (means of VAM and non-VAM plants) of both cultivars were significantly reduced by *R. solani* infection (Table 2). In healthy plants of both cultivars, root fresh weights were not significantly affected by inoculation with VAM fungi. However, in *R. solani*-infected plants of Goldrush, VAM fungi significantly increased root fresh weight, compared with non-VAM plants. This effect was more pronounced in plants inoculated with *G. etunicatum*. Compared with non-VAM plants (4.52 g), *G. etunicatum* and *G. intraradices* increased root fresh weight by 140.3% (10.86 g) and 76.5% (7.98 g), respectively. Such an effect of VAM fungi on root fresh weight was not observed for LP89221.

Table 3 Effect of *Glomus etunicatum* and *G. intraradices* on concentrations of shoot macroelements (P, K, Ca) and oligoelements (Mn, Zn, Fe) in the cultivar Goldrush, either non-infected (healthy plants) or infected with *Rhizoctonia solani*. Means in each column followed by the same letter are not significantly different according to an LSD test (P <0.05). P, K and Ca in mg/g dry wt.; Mn, Zn and Fe in µg/dry wt. Differences between means of non-infected (healthy plants) and *R. solani*-infected plants are significant (* P <0.05), highly significant (*** P <0.001) or not significant (NS)

Treatment	P		K		Ca		Mn		Zn		Fe	
	Healthy	Infected	Healthy	Infected	Healthy	Infected	Healthy	Infected	Healthy	Infected	Healthy	Infected
G. etunicatum	2.22a	2.54c	49.23a	52.52a	29.46a	22.89a	68.09a	58.98a	86.46a	85.55a	949.30a	1040.5a
G. intraradices	2.23a	2.89b	46.54a	40.88b	27.59a	24.36a	54.14a	45.69a	81.69a	85.68a	763.70a	1117.7a
Control	2.50a	3.74a	52.98a	35.10b	27.63a	18.90a	57.76a	57.84a	83.62a	97.45a	734.60a	1550.7a
Means	2.32	3.06	49.59	42.83	28.23	22.05	60.00	54.17	83.92	89.56	815.90	1236.3
	***		***		***		NS		NS		*	

Table 4 Effect of *Glomus etunicatum* and *G. intraradices* on concentrations of shoot macroelements (P, K, Ca) and oligoelements (Mn, Zn, Fe) in the cultivar LP89221, either non-infected (healthy plants) or infected with *Rhizoctonia solani*. Means in each column followed by the same letter are not significantly different according to an LSD test (P <0.05). P, K and Ca in mg/g dry wt.; Mn, Zn and Fe in µg/dry wt. Differences between means of non-infected (healthy plants) and *R. solani*-infected plants are significant (* P <0.05) or not significant (NS)

Treatment	P		K		Ca		Mn		Zn		Fe	
	Healthy	Infected	Healthy	Infected	Healthy	Infected	Healthy	Infected	Healthy	Infected	Healthy	Infected
G. etunicatum	2.89a	3.10a	34.13a	36.22a	24.26a	22.09a	64.85a	57.28a	82.48a	88.70a	1037.1a	943.4a
G. intraradices	2.96a	2.65a	34.16a	31.26b	22.69a	19.15a	59.76ab	48.01a	76.56a	67.20b	1037.9a	1008.6a
Control	2.97a	2.03b	35.92a	31.29b	18.19b	17.19a	45.58b	46.40a	65.49b	71.80b	305.4b	951.1a
Means	2.94	2.59	34.74	32.92	21.72	19.48	56.73	50.56	74.84	75.90	793.5	967.7
	*		NS		NS		NS		NS		NS	

Effect of VAM fungi on mineral status

Goldrush and LP89221 responded differently to inoculation with VAM fungi and to *R. solani* infection in terms of shoot mineral content (Tables 3, 4). In Goldrush, shoot contents of P, K, Ca, and Fe (means of VAM and non-VAM plants) were significantly affected by *R. solani* infection. P and Fe contents were significantly higher in *R. solani*-infected plants, whereas K and Ca contents were significantly lower (Table 3). In healthy plants of Goldrush, VAM fungi did not significantly influence shoot mineral content. On plants inoculated with *G. etunicatum* and *R. solani*, P and K contents were significantly lower and higher, respectively. P content of plants inoculated with *G. intraradices* and *R. solani* was also significantly lower relative to the control. In LP89221, means of shoot contents of K, Ca, Mn, Zn, and Fe were not influenced by *R. solani* infection, whereas means of P content was significantly lower in *R. solani*-infected plants (Table 4). In healthy plants of LP89221, P and K contents were not significantly affected by inoculation with VAM fungi, while Ca, Zn, and Fe contents were significantly increased. Mn content was significantly higher in plants inoculated with *G. etunicatum* than in the control (Table 4). In *R. solani*-infected plants of LP89221, VAM fungi did not significantly influence shoot contents of Ca, Mn, and Fe, whereas *G. etunicatum* significantly increased P, K, and Zn contents.

Discussion

This study demonstrates that inoculation with VAM fungi reduced development of *R. solani* disease on micropropagated potato plantlets. The results also show the beneficial effect of VAM fungi on growth and development of micropropagated potato plantlets, as have previous investigations on the effects of VAM fungi on potato growth (Graham et al. 1976) and yield (Vosátka and Gryndler 1999; Niemira et al. 1995; Graham et al. 1976).

The two potato cultivars differed in their response to VAM fungi. Indeed, plantlets of Goldrush were more influenced by VAM fungi than those of LP89221 in terms of increase in shoot fresh biomass, root dry biomass, and number of tubers produced. Similarly, differences in growth and yield responses to VAM fungi have been observed recently on various cultivars of strawberry (Mark and Cassells 1996; Norman et al. 1996), wheat (Hetrick et al. 1993), banana (Declerck et al. 1995), finger millet (Tewari et al. 1993; Krishna et al. 1985), and cowpea (Rajapakse and Miller 1987). On the other hand, the VAM fungus *G. etunicatum* enhanced more strongly plant growth and yield than *G. intraradices*. Although both VAM fungi increased the number of tubers produced in Goldrush, only *G. etunicatum* increased shoot fresh weight and root dry weight. Furthermore, in *R. solani*-infected plantlets of Goldrush, inoculation with *G. etunicatum* produced higher tuber and root fresh weights than those inoculated with *G. intraradices*. In LP89221, only tuber fresh weight was consistently increased by *G.*

etunicatum in infected and healthy plants. These results suggest a kind of compatibility between potato cultivars and VAM fungi even in the presence of *R. solani*. Such a compatibility between VAM fungi and host plant was previously observed in other plants such as onion (Yao 1996) and maize cultivars (Khalil et al. 1994). Beneficial effects of *G. etunicatum* on plantlets of Goldrush did not seem to be correlated with increased mineral uptake since, except for K, *G. etunicatum* did not significantly influence shoot mineral contents in either healthy or *R. solani*-infected plantlets. It is also interesting to note that inoculation of VAM fungi significantly stimulated production of tubers. A promoting effect of VAM fungi on potato tuber initiation was observed previously (Niemira et al. 1995; Graham et al. 1976). Considering that tuber initiation is hormonally mediated (Ewing 1995), it may be hypothesized that *G. etunicatum* and *G. intraradices* affected hormone balance in potato plantlets, leading to increased production of tubers. Previously, Allen et al. (1982, 1980) proposed that phytohormone changes in leaves and roots alter substantially the physiology of mycorrhizal *Bouteloua gracilis*, a common western United States range grass.

Mycorrhization influenced *R. solani* severity on potato plantlets. An interesting decrease in disease severity and mortality was observed especially with plantlets of Goldrush inoculated with *G. etunicatum*. Although *G. intraradices* did not reduce disease severity, it decreased mortality and enhanced tuber and root fresh weights in Goldrush. In addition, the decrease in disease severity and improvement of growth and yield observed in plantlets inoculated with *G. etunicatum*, after challenge with *R. solani*, suggest that inoculation of Goldrush with VAM fungi results in plant protection and/or tolerance. Norman et al. (1996) also reported that VAM fungi reduced adverse effects of *Phytophthora fragariae* on infected plants of strawberry cultivars, as indicated by better growth. Plants of soybean colonized by *G. mosseae* tolerated *R. solani* infection better than non-VAM plants (Zambolim and Schenck 1983). Trotta et al. (1996) indicated that inoculation of tomato plants with *G. mosseae* improved resistance against *Phytophthora nicotianae* var. *parasitica*.

A few lines of evidence indicate that increased disease tolerance in mycorrhizal plants may be attributed to increased P nutrition in the host plant (Zambolim and Schenck 1983). This mechanism is unlikely to be involved in the present study, as shoot P concentrations of mycorrhizal plantlets were significantly lower in *R. solani*-infected plantlets than healthy plantlets of Goldrush. The involvement of other mechanisms, such as morpho-physiological or biochemical changes, must be considered. *G. etunicatum* inoculation was particularly beneficial to infected plantlets of Goldrush, which were more susceptible to *R. solani* disease than plantlets of LP89221. This result suggests that VAM fungi inoculation is mainly beneficial to plants showing a high level of susceptibility. Mark and Cassells (1996) and Norman et al. (1996) also observed that VAM fungi were especially beneficial to cultivars of strawberry that were highly susceptible to *P. fragariae* in terms of resistance/tolerance.

Beneficial effects of VAM inoculation on potato growth, yield, and protection against *R. solani* infection were observed in this study, although the level of root colonization was relatively low. Niemira et al. (1995), using a peat-based medium containing *G. intraradices* to produce potato minitubers, observed yield increase even in the presence of very low levels of mycorrhization. St-Arnaud et al. (1994) and Mark and Cassells (1996) reported a lack of correlation between the extent of mycorrhizal colonization and host plant disease reduction. On the other hand, Dugassa et al. (1996) reported that the influence of VAM symbiosis on plant health depends more on host-plant and pathogen genotype than on VAM fungal colonization level.

As observed in the case of growth parameters, the effect of VAM fungi on shoot mineral concentration varied with the potato cultivar and the presence or not of *R. solani*. VAM fungi did not affect shoot mineral content of healthy plants of Goldrush, whereas they increased Ca, Mn, Zn, and Fe shoot content of LP89221 plantlets. These results suggest that increased shoot content in these mineral elements was not involved in the observed stimulation of plant growth and yield. However, the possibility that increased shoot contents of Ca, Mn, Zn, and Fe led to an increased tuber fresh weight in LP89221 plantlets can not be ruled out. In *R. solani*-infected plantlets of both cultivars, *G. etunicatum* increased K shoot content. Although this observation does not indicate conclusively a link between K shoot content and reduction in disease severity, adequate K supply does promote cell wall thickening that helps plants to resist disease (Shuman 1994). VAM fungi, particularly *G. etunicatum*, significantly decreased and increased P shoot content of plantlets of Goldrush and LP89221, respectively. As *G. etunicatum* inoculation also decreased *R. solani* disease severity in Goldrush, it seems that P absorption is not involved in the increased disease resistance/tolerance observed (Caron et al. 1985).

In summary, the results show that the VAM fungi-potato cultivar combination influences plant responses to mycorrhizal inoculation and provide evidence that inoculation of plantlets of the potato cultivar Goldrush with *G. etunicatum* enhanced growth and yield and improved resistance/tolerance to *R. solani* infection. Thus, inoculation with an appropriate VAM fungus may help young potato plants overcome damage caused by *R. solani*, one of the most widely spread soilborne pathogen of potatoes. This is the first study to show that VAM fungi improve protection in potato plants highly susceptible to pathogenic fungi.

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