Effects of *Glomus intraradices* and onion cultivar on *Allium* white rot development in organic soils in Ontario

M.D.L.A. Jaime, T. Hsiang, and M.R. McDonald

Abstract: Commercial products containing formulations of the vesicular–arbuscular mycorrhiza (AM) *Glomus intraradices* were assessed for their effectiveness in suppressing *Allium* white rot (WR) on onions (*Allium cepa*) in organic soils and compared with the fungicide Folicur 3.6F (430 g a.i./L tebuconazole) under field conditions. The trials were conducted during 2000 and 2001 in commercial onion fields in the Holland–Bradford Marsh in Ontario. The AM product MIKRO-VAM, which is used in transplanted onions, reduced the incidence of WR by almost 50% compared with the untreated control and was comparable with that of the fungicide treatment, Folicur 3.6F, applied according to label recommendations. This is one of the few studies to demonstrate season-long disease suppression with AM under field conditions, and it is the first to show that the AM products can be as effective as a fungicide treatment under commercial production practices. A consistent difference in incidence of WR was found between the cultivars 'Hoopla' and 'Fortress' onions. 'Hoopla' was more susceptible to WR than 'Fortress' in 10 of 13 field trials and all trials where WR incidence on 'Hoopla' was ≥4%. There was a significant negative correlation between disease incidence and AM root colonization, suggesting that AM colonization was an important factor in the reduction of WR observed in this study.

Key words: vesicular–arbuscular mycorrhizae, cultivar resistance, *Allium* white rot, *Sclerotium cepivorum,* biological control.

Résumé : Des produits commerciaux contenant des préparations du champignon mycorhizien à vésicules et arbuscules (MVA) *Glomus intraradices* ont été évalués, au champ, en ce qui a trait à leur capacité de supprimer la pourriture blanche (PB) chez les oignons (*Allium cepa*) cultivés dans des sols organiques, et comparés au fongicide Folicur 3.6F (430 g matière active/L tébuconazole). Les essais ont eu lieu en Ontario, en 2000 et 2001, dans les cultures commerciales d'oignons de la région du marais Holland–Bradford. Le MIKRO-VAM, contenant du MVA et utilizé lors de la transplantation des oignons, a réduit l'incidence de la PB de près de 50 % relativement aux témoins non traités, ce qui se compare au résultat obtenu avec le traitement au Folicur 3.6F appliqué selon les instructions du fabricant. Cette étude en est une des rares qui démontre, dans des conditions naturelles, l'efficacité du MVA en ce qui a trait à la suppression de la maladie durant toute une saison, et la première à montrer que les produits contenant le MVA peuvent être tout aussi efficaces que les fongicides dans les cultures commerciales. Une différence constante sur le plan de l'incidence de la PB a été observée chez les cultivars 'Hoopla' et 'Fortress'. Le cultivar 'Hoopla' était plus réceptif à l'égard de la PB que le cultivar 'Fortress' dans 10 des 13 essais en champ de même que dans tous les essais où l'incidence chez le cultivar 'Hoopla' était de ≥4 %. Il y avait une corrélation négative significative entre l'incidence de la maladie et la colonization des racines par le MVA, ce qui semble indiquer que cette colonization était un facteur important dans la réduction de la PB observée au cours de cette étude.

Mots-clés : mycorhizes à vésicules et arbuscules, résistance des cultivars, pourriture blanche de l'oignon, *Sclerotium cepivorum*, lutte biologique.

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Introduction

Allium white rot (WR), which is caused by the soilborne pathogen *Sclerotium cepivorum* Berk, is one of the most important diseases wherever edible *Allium* crops are grown and is an economically limiting factor in production areas around the world (Coley-Smith 1990). The control of this disease has been difficult both technically and economically and has posed a challenge to researchers because of the persistence of sclerotia in soils, even in the absence of a host, and the potential for sclerotia to infect host plants at any time (Coley-Smith and King 1969).

Several methods have been evaluated for the control of WR, including cultural controls, the use of resistant cultivars, chemical controls, biological controls, and the use of sclerotial germination stimulants. In several countries, including the United States, New Zealand, Brazil, Egypt, and Mexico, management of WR has been based mostly on the use of chemicals and, more recently, on germination stimulants (Abd-El Razik et al. 1988a, 1988b; Crowe et al. 1994; Davis et al. 2007; Fullerton and Stewart 1991; Hovius and McDonald 2002; Perez et al. 1996; Sinigaglia et al. 1986). In Canada, the fungicide Botran 75W (dichloran, 750 g a.i./kg) is the only product registered for WR control. However, when applied according to label recommendations, this fungicide does not always provide satisfactory disease control and is expensive (Slade et al. 1992; Valdes and Edgington 1986). Tebuconazole is a demethylation inhibitory fungicide that has been approved for WR control in some countries, including the United Kingdom and the United States (Clarkson et al. 2006). This fungicide has shown satisfactory WR control when applied to the soil or to garlic (*Allium sativum* L.) cloves (Dennis 2001; Jackson et al. 2001; Melero-Vara et al. 2000).

Effective biological controls would be beneficial for the Canadian onion industry, especially if combined with other management methods. One group of organisms with potential as biological control agents are vesicular–arbuscular mycorrhizae, more commonly known as arbuscular mycorrhizae (AM). These fungi are the most common and widespread type of mycorrhizae. They establish a mutualistic symbiosis with the roots of about 80% of land plants in different ecosystems (Bonfante and Perrotto 1995) and interact with almost all plant families including many important agricultural species (Brown 1992). Mycorrhizal fungi are promising candidates for biological control because they are environmentally friendly, ubiquitous symbionts that establish stable, long-term associations with the roots of most plants (Traquair 1995).

The benefits of mycorrhizal symbioses have received increased attention because of improved plant nutrition and also because they may increase the resistance of plants to root pathogens and abiotic stresses (Azcón-Aguilar and Barea 1996; Caron 1989; Harley and Smith 1983; Linderman 1994). Over the last three decades, there has been a growing, but reserved, interest in the role of the mycorrhizal fungi as biological control agents (Caron 1989; Dehne 1982; Duchesne 1994; Jalali and Jalali 1991; Linderman 1994, 2000; Schenck 1987).

Reduction of disease symptoms as a result of mycorrhizal association has been described for a range of protist and fungal pathogens belonging to the genera *Phytophthora*, *Gaeumannomyces*, *Fusarium*, *Thielaviopsis*, *Pythium*, *Rhizoctonia*, *Sclerotium*, *Verticillium*, *Aphanomyces*, *Pyrenochaeta*, *Ganoderma*, *Macrophomina*, *Bipolaris*, *Phoma*, *Urocystis*, *Microcyclus*, *Olpidium*, and *Cylindrocarpon* (Singh et al. 2000); bacterial pathogens in the genera *Erwinia* (Garcia-Garrido and Ocampo 1989b) and *Pseudomonas* (Garcia-Garrido and Ocampo 1989a); and nematodes in the genera *Pratylenchus*, *Rotylenchus*, *Radopholus*, *Heterodera*, *Tylenchorynchus*, *Tylenchulus*, *Aphelenchus*, and *Meloidogyne* (Singh et al. 2000). Evidence exists to demonstrate the potential of AM as a biological agent against soilborne root diseases; however, examples of successful practical applications are scarce (Hooker et al. 1994; Linderman 1994) because of the complexity of the tripartite mycorrhiza–soil–plant association and the direct influence of prevailing environmental conditions.

The main objective of this study was to assess the efficacy of commercially available AM products containing formulations of *Glomus intraradices* Schenck & Smith for suppression of WR of onions (*Allium cepa* L.) in organic soils and to compare their efficacy to that of the fungicide Folicur 3.6F (430 g a.i./L tebuconazole). The second objective was to determine if there was a difference in resistance to WR between two onion cultivars: 'Fortress' and 'Hoopla'. The third objective was to determine the relationship between the application of *G. intraradices* and root colonization by AM and identify any relationship between disease incidence and root colonization.

Materials and methods

Field trials were conducted in the Bradford–Holland Marsh, Ontario, Canada (44°15′N, 79°35′W), in 2000 and 2001 with four commercial AM products containing *G. intraradices*: MIKRO-VAM (MIKRO-TEK, Timmins, Ont.), PRO-MIX PGX with MYCORISE 1000, PRO-MIX PGX with MYCORISE 500, and PRO-MIX PGX with MYCORISE 255 (Premier Tech, Rivière-du-Loup, Que.). The MYCORISE products differed only in the concentration of spores of *G. intraradices*, i.e., MYCORISE 1000 contains 1000 spores/L of PRO-MIX PGX soilless growing medium. Onions were grown as transplants and then planted out into commercial onion fields of muck soil (pH 5.5–6.5, 60% organic matter). In 2001, other formulations of AM containing *G. intraradices*, MYCORISE PRO and a seed coating of MIKRO-VAM, were also evaluated on direct seeded onions.

Field trials with transplanted onions

'Fortress' (Stokes Seeds, Thorold, Ont.) and 'Hoopla' (Solar Seeds, Eustis, Fla.) onions were seeded in plastic plug trays with 288 cells (2 cm^2 by 4.5 cm deep/cell; Landmark Plastic Co-op, Akron, Ohio) on 18 and 19 April 2000 and 17–19 April 2001. Trays were filled with premixed AM products containing *G. intraradices*: PRO MIX PGX with MYCORISE 1000, PRO-MIX PGX with MYCORISE 500, and PRO-MIX PGX with MYCORISE 255 prior to seeding (Table 1). PRO-MIX PGX was used as the growing medium for all treatments. For the MIKRO-VAM treatment, trays were half-filled with growing medium and then compacted, after which 1 mL/plug of MIKRO-VAM inoculum was

Table 1. Treatments, rates, and active ingredients used in the vesicular–arbuscular transplanted and direct-seeded trials conducted in 2000 and 2001.

Treatment[a]	Active ingredient	Rate	Trial	2000 sites	2001 sites	Source
MYCORISE 1000	*Glomus intraradices* (1000 spores/L of soilless mix)	1.25 L/tray, 4.3 propagules/cell	Transplanted	123	456	Premier Tech
MYCORISE 255	*G. intraradices* (255 spores/L of soilless mix)	1.25 L/tray, 1.1 propagules/cell	Seeded	123	None	Premier Tech
MYCORISE 500	*G. intraradices* (500 spores/L of soilless mix)	1.25 L/tray, 2.4 propagules/cell	Transplanted	None	456	Premier Tech
MIKRO-VAM	*G. intraradices* (1000 propagules/g inoculum)	288 g/tray (1 g/cell), 1000 propagules/cell	Transplanted	123	456	MIKRO-TEK
Folicur 3.6F (fungicide check)	Tebuconazole (430 g a.i./L)	1 L/ha	Transplanted	123	456	Bayer
Untreated control			Transplanted	123	456	
MIKRO-VAM film coat	*G. intraradices* (25–50 propagules/seed)	28 125 × 10^3 propagules/ha	Seeded	None	789	MIKRO-TEK
MYCORISE PRO	*G. intraradices* (15 propagules/gr)	50 L/ha product, 750 × 10^3 propagules/ha	Seeded	None	789	Premier Tech
Dithane DG 75%	Mancozeb (750 g a.i./kg)	8.8 kg/ha product	Seeded	None	789	Rohm & Haas
Folicur 3.6F (fungicide check)	Tebuconazole (430g a.i./L)	1 L/ha product	Seeded	None	789	Bayer
Untreated control						

[a]All treatments were applied at seeding, except for the fungicide Folicur, which was band sprayed 5 and 10 weeks after transplanting.

added. One seed per cell was placed on top of the inoculum and the cells were filled with growing medium.

Seeded trays were placed in a greenhouse for 6 weeks with ambient light and temperatures ranging from 15 to 30 °C; the mean daytime temperature was 24 °C. The onion tops were clipped at 4, 5, and 6 weeks after seeding to encourage growth. Potassium nitrate 13.5:0:46 (N:P:K; Plant Products Inc., Brampton, Ont.) was applied once a week starting 2.5 weeks after seeding (50 mg/L initially and 100 mg/L for the remainder). At 6 weeks after seeding, the plants were placed outside for 1 week to harden before transplanting. Lorsban 4E (chlorpyrifos 480 g a.i./L) was applied for onion maggot (*Delia antiqua* (Meigen)) control (1.6 mL in 500 mL of water per tray) before transplanting. The onion plants were hand transplanted into fields that were naturally infested with *S. cepivorum* (sites 1, 2, and 3 in 2000 and 4, 5, and 6 in 2001; Table 2).

The fungicide Folicur 3.6F (430g a.i./L tebuconazole; Bayer Crop Science, Calgary, Alta.) was applied at a rate of 430 g a.i /ha in 2500 L/ha of well water at 5 and 10 weeks after transplanting, as recommended by Davies et al. (1998). Folicur 3.6F treatment dates are listed in Table 2. All treatments were applied using a Solo back pack sprayer with a Tee-Jet 8010 nozzle, held approximately 20 cm above the plant base to give a 30–35 cm wide band. Crop-management practices for management of diseases (except WR), weeds, and insect pests were applied by the grower following the recommendations of the Ontario Ministry of Agriculture and Food (OMAF 2000). Preplant fertilizer, including phosphorus, was applied to all fields by the growers according to OMAF (2000) recommendations.

Each treatment plot consisted of one bed of 4 rows × 2 m of onions with a spacing of 42 cm between rows (1.7 m/bed). Onions were planted at 25 plants/m, to provide 200 onions/plot. The treatments given in Table 1 were replicated six times for each cultivar in a randomized complete block design. Additional trials with 'Hoopla' and 'Fortress' onions were transplanted in other commercial fields on 29–30 May (site 10) and 1 June (site 11) in 2000.

White rot incidence (percentage of bulbs with symptoms) and severity was assessed at harvest by pulling and observing all onion bulbs in each plot. White rot severity was assessed on each bulb based on the percentage of each bulb infected: low (1%–10%), intermediate (11%–50%), and high (51%–100%). Weekly observations were made of all trials to assess preharvest mortality caused by WR. Onion bulbs from 1 m row in each treatment plot were harvested and weighed for yield assessment.

Field trials with direct-seeded onions

'Fortress' and 'Hoopla' onions were seeded into three commercial onion fields (sites 7, 8, and 9) using a push V-belt seeder delivering 46 seeds/m randomly spaced and at a depth of 1.5–2 cm. Seeding dates are given in Table 2. MYCORISE PRO and Dithane DG were applied on the V-belt with the seed. Treatments are given in Table 1. Folicur 3.6F was applied in a band twice at 8 and 12 weeks after seeding, as described for the transplanted trial. Crop management was carried out by the grower and followed provincial recommendations (OMAF 2000).

Table 2. Dates of (A) seeding for transplantation trials and Lorsban treatment and first root sampling for all plants and (B) transplantation, Folicur treatments, midseason root sampling, and harvest assessment for vesicular–arbuscular transplanted and direct-seeded trials conducted in 2000 and 2001.

(A) Seeding, Lorsban treatment, and first root sampling dates.

	2000	2001
Seeding	18–19 April	17–19 April
Lorsban treatment	26 May	25 May
First root sampling	26 May	29 May

(B) Transplantation, Folicur treatment, midseason root sampling, and harvest assessment dates.

	Transplant trials in 2000			Transplant trials in 2001			Direct-seeded trials in 2001		
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9
Direct seeding	—	—	—	—	—	—	2 May	4 May	10 May
Transplant	29–30 May	5–6 June	7 June	29 May	29–30 May	31 May	—	—	—
First Folicur 3.6F treatment	5 July	11 July	12 July	6 July	6 July	9 July	25 June	25 June	25 June
Midseason root sampling	24 July	25 July	26 July	6 Aug.	8 Aug.	10 Aug.	25 June	25 June	25 June
Second Folicur 3.6F treatment	8 Aug.	15 Aug.	15 Aug.	10 Aug.	9 Aug.	13 Aug.	24 July	24 July	24 July
Harvest assessment	6–8 Sept.	22–23 Sept.	18–19 Sept.	10–12 Sept.	18–19 Sept.	3–4 Sept.	5 Sept.	6–7 Sept.	26 Sept.

Note: First Folicur treatment dates were 5 weeks after transplantation and 8 weeks after direct seeding. Second Folicur treatment dates were 10 weeks after transplantation and 12 weeks after direct seeding.

Each treatment plot consisted of 2 rows × 4 m of onions with 42 cm between rows. The five treatments given in Table 1 were replicated five times for each cultivar in a randomized complete block design. Additional trials with 'Hoopla' and 'Fortress' onions were seeded on 3 and 4 May 2000 in other commercial onion fields (sites 12 and 13) with the same plot size and number of replications. Onion bulbs were assessed for WR incidence and severity at maturity as described above.

Mycorrhizal colonization

The root systems of 10 onions were excavated from each treatment replication, taking care to ensure that fine (<0.5 mm diameter) roots were well represented in the samples and to exclude captured roots of other species. Fine roots were carefully removed by forceps from the root samples to obtain approximately 2 g (fresh mass) of fine roots for each treatment replication. These roots were washed to remove adhering soil (Brundrett et al. 1996) and kept in a preservative solution (50% isopropanol) until they were processed.

Selected fine roots were placed into an OmniSette tissue cassette for clearing and staining. Roots were cleared for 30 min in potassium hydroxide (10% *w*/*v*) and heated in a water bath to 70–90 °C. After clearing, roots were rinsed with tap water and then transferred to the staining solution (Brundrett et al. 1996). Cleared roots were stained with chlorazol black E (CBE) in a lactoglycerol 0.03% (*w*/*v*) solution (Brundrett et al. 1984). The staining solution was heated to 70–90 °C in a water bath, with the roots remaining in the solution for 45 min. After staining, roots were placed in a destaining solution (50% glycerol solution) to remove excess stain and stored until slides were mounted.

Root pieces of variable length were selected at random from a stained sample and mounted on microscope slides in groups of 6–10 (5 slides per replication per treatment). A Leica (40×) compound microscope was used to make 20 observations per slide. The presence or absence of mycorrhizal colonization (vesicles, arbuscules, or hyphae) at particular fixed points was recorded, and the results were expressed as a percentage of observations.

Statistical analysis

The results for disease incidence and mycorrhizal colonization were subjected to angular transformation calculated as the arcsine of the square root of the percentage. The transformed variables and yield were analysed using the general linear models procedure of SAS for Windows version 8 (SAS Institute Inc., Cary, N.C.). The type I error rate (α) was 0.05 for all statistical tests. When a significant treatment or cultivar effect was found, the differences were further explored using Fisher's least significant difference (LSD) test. If there was no significant treatment × trial interaction ($P > 0.05$), data from different trials were combined. Similarly, if no treatment × cultivar interaction was found, the two cultivars were combined for analysis to increase the power of the test. Results of disease incidence are from combined data of all trials and both cultivars unless otherwise indicated. Pearson's correlation analysis (PROC CORR) was performed to measure the intensity and type of association between mycorrhizal colonization and

disease incidence. A graphical analysis (PROC PLOT) was performed to confirm results of correlation analysis. The reported results are the back-transformed means of the data.

Results

Weather conditions varied considerably between the 2000 and 2001 field seasons. In 2000, unusually cool and wet conditions were present, which were favourable for the development of WR and other fungal and bacterial diseases. In 2001, it was dry and hot, which was unfavourable for the development of WR. Total precipitation from 1 May to 31 August was 475 mm in 2000 and 240 mm in 2001. The 10 year mean precipitation for the same period was 311 mm. Because of the different weather conditions between the two field seasons, the results for each year are presented separately.

Field trials with transplanted onions

Weather conditions during the 2000 field season resulted in moderate incidence of WR at two of the three field sites: 22.3% and 36.4% at sites 1 and 2, respectively (Table 3). The first visible symptoms of WR (mycelial growth at the base of the onion plant) were found on 6 July, and the mean disease incidence in commercial onion fields in the Bradford–Holland Marsh was >35%. At the third field site, disease incidence was <2% and no differences among treatments were found. Therefore, results from this field were removed from further analysis.

At sites 1 and 2, a significant difference in disease incidence between cultivars ($P < 0.0001$) was found, with a higher disease incidence in 'Hoopla' than in 'Fortress' (Table 3). The incidence of WR was significantly different between sites, with the mean incidence for site 2 (21.3%) greater than site 1 (15.5%). There were no significant treatment × cultivar, cultivar × site, or treatment × site interactions, indicating that the treatments and cultivars performed consistently at both sites.

There was a significant effect of treatment on disease incidence. Incidence of WR was lower on onion plants inoculated with the AM products when compared with the untreated onions (Table 3). Disease incidence in the mycorrhizae treatments was similar to that on onions treated with Folicur 3.6F (Table 3). White rot incidence at harvest was reduced by almost 50% on onions treated with MIKRO-VAM, PRO-MIX PGX with MYCORISE 1000, and Folicur 3.6F. The PRO-MIX PGX with MYCORISE 255 treatments reduced disease incidence at site 1 compared with the untreated control; however, at site 2, this treatment had a higher incidence of WR than the untreated control (Table 3).

There were no differences in the numbers of bulbs in each treatment ($P = 0.38$). This indicates that there was no other cause of mortality of onion bulbs, such as onion maggot. A significant difference ($P = 0.0001$) was found in the number of bulbs for each field, with a greater number of bulbs per plot at site 1 (188) compared with site 2 (166).

There was no effect of treatment on yield (data not shown), although a significant difference between cultivars was found. The yield mean for 'Hoopla' (2.4 kg/m row) was higher than 'Fortress' (2.2 kg/m row). There were no significant differences in disease severity among treatments, sites, or cultivars (data not shown).

Table 3. Mean incidence of *Allium* white rot on transplanted 'Fortress' and 'Hoopla' onions at harvest at sites 1 and 2, Bradford–Holland Marsh, Ontario, in 2000.

	Disease incidence (%)	
	Site 1	Site 2
Treatment		
Untreated control	22.3 b	26.8 bc
Folicur 3.6F	11.6 a	15.6 a
MIKRO-VAM	13.3 a	13.6 a
MYCORISE 1000	14.9 a	18.5 ab
MYCORISE 255	16.4 a	36.4 c
Cultivar		
'Fortress'	7.0 b	12.4 b
'Hoopla'	28.5 a	36.2 a

Note: Values in a column followed by a different letter are significantly different at $P = 0.05$ according to a Fisher's protected LSD test. The two cultivars ('Fortress' and 'Hoopla') were compared with each other.

The weather conditions during the 2001 field season were dry and hot and were not favourable for the development of WR. Therefore, disease incidence was low at all three sites (Table 4). As expected, no significant treatment effect was found (Table 4). However, even at these low levels of disease, there was a difference in disease incidence between cultivars at two of these sites (sites 4 and 6) with higher disease incidence in 'Hoopla' than in 'Fortress'. There was a cultivar × site interaction; no difference in disease incidence between 'Hoopla' and 'Fortress' was found at site 5 (Table 4).

A significant effect of cultivar on yield was found, where 'Hoopla' onions (2.76 kg/m) were consistently heavier than 'Fortress' (2.32 kg/m). A treatment × site interaction for yield was detected. At site 6, there was an effect of treatment on yield that was not seen at the other two sites. The lowest yield was found in the plots treated with Folicur 3.6F (2.2 kg/m); however, the rest of the treatments did not significantly differ from the untreated control (data not shown).

Field trials with direct seeded onions

Disease incidence was low at all sites in 2001 because the weather was unfavourable for disease development. There were differences in disease incidence among sites but not among treatments at any site presumably because of overall low disease pressure. Site 8 had the highest overall mean, which was only 5.2%. A significant cultivar × site interaction was also detected ($P < 0.0001$) because no significant difference in disease incidence × cultivar was found at site 9 (data not shown). No significant difference in disease severity was found among treatments, sites, or cultivars (data not shown). Differences in cultivar susceptibility to WR were found in these trials where the onions were direct seeded, as in the transplanted trials. 'Hoopla' had a higher disease incidence than 'Fortress' at sites 7 and 8 (Table 5).

Differences in disease incidence between the cultivars were also found in field trials with 'Hoopla' and 'Fortress'

Table 4. Mean *Allium* white rot incidence in transplanted onions at harvest at the Bradford–Holland Marsh, Ontario, in 2001.

	Disease incidence for 'Hoopla' (%)			Disease incidence for 'Fortress'(%)		
	Site 4	Site 5	Site 6	Site 4	Site 5	Site 6
Treatment						
MYCORISE 1000	4.0 a	2.1 a	1.3 a	0.7 a	1.4 a	1.0 a
MYCORISE 500	3.3 a	1.2 a	1.8 a	0.4 a	2.3 a	0.3 a
MIKRO-VAM	1.3 a	0.4 a	1.6 a	1.8 a	1.0 a	0.3 a
Folicur 3.6F	1.9 a	1.1 a	0.9 a	0.1 a	0.8 a	0.3 a
Untreated control	1.8 a	2.6 a	1.7 a	0.5 a	2.0 a	0.0 a
Cultivar						
'Fortress'	0.7 b	1.5 a	0.4 b	na	na	na
'Hoopla'	2.5 a	1.5 a	1.5 a	na	na	na

Note: Values within a column followed by a different letter are significantly different according to a Fisher's Protected LSD test ($P < 0.05$). The two cultivars ('Fortress' and 'Hoopla') were compared with each other. na, not available.

Table 5. Mean incidence of *Allium* white rot on transplanted and direct seeded 'Hoopla' and 'Fortress' onions at harvest, with or without AM inoculation, Bradford–Holland Marsh, Ontario, Canada, 2000–2001.

			Disease incidence			AM
Site	Year	Trial	'Hoopla'	'Fortress'	*P*	inoculation
1	2000	Transplanted	28.5	7	<0.001	Yes
2	2000	Transplanted	36.2	12.4	<0.001	Yes
4	2001	Transplanted	2.4	0.7	<0.001	Yes
5	2001	Transplanted	1.5	0.4	<0.001	Yes
7	2001	Direct seeded	10.9	0.9	<0.001	Yes
8	2001	Direct seeded	5.2	2.4	<0.05	Yes
10	2000	Transplanted	32.7	5.5	<0.001	No
11	2000	Transplanted	39.8	12.2	<0.001	No
12	2000	Direct seeded	21.2	9.3	<0.001	No
13	2000	Direct seeded	40.9	29.4	<0.001	No

Note: Data from sites 3, 6, and 9 are not shown because WR incidence was very low or zero. The *P* value refers to the level of significance in the difference between 'Hoopla' and 'Fortress'.

where the onions were not treated with AM. 'Hoopla' had higher disease incidence compared with 'Fortress' in transplanted onions at sites 10 and 11 and in direct seeded onions, which also were not treated with AM, at sites 12 and 13 (Table 5).

Mycorrhizal colonization assessment

In 2000, an assessment of mycorrhizal colonization was performed on roots sampled before transplanting and in midseason from the two fields evaluated in the transplanted trials, where significant treatment differences were found. For the 2001 field season, assessment of mycorrhizal colonization was performed on onion roots before transplanting and from midseason samples. However, because of the low disease pressure, there were no significant differences in disease incidence among treatments, and hence, no further correlation analysis was performed (Table 5).

Assessment of the mycorrhizal colonization of roots on the onions sampled before transplanting showed that all treatments had higher levels of colonization compared with the untreated control (Table 6). There was also a treatment effect on mycorrhizal colonization at midseason. Colonization with MIKRO-VAM was significantly higher at midseason compared with the untreated controls (Tables 6 and 7).

The mycorrhizal colonization of roots was different for the two cultivars for roots sampled before transplanting and roots sampled at midseason (Table 7), with consistently higher colonization in 'Fortress' compared with 'Hoopla' (Table 7). There was greater root colonization at site 2 (26.2%) than at site 1 (14.1%).

Relationship between mycorrhizal colonization and disease incidence

Higher levels of mycorrhizal colonization were associated with lower levels of disease in the 2000 trials. A significant negative correlation was found at both field sites when all treatments were included ($r = –0.27$, $P = 0.04$; Table 8). Higher levels of mycorrhizal colonization were associated with lower disease incidence.

When untreated controls were removed from the analysis to remove any effect of natural colonization from the field soil, the relationship was stronger ($r = –0.33$, $P = 0.03$).

Table 6. Mean mycorrhizal colonization of onion roots before transplantation, and midseason and mean incidence of *Allium* white rot at harvest in 2000 and 2001 in Bradford–Holland Marsh, Ontario.

	AM colonization before transplant (%)		AM colonization midseason (%)		Disease incidence (%)	
Treatment	2000	2001	2000	2001	2000	2001
MIKRO-VAM	14.0 a	28.5 a	28.4 a	29.8 a	13.1 b	1.13 a
MYCORISE 1000	25.0 a	8.5 b	18.0 b	26.1 a	14.3 b	1.43 a
MYCORISE 255	17.0 a	6.5 b	9.8 ab	16.9 b	25.3 a	1.38 a
Folicur 3.6F	na	na	na	na	13.1 b	0.70 a
Untreated control	0.5 b	0.5 c	12.6 b	12.9 b	24.0 a	0.80 a

Note: Values in a column followed by a different letter are significantly different at $P = 0.05$ according to the Fisher's Protected LSD test. na, not applicable.

Table 7. Mean mycorrhizal colonization by treatment and by cultivar of onion roots at sites 1 and 2 in Bradford–Holland Marsh, Ontario, in 2000.

	Mycorrhizal colonization (%)	
	Before transplantation	Midseason
Treatment		
Untreated control	0.5 b	12.6 b
MYCORISE 1000	25.0 a	18.0 b
MYCORISE 255	17.0 a	19.8 ab
MIKRO-VAM	14.0 a	28.4 a
Cultivar		
'Hoopla'	6.5 b	15.0 b
'Fortress'	21.8 a	23.6 a

Note: Values in a column followed by a different letter are significantly different at $P = 0.05$ according to a Fisher's protected LSD test. The two cultivars ('Fortress' and 'Hoopla') were compared with each other.

Table 8. Pearson's correlation coefficient (r) and levels of significance (P) between mycorrhizal colonization and incidence of *Allium* white rot in onions at two sites in Bradford–Holland Marsh, Ontario, in 2000.

	r	P
Both sites		
All treatments	–0.2736	0.036
No controls	–0.3316	0.030
Site 1		
All treatments	–0.3623	0.042
No controls	–0.5004	0.013
Site 2		
All treatments	–0.4431	0.021
No controls	–0.4647	0.045
'Hoopla'		
All treatments	–0.0832	0.70
No controls	–0.0252	0.92
'Fortress'		
All treatments	–0.0394	0.83
No controls	–0.0203	0.99

The untreated control was a considerable source of variation (Table 8) because it was colonized by other natural AM that may not have behaved the same way as the commercial products that were tested.

When the two sites were compared separately, a higher correlation coefficient was found at individual sites ($r = –0.36$, $P = 0.04$ at site 1; $r = –0.44$, $P = 0.02$ at site 2) than when combined. Again, the correlation coefficient was higher when untreated controls were omitted ($r = –0.50$, $P = 0.01$ at site 1; $r = –0.47$, $P = 0.04$ at site 2; Table 8).

Because significant differences in mycorrhizal colonization between cultivars were found, disease incidence and mycorrhizal colonization data were also subjected to correlation analysis by cultivar. No significant correlation was found (Table 8). When the data were graphed, no correlation pattern was found in the data for 'Hoopla' (data not shown). Observation of the data for 'Fortress' showed a slightly negative correlation pattern, but this was not significant. The pooled data from the two cultivars had a significant correlation with higher colonization associated with lower disease, but separately, neither cultivar showed a significant correlation between mycorrhizal colonization and disease incidence. These data suggest that the important difference is between cultivars: with 'Hoopla' was more susceptible to disease and less colonized by AM, and 'Fortress' was less susceptible to disease and more colonized by AM.

Discussion

This study demonstrated that the use of a commercially available AM product, MIKRO-VAM, in transplanted onions reduced the incidence of WR by almost 50% compared with the untreated control. The other products, PRO-MIX PGX with MYCORISE 1000 or MYCORISE 255, also reduced WR at one of two sites. This is the first study to demonstrate season-long control of *Allium* white rot as a result of colonization by mycorrhizae. The results are consistent with those of Torres-Barragan et al. (1996) using AM for the management of WR. That study showed that AM could provide protection for 11 weeks but not until harvest. In the current study, onions were exposed to infested soil for a minimum of 14 weeks after transplanting. The protection obtained with MIKRO-VAM containing *G. intraradices* was comparable with the protection by the fungicide Folicur 3.6F applied according to label recommendations. However, it must be noted that neither the fungicide nor the AM treatment reduced the incidence of WR by >50%, which points

to the difficulty in controlling WR in commercial onion production.

Several studies have reported that standard agricultural practices can decrease mycorrhizal colonization and mycorrhizal inoculum (spores and vegetative propagules in roots and mycelium), consequently reducing the potential of using AM for biological control and for other beneficial effects, such as increased plant growth and plant nutrition (Hamel 1996; Hamel et al. 1997; Hayman 1983; Linderman 1994; Vyas and Vyas 2000). In this study, AM were shown to be effective in suppressing WR under commercial field conditions where mycorrhizal and nonmycorrhizal plants were exposed to all normal agricultural practices, such as the application of fertilizer, herbicides, insecticides, and fungicides for crop management.

The inconsistent performance of the PRO-MIX PGX with MYCORISE treatments, which significantly decreased disease compared with the control at one site but not at the other, could have been due to an insufficient level of mycorrhiza inoculum. In inoculum studies performed by Saleh and Sikora (1984), it was shown that low inoculum concentrations resulted in low root colonization and had no effect on the nematode, *Meloidogyne incognita* (Kofoid & White) Chitwood. At high concentrations and high root colonization levels, egg and nematode densities were greatly suppressed. A similar situation could have occurred with PRO-MIX PGX with MYCORISE 1000 and 255, where the recommended application rates were equivalent to 4.3 and 1.2 propagules/transplant cell, compared with 1000 propagules/cell for MIKRO-VAM. Mycorrhizal colonization was observed in onions treated with MYCORISE, but the amount of inoculum may have been too low to achieve an effective reduction of disease.

A consistent difference in incidence of WR was found between 'Hoopla' and 'Fortress', which confirmed earlier preliminary findings (Earnshaw et al. 2000; Hovius and McDonald 1998a, 1998b; Jaime et al. 2000). 'Hoopla' appears to be more susceptible to WR, whereas 'Fortress' appears to be consistently more resistant. The performance of the two cultivars was consistent in 10 of the 13 transplanted and direct-seeded trials established during the two field seasons, despite differences in environmental conditions and disease pressure and whether or not the onions were inoculated with AM. In cases where differences between cultivars were not detected, incidence of WR was very low.

A significant difference in mycorrhizal colonization was found between cultivars, where 'Fortress' had higher AM colonization than 'Hoopla'. Crop species and cultivars within species can differ remarkably in their ability to respond to AM colonization (Parke and Kaeppler 2000). The host genotype controls the rate and extent of mycorrhiza formation, and the magnitude of mycorrhizal dependency varies between and within plant species (Menge et al. 1978; Plenchette et al. 1983). Previous researchers have suggested that better agronomic characteristics and higher disease resistance are negatively correlated with AM colonization compatibility (Baon et al. 1993; Toth et al. 1990), but the results of this study do not support that hypothesis.

Mycorrhizal colonization of onion roots growing in the greenhouse was higher in all inoculated treatments compared with the untreated control. The AM treatments resulted in moderate mycorrhizal colonization (18%–28%) where the untreated control had only 0.5% colonization, which could be attributed to naturally occurring inoculum in the growing medium (PRO-MIX PGX). In the midseason mycorrhizal assessments, an increase in mycorrhizal colonization in the untreated controls was observed, likely from indigenous AM fungi present in the field. Arbuscular mycorrhizal colonization in the treatment plots was moderate to low (18%–28%) compared with previous reports from non-sterile soils (58%–76%) (Hayman 1983; Torres-Barragan et al. 1996). The experimental fields in this study were exposed to normal onion production practices, including pesticide and fertilizer application, which has been reported to decrease mycorrhizal colonization and mycorrhizal inoculum (Hamel et al. 1997; Hayman 1983; Linderman 1994; Vyas and Vyas 2000), whereas the trials conducted by Hayman (1983) and Torres-Barragan et al. (1996) were not exposed to these practices.

There is still disagreement about whether significant differences in resistance to WR exist in onion and the extent of any genetic potential for resistance within the genus (Brix and Zinkernagel 1992). Although some reports have demonstrated substantial differences (Earnshaw et al. 2000; Hovius and McDonald 1998b; Utkhede and Rahe 1978; Van Der Meer et al. 1983), others have reported little or no difference in resistance (Coley-Smith and Esler 1983; Semb et al. 1978). The results of the present study suggest that the low incidence of disease in 'Fortress' and the higher AM colonization are most likely determined by the genotype of the cultivar. This demonstrates that consistent differences in resistance in onions to WR do exist and that these differences in resistance may be a potential source in resistance breeding programs with onions.

This is the first research to quantify a relationship between AM colonization and disease incidence under commercial field conditions. The significant negative correlation between disease incidence and AM root colonization suggests that AM colonization was important in the reduction of WR observed in this study. Only 7%–11% (r^2 = 0.07–0.109 for both sites combined) of the variation in disease incidence could be explained by the extent of AM colonization; this is a low but significant value. The increase in Pearson's correlation coefficient when untreated controls were removed suggests that the observed reduction of WR incidence is due to the AM treatments and not due to the indigenous AM species.

The results of the present study agree with previous research where an increase in root colonization was related to a decrease in disease levels (Thompson and Wildermuth 1988). The nonsignificant correlation with each cultivar suggests that other factors, such as host genotype, were involved in the disease incidence observed. Testing with more cultivars would be needed to confirm this effect. The data suggest that the greater resistance in 'Fortress' may be related to a greater compatibility for mycorrhizal colonization.

This study did not investigate possible mechanisms of biological control as a result of colonization by mycorrhizae. Several mechanisms have been suggested to explain how mycorrhizal colonization of roots could suppress disease. One possible mechanism is a change in the physiology of the host. If AM colonization changes the quality and quan-

tity of onion root exudates, this could affect the incidence of WR because sclerotia of *S. cepivorum* are stimulated to germinate by *Allium* root exudates (Caron 1989; Coley-Smith 1990). Previous work has demonstrated a significant reduction of root exudates from AM colonized plants compared with exudates from non-AM plants in vitro (Norman and Hooker 2000). Changes in microbial populations associated with AM colonization is another mechanism that may account for reduction of WR. Linderman (2000) showed an increase in the number and proportion of bacteria in the mycorrhizosphere that inhibit *S. cepivorum* in vitro in onions colonized by AM compared with those without AM. There could be a direct suppression of the pathogen resulting from antibiosis, competition, or parasitism by the bacteria (Linderman 2000). Preliminary results from the evaluation of microbial populations in the rhizosphere and mycorrhizosphere samples from this study show a clear shift in the number and proportion of antagonistic bacteria over time (R.G. Linderman, USDA-ARS Horticultural Crops Research Laboratory, Corvallis, Oregon (retired), personal communication). Considering that onions have high levels of natural mycorrhizal colonization (Hayman 1983), other possible mechanisms involved in reducing onion WR may include competition of AM for infection sites and photosynthates, the induction of defence mechanisms in the host, morphological changes in the root system, damage compensation, or others (Whipps 2004). Further research is needed to understand which mechanisms are important in the AM – *S. cepivorum* – onion interaction.

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