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Mycorrhiza

Plant life span and response to inoculation with vesicular-arbuscular mycorrhizal fungi

I. Annual versus perennial grasses

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Summary. To determine the relative responsiveness to and dependency on vesicular-arbuscular mycorrhizae (VAM) of annual and perennial plants, this study compared the responses of congeneric, sympatric pairs of species in the grass genera *Panicum* and *Bromus* to inoculation with two VAM fungal isolates from the genus *Glomus*. When inoculated with *G. intraradices*, the perennials *P. virgatum* and *B. inermus* showed significantly greater response at both high and low phosphorus (P) than did the annuals *P. capillare* and *B. secalinus*. Responsiveness of perennials was significant at both P levels, whereas annuals responded significantly only at low P. Neither *Bromus* species responded strongly to inoculation with *G. etunicatum*. Overall, the perennial grasses were more responsive and dependent than were the annuals. A survey of 26 studies including 84 plant-VAM fungus combinations yielded similar patterns of responsiveness in relation to P level and plant life span, especially for grasses. The greater responsiveness of perennial grasses to VAM infection must be considered within the suite of life history traits used to erect hypotheses concerning successional replacement of annuals by perennials in graminoid-dominated ecosystems.

Key words: Vesicular-arbuscular mycorrhizae – Grasses – Plant life span – Responsiveness – Dependency

Introduction

Although it is now almost trivial to state that many vascular plants respond significantly to infection by vesicular-arbuscular mycorrhizal (VAM) fungi, few general models for predicting the magnitude of, and controls on, those responses are currently available, other than indications of where various families of vascular plants fall along a continuum of responsiveness or dependence (often referred to as "Mycotrophy"). This lack of a broad synthesis is, in part, due to the diverse factors which can influence the responsiveness of a plant to infection, including soil phosphorus (P) availability, pH, moisture, temperature, stage of development, etc. (reviewed by Hayman 1983).

One major factor which may influence the magnitude of the plant's response to infection may be ramet longevity or life span, an integral part of a plant's life history. For example, as secondary succession proceeds in a mesic, humid environment, the mean life span of the species present generally increases (e.g. Vankat and Snyder 1991). Concomitantly, availability of most mineral nutrients in the soil generally decreases with successional time (Grime 1979). Thus, life history and succession theory lead us to predict that longer-lived, later-successional perennials should have greater dependence on and response to VAM infection than ruderal, early successional annuals. A robust test of this hypothesis requires the comparison of congeneric, sympatric pairs of annuals and perennials from a predominantly mycorrhizal family, so as to minimize other differences between species which may have arisen through recent evolutionary events or current habitat factors (Newman and Riddell 1987). For this we have chosen to examine grasses, of which 91% of species examined to date have been classified as facultatively or obligately mycorrhizal (Newman and Riddell 1987).

The terminology used in this study to that suggested by Janos (1988). The growth or nutrient uptake response to VAM inoculation at any given level of P availability is termed "responsiveness". The "dependence" of a plant, population, or species is defined as the range of soil P availability (or other factor) over which that plant exhibits significant responsiveness. Thus, a plant may be highly responsive to VAM infection at low soil P but still have low mycorrhizal dependence if it is insensitive to VAM infection at moderate and high P levels.

Within that context, the specific questions to be addressed in this study were: (1) Do annual and perennial congeneric, sympatric species of grasses exhibit different responsiveness to inoculation with common VAM fungi? (2) Do annuals and perennials differ in VAM dependence; that is, in responsiveness in relation to P availability? (3) Are pattern of responsiveness and dependence among plant species pairs significantly af-

fected by changing the fungal isolate used for inoculation?

Materials and methods

Seeds of four grasses which are common and widespread in eastern North America were obtained from F and J Seed Service, Woodstock, Ill. *Bromus inermus* Leyss (smooth or awnless brome) and *Panicum virgatum* L (switchgrass) are perennials found in both grasslands and abandoned agricultural fields; the seeds of these species used in this study came from prairies in Kansas and eastern Texas, respectively. *Bromus secalinus* L (cheat) and *Panicum capillare* L (witchgrass or Mousseline) are annual grasses common as weeds in grain fields and waste places. The seeds of the two species used in this study came from abandoned agricultural fields in Illinois. The two *Panicum* species are native to North America, whereas the two *Bromus* spp. were introduced from Europe.

Glomus intraradices Schenck and Smith is among the most common *Glomus* species in the southeastern United States and will form VAM with a wide range of hosts (Schenck and Smith 1982). We have observed *G. intraradices* in roots of *P. virgatum* and *P. capillare*. *Glomus etunicatum* Becker and Gerdemann is a VAM fungus found in agricultural fields and prairies throughout the eastern United States. It forms symbiotic relationships with many agricultural (e.g., *Zea mays* L.) and prairie species (e.g. *Andropogon scoparius* Michx.) (Becker and Gerdemann 1977). Both cultures were obtained from J. H. Gerdemann at the University of Illinois and were isolated from agricultural field crops. The *G. intraradices* culture had originally been identified as *G. fasciculatum*, but was subsequently re-identified (S. B. Rabatin, personal communication).

Seeds were planted in flats of acid-washed sand and transplanted to 10-cm-diameter pots of 4:1 sand:perlite (v:v) when the first true leaves appeared. Each plant to be VAM-inoculated was given 30 ml of an inoculum slurry which contained at least 300 *Glomus* spores. Plants which were to remain free of VAM infection were given an equal amount of a slurry which had been passed through a 15-μm filter to remove VAM spores (Jensen 1982).

The plants were grown for 8 weeks during the summer in a glasshouse at ambient temperature and light intensity. They were fed weekly with a nutrient solution (Ruakura Solution) designed for sand culture (Smith et al. 1983) modified so as to supply P at rates similar to that found in relatively fertile and infertile forest sites in Ohio (Boerner 1990); high P: 5.0 mg $P.l^{-1}$ in solution and 11.0 mg P total over the course of the experiment versus low P: 2.0 $mg.l^{-1}$ in solution and 4.4 mg P total addition. Each species-VAM inoculum-P level combination was replicated 16 times in a completely randomized design.

The plants were harvested 8 weeks after inoculation. Shoots and a subsample of roots were weighed fresh, dried at 70° C for 72 h, then weighed again. The remainder of the roots were weighed fresh, then preserved in formalin:acetic acid:ethyl alcohol (FAA). The preserved root material was later stained with trypan blue in lactoglycerin and examined microscopically to verify presence or absence of VAM structures (Giovanetti and Mosse 1980). All VAM-inoculated plants had at least 15% of root length infected; plants from non-VAM treatment combinations which had any detectable infection were discarded. The dried root and shoot material was digested in 30% $H_2O_2 + H_2SO_4$, and phosphate concentrations in digests determined by the stannous chloride method (American Public Health Association 1976).

All response variables were tested for normality, then analyzed by analysis of variance and the Ryan-Einot-Gabriel-Welsch Modified F test (Statistical Analysis-System 1985). As the experiments were performed sequentially rather than simultaneously, no direct statistical comparisons among experiments were conducted. All significant differences noted are at $P<0.05$, except where otherwise noted.

Results

Panicum spp. and Glomus intraradices

VAM-inoculated *P. virgatum* (perennial) plants attained significantly greater total mass, shoot mass, and root mass than did non-inoculated plants at both P levels (Fig. 1). VAM-inoculated *P. virgatum* plants grown at low P produced as much root mass as non-inoculated plants at high P. Increases in total mass production attributable to VAM inoculation were much greater than increases in root length production. The mass increases were 72% for high P and 118% for low P as against root length increases of 16% for high P and 37% for low P. Total P uptake and tissue P concentrations were also significantly affected by VAM inoculation. P supply rate affected tissue P concentrations in non-VAM plants, but not in VAM-inoculated plants.

P. capillare (annual) was less responsive to VAM inoculation. At high P, there were no significant differences in *P. capillare* biomass components attributable to VAM inoculation (Fig. 1). At high P, only tissue P concentration was significantly affected by VAM inoculation. *P. capillare* plants did respond significantly to VAM inoculation in the low P treatment: total mass, shoot mass, and total P uptake were greater in VAM-inoculated plants than in non-VAM plants. Overall, the perennial *P. virgatum* exhibited greater mycorrhizal dependency than did the annual *P. capillare*; that is, *P. virgatum* showed significant responsiveness at both P levels while *P. capillare* did so only at low P.

Bromus spp. and G. intraradices

B. inermus plants (perennial) grown at high P and inoculated with *G. intraradices* were significantly larger and took up significantly more P than uninoculated plants (Fig. 2). At low P, only P uptake and tissue P concentrations were increased significantly as a result of inoculation.

At high P, total mass and root mass production by *B. secalinus* plants (annual) were reduced and tissue P concentration was increased by *G. intraradices* inoculation (Fig. 2). At low P, the only response of *B. secalinus* plants to inoculation was an increase in tissue P concentrations. Overall, the perennial *B. inermus* plants exhibited greater mycorrhizal dependency than did the annual *B. secalinus*.

Bromus spp. and G. etunicatum

There were no significant responses, ether positive or negative, of *B. inermus* plants (perennial) to inoculation with *G. etunicatum* at high P supply rate (Fig. 3). At low P, *B. inermus* total mass production was inhibited by inoculation with *G. etunicatum*; no other response parameter was affected by inoculation at low P.

Total mass and root mass of non-VAM *B. secalinus* plants (annuals) were significantly greater that those of

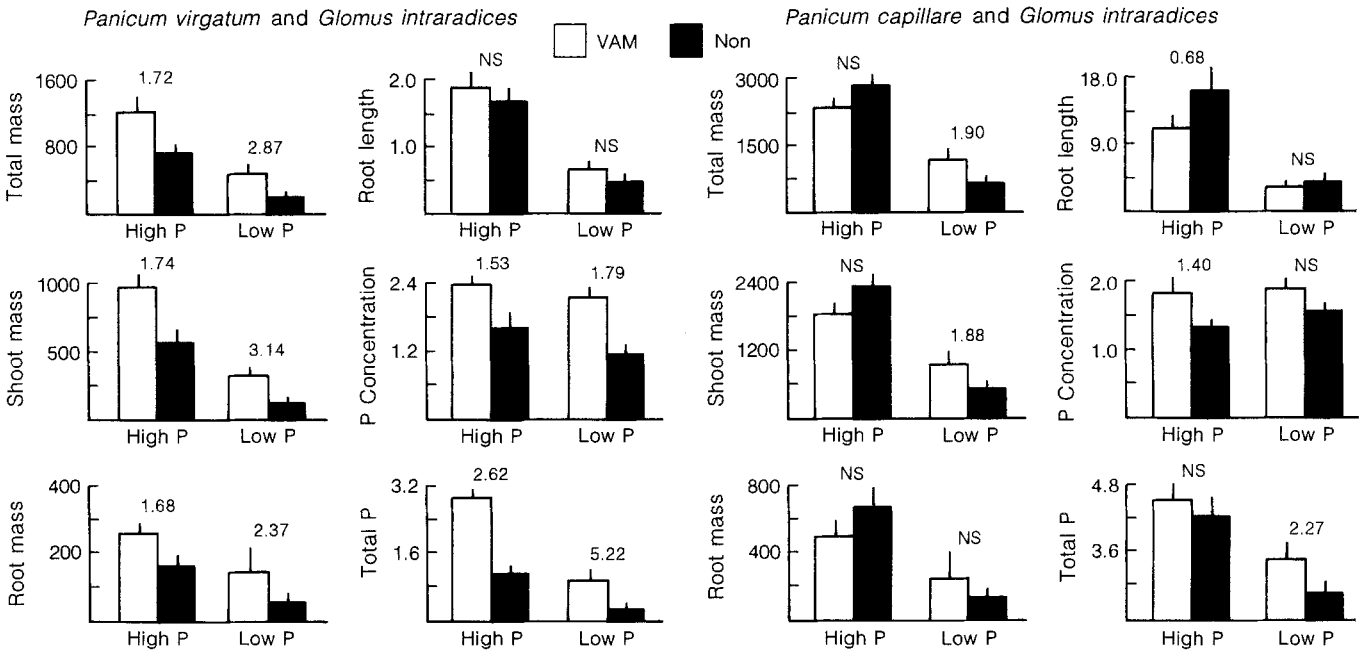

Fig. 1. Response of *Panicum virgatum* (perennial) and *Panicum capillare* (annual) in relation to inoculation with *Glomus intraradices*. *Histogram bars* represent means of 16 replicates; standard errors are indicated by the *vertical lines*. Levels of significant responsiveness are indicated (see text). NS, No significant responsiveness. Units are all in mg.plant^{-1} except root length (m) and tissue P concentration (mg·g dry mass^{-1})

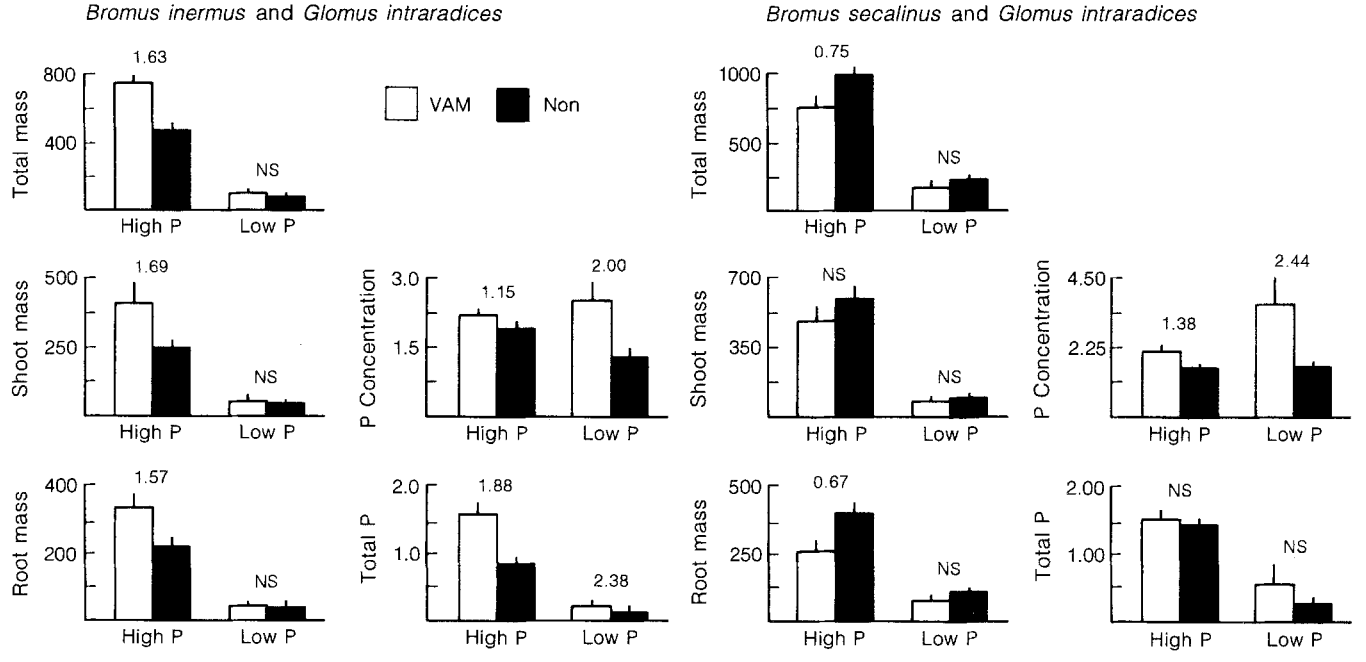

Fig. 2. Total plant mass (mg) and total P uptake (mg) of *Bromus inermus* (perennial) and *Bromus secalinus* (annual) in relation to inoculation with *Glomus intraradices*. Format as in Fig. 1

G. etunicatum-inoculated plants at high P; tissue P concentrations and total P uptake were not significantly affected by inoculation at high P (Fig. 3). In the low P treatment, inoculated *B. secalinus* plants took up more total P than uninoculated plants; no other *B. secalinus* response parameter was significantly affected by *G. etunicatum* inoculation at low P. The perennial *B. inermus* exhibited little responsiveness and essentially no dependency on *G. etunicatum*; responsiveness of annual *B. secalinus* plant to *G. etunicatum* was also slight, though greater than that of the perennial.

Comparison of responses to inoculation

The perennial species, *P. virgatum* and *B. inermus*, both responded positively to inoculation with *G. intraradices*

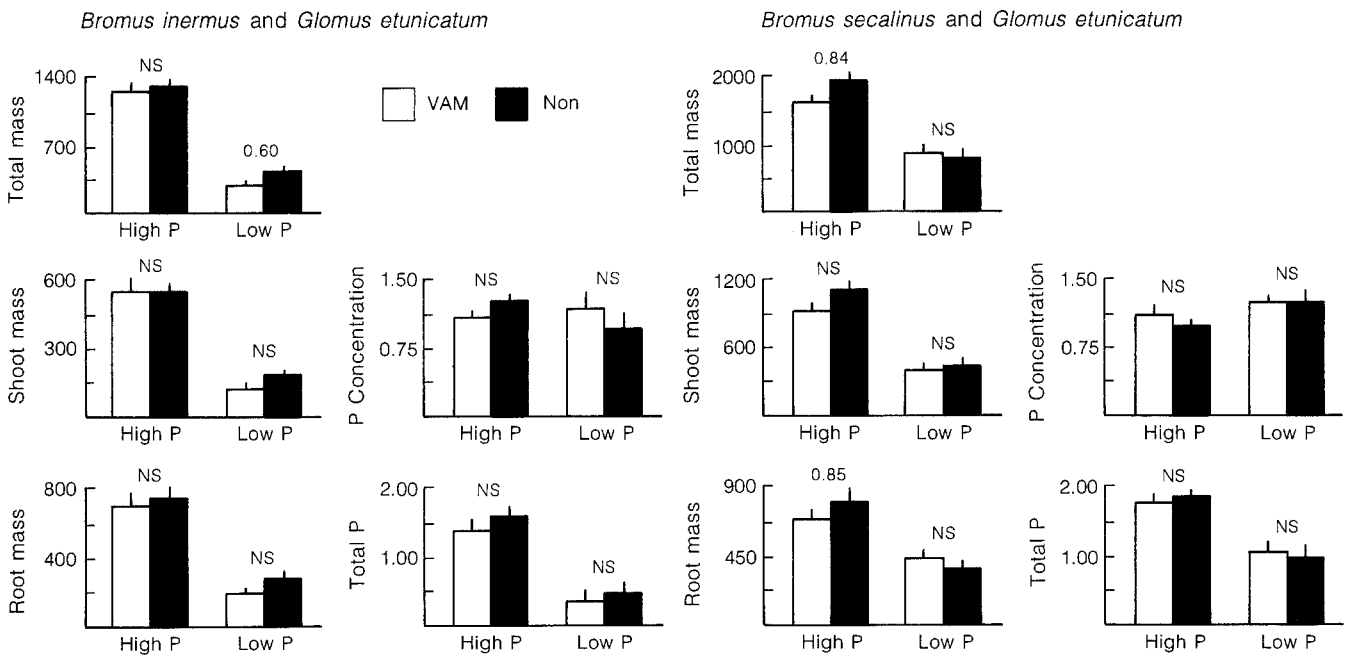

Fig. 3. Total plant mass (mg) and total P uptake (mg) of *Bromus inermus* (perennial) and *Bromus secalinus* (annual) in relation to inoculation with *Glomus etunicatum*. Format as in Fig. 1

Table 1. Comparisons of responses of two *Bromus* species and two *Panicum* species to inoculation with two *Glomus* species. Positive growth responses are indicated by +, negative responses by −, and the lack of significant response by 0; responses to high and low P treatments are separated by "/"

Perennials	*P. virgatum* and *G. intraradices*	*B. inermus* and *G. intraradices*	*B. inermus* and *G. etunicatum*
Total plant mass	+/+	+/0	0/−
Shoot mass	+/+	+/0	0/0
Root mass	+/+	+/0	0/0
P uptake	+/+	+/+	0/0
Tissue P concentration	+/+	+/+	0/0
Totals	5+/5+	5+/2+	0/1−
Annuals	*P. capillare* and *G. intraradices*	*B. secalinus* and *G. intraradices*	*B. secalinus* and *G. etunicatum*
Total plant mass	0/+	−/0	−/0
Shoot mass	0/+	0/0	0/0
Root mass	0/0	−/0	−/0
P uptake	0/+	0/0	0/0
Tissue P concentration	+/0	+/+	0/0
Totals	1+/3+	1+, 2−/1+	2−/0

at both P supply levels (Table 1). In contrast, *B. inermus* did not respond at all to inoculation with *G. etunicatum* at high P, and gave a mild negative response to inoculation at low P.

The pattern of responses of the annual species to inoculation was less consistent. At high P, inoculation of *P. capillare* and *B. secalinus* with *G. intraradices* resulted in modest, though significant, increases in tissue P concentration; this response was not observed in *B. secalinus* plants given *G. etunicatum* and high P (Table 1). In contrast, at high P, both total and root mass production by *B. secalinus* was inhibited by inoculation with either fungus, while productivity of *P. capillare* was unaffected by inoculation.

At low P, all three annual plant-fungus combinations exhibited some positive response to inoculation in P uptake or tissue P concentration, but only *P. capillare* responded to inoculation with significant increases in biomass production. Overall, the perennials responded more positively to inoculation with *G. intraradices* than

Table 2. Responsiveness to mycorrhizal infection in relation to P level and plant life span. Responsiveness is the ratio of performance of inoculated plants to paired uninoculated plants. ND, No data

Plant species	Fungus species	Parameter measured	Low(er) P	High(er) P	Reference
Cultivated annuals					
Hordeum vulgare (barley)	*Glomus caledonius*	Biomass	1.40	1.06	Jakobsen 1983
		Seed prod.	1.23	1.05	
		P conc.	1.87	1.62	
Hordeum vulgare (barley)	*Glomus constrictus*	Biomass	1.54	ND	Jensen 1982
		Total P	1.54	ND	Jensen 1982
	Glomus fasciculatus 185	Biomass	1.43	ND	Jensen 1982
		Total P	1.67	ND	Jensen 1982
	Glomus fasciculatus 0-1	Biomass	1.47	ND	Jensen 1982
		Total P	1.53	ND	Jensen 1982
	Gigaspora margarita	Biomass	0.92	ND	Jensen 1982
		Total P	0.83	ND	Jensen 1982
Zea mays (corn)	*Glomus mosseae*	Biomass			
		(control)	0.96–1.00	0.87–1.17	Daniels Hetrick et al. 1984
		(droughted)	1.01–1.23	0.96–1.02	
Zea mays (corn)	*Glomus etunicatum*	Biomass			
		(control)	1.23	0.99	Daniels Hetrick et al. 1987
		(droughted)	1.21	0.96	
Sorghum vulgare (sudan grass)	*Glomus etunicatum*	Biomass			Daniels Hetrick et al. 1987
		(control)	1.14	ND	
		(droughted)	0.95	ND	
Allium cepa (yellow onion)	*Glomus macrocarpum*	Biomass	2.45	1.06	Schubert and Hayman 1986
	Glomus E3		2.26	0.79	
	Gigaspora margarita		2.02	1.46	
	Glomus clarum		1.45	0.86	
	Glomus caledonium		2.51	1.10	
	Glomus mosseae		2.21	1.47	
Allium porrum (leek)	*Glomus epigeaum*	P conc.	0.96–1.65	0.89–1.01	Plenchette et al. 1983
	Glomus monosporum		0.97–1.65	0.86–1.01	
Tagetes patulus (marigold)	*Glomus monosporum*	P conc.	0.93–1.43	0.80–0.93	Plenchette et al. 1983
	Glomus epigeaum		1.06–1.29	0.92–0.98	
Helianthus annuus (sunflower)	*Glomus fasciculatum*	Shoot mass	0.69–1.47	0.60–0.89	Koide 1985
Pisum sativum (pea)	Field inocula	Shoot mass	1.04	1.01	Jakobsen 1986
		Total P	1.56	1.35	
Gossypium hirsutum (cotton)	*Gigaspora margarita*	P conc.	1.82	ND	Smith and Roncadori 1986
	Glomus intraradices		1.91	ND	
	Glomus ambisporum		1.79	ND	
Wild annuals					
Geranium robertianum (herb robert)	*Glomus occultum*	Biomass	0.85–1.33	ND	Boerner 1990
		Total P	1.01–1.51	ND	
Panicum capillare (witchgrass)	*Glomus intraradices*	Biomass	1.88	0.77	This study
		Total P	1.84	1.04	This study
		Shoot mass	1.88	0.80	This study
		Root mass	2.01	0.76	This study
		Root length	0.96	0.68	This study
		P conc.	1.19	1.40	This study
Bromus secalinus (cheatgrass/chess)	*Glomus intraradices*	Biomass	0.92	0.75	This study
		Total P	0.88	0.91	This study
		Shoot mass	0.95	0.81	This study
		Root mass	0.86	0.67	This study
		P conc.	2.44	1.38	This study
Bromus secalinus (cheatgrass/chess)	*Glomus etunicatum*	Biomass	1.07	0.84	This study
		Total P	1.54	0.88	This study
		Shoot mass	0.91	0.84	This study
		Root mass	1.22	0.85	This study
		P conc.	0.99	1.16	This study

Table 2 (continued)

Plant species	Fungus species	Parameter measured	Low(er) P	High(er) P	Reference
Cultivated herbaceous perennials					
Medicago sativa (alfalfa)	Mixed culture	Biomass Total P	1.17–1.28 1.05–1.18	1.03–1.09 0.88–1.10	Kucey and Diab 1984
Wild Herbaceous perennials					
Thysanotus sp. (Anthericeae)	*Glomus clarum*	Biomass Root mass	2.07 2.84	ND ND	McGee 1988
Agropyron smithii (western wheatgrass)	*Glomus mosseae*	Biomass Tiller no.	1.11–1.57 1.52–2.10	1.05–1.23 1.24–1.66	Miller et al. 1987
Agropyron smithii (western wheatgrass)	ND	Biomass (control) (droughted)	 1.17 1.56	 1.00 1.34	Duce 1987
Agropyron smithii (western wheatgrass)	Soil and mixed spores	Biomass (control) (competition)	 ND ND	 0.90–0.96 1.17–1.37	Allen and Allen 1984
Bouteloua gracilis (blue grama)	Soil and mixed spores	Biomass (control) (competition)	 ND ND	 0.89–1.02 1.15–1.41	Allen and Allen 1984
Plantago ovata (plantain)	Mean of 3 species	Height Seed mass	2.07–2.15 1.72–2.83	ND ND	Bloss 1982 Bloss 1982
Poa laevis (blue tussock grass)	Field inocula	Biomass	2.74	1.15	Crush 1973
Festuca novae-zealandica (silver tussock grass)	Field inocula	Biomass	2.14	0.98	Crush 1973
Anthoxanthum odoratum (tussock grass)	Field inocula	Biomass	ND	1.00	Crush 1973
Chionochloa rigida (tussock grass)	Field inocula	Biomass Shoot mass	2.16 1.59	ND ND	Crush 1973
Andropogon gerardi (big bluestem grass)	*Glomus etunicatum*	Biomass (control) (droughted)	 6.57 6.36	 1.26 1.20	Daniels Hetrick et al. 1987
Panicum virgatum (switchgrass)	*Glomus intraradices*	Biomass Total P Shoot mass Root mass Root length P conc.	2.87 3.65 3.14 2.37 1.37 1.79	1.72 1.67 1.74 1.68 1.16 1.53	This study This study This study This study This study This study
Bromus inermus (smooth bromegrass)	*Glomus fasciculatum*	Shoot mass Total P	ND ND	0.85 0.93	Bildusas et al. 1986
Bromus inermus (smooth bromegrass)	*Glomus intraradices*	Biomass Total P Shoot mass Root mass P conc.	1.08 2.09 1.18 1.20 2.00	1.63 2.38 1.69 1.57 1.15	This study This study This study This study This study
Bromus inermus (smooth bromegrass)	*Glomus etunicatum*	Biomass Total P Shoot mass Root mass P conc.	0.60 0.92 0.62 0.58 1.20	0.99 0.99 1.01 0.97 0.89	This study This study This study This study This study
Cultivated woody perennials					
Pyrus malus (apple)	*Glomus epigeaum* *Glomus* species 3	P conc. P conc.	1.25–1.34 1.23–1.27	0.90–1.11 0.86–0.97	Plenchette et al. 1983
Malus domestica (apple)	*Glomus mosseae* *Glomus maculosum* *Glomus manihotus* *Gigaspora calospora* *Glomus bitunicatum* *Glomus occultum* (IN) *Glomus occultum* (WA)	Biomass	2.05 1.74 2.11 1.33 1.35 2.15 1.21	1.04 1.30 0.74 1.17 1.01 0.98 1.09	Miller et al. 1985

Table 2 (continued)

Plant species	Fungus species	Parameter measured	Low(er) P	High(er) P	Reference
Citrus aurantium (sour orange)	*Glomus intraradices*	Biomass	12.1	ND	Graham and Syversten 1985
Citrus reshni (Cleopatra mandarin)	*Glomus intraradices*	Biomass	12.1	ND	Graham and Syversten 1985
Poncirus trifoliata (Trifoliate orange)	*Glomus intraradices*	Biomass	8.2	ND	Graham and Syversten 1985
Poncirus trifoliata X *Citrus sinensis* (Carrizo citrange)	*Glomus intraradices*	Biomass	6.2	ND	Graham and Syversten 1985
Poncirus trifoliata X *Citrus paradsi* (Swingle citrumelo)	*Glomus intraradices*	Biomass	4.7	ND	Graham and Syversten 1985
Wild woody perennials					
Platanus occidentalis (sycamore)	*Glomus mosseae*	Biomass	1.17	ND	Pope et al. 1983
	Glomus fasciculatum		1.20	ND	
	Glomus etunicatum		1.31	ND	
	Glomus macrocarpum		1.61	ND	
	Glomus epigaeum		1.05	ND	
	Gigaspora margarita		0.84	ND	
Fraxinus pensylvanica (green ash)	*Glomus mosseae*	Biomass	3.79	ND	Pope et al. 1983
	Glomus fasciculatum		2.00	ND	
	Glomus etunicatum		3.17	ND	
	Glomus macrocarpum		7.61	ND	
	Glomus epigaeum		3.18	ND	
	Gigaspora margarita		3.66	ND	
Liriodendron tulipifera (yellow poplar)	*Glomus mosseae*	Biomass	2.82	ND	Pope et al. 1983
	Glomus fasciculatum		1.74	ND	
	Glomus etunicatum		4.58	ND	
	Glomus macrocarpum		5.78	ND	
	Glomus epigaeum		4.38	ND	
	Gigaspora margarita		3.21	ND	
Liquidambar styraciflua (sweetgum)	*Glomus mosseae*	Biomass	2.56	ND	Pope et al. 1983
	Glomus fasciculatum		2.65	ND	
	Glomus etunicatum		3.15	ND	
	Glomus macrocarpum		8.64	ND	
	Glomus epigaeum		3.51	ND	
	Gigaspora margarita		2.31	ND	
Fraxinus americana (white ash)	*Glomus fasciculatus*	Total P	2.94–3.46	1.42–10.56	Ponder 1984
Juglans nigra (black walnut)	*Glomus fasciculatus*	Total P	1.76–2.10	1.21–1.80	Ponder 1984
Leucaena leucocephala (tropical legume)	*Glomus fasciculatum*	Shoot mass	7.63	ND	Huang et al. 1985
		Root mass	3.58	ND	
		Leaf area	11.12	ND	
		Total P	9.73	ND	
Parthenium argentatum (guayule)	*Glomus intraradices*	Biomass			
		(low salinity)	1.84	1.06	Pfeiffer and Bloss 1988
		(high salinity)	5.36	1.10	
Hedysarum boreale (steppe shrub)	Field inocula and *Rhizobium*	Shoot mass	ND	2.30	Carpenter and Allen 1988
		Leaf mass	ND	2.19	
		Total P	ND	2.62	
Artemisia tridentata (big sagebrush)	Field inocula	Biomass	ND	1.44	Stahl et al. 1988
		Total P	ND	1.43	
Coprosma robusta (New Zealand shrub)	Field inocula	Biomass	13.33	5.29	Crush 1973

Table 2 (continued)

Mean by lifespan	No. of plant-fungus combinations	Mean responsiveness at	
		Low(er) P	High(er) P
Annuals (literature)	24	1.37	1.06
Annuals (this study)	3	1.34	0.91
Herb. perennials (literature)	13	2.44	1.13
Herb perennials (this study)	3	1.67	1.42
Woody perennials (literature)	46	3.86	1.80

did the annuals. The response to inoculation with *G. etunicatum* was more negative in the annual than the perennial at high P, but the opposite at low P.

Discussion

The existence of a continuum of mycotrophy, or dependence, has been recognized since the early years of mycorrhizal research (Stahl 1900). In the context of a yield plot which portrays P availability on the abscissa and plant yield on the ordinate, this continuum of mycotrophy is the horizontal gradient. As Janos (1988) has pointed out, there also exists a vertical gradient, a continuum of responsiveness, which may be independent of, or interactive with, the horizontal continuum of dependence. Results from the six plant species fungal isolate combinations described here suggest that perennial plants may exhibit both greater dependency and greater responsiveness than the annuals. Within each genus there was the tendency for the perennials to show quantitatively greater responses than annuals at either P level (responsiveness), and to show a larger number of positive responses at the two P levels tested (dependency). These results are consistent with those which indicate that grass species vary in their responsiveness (Miller 1987) and that perennial grasses are more responsive than annuals (Benjamin and Allen 1987). Even with these corroborative data, however, this interpretation is based on a relatively small number of plant-fungus combinations. How do these data compare with a broader survey of the literature?

A sample of 26 studies which encompass experiments involving 84 plant-fungus-response parameter combinations suggests this may be a general trend (Table 2). Among these studies, annuals tended to have less responsiveness than herbaceous perennials, which in turn tended to be less responsive than woody perennials. Also, plant-fungus combinations given higher P levels generally responded less strongly than plant-fungus combinations given lower P. This pattern is particularly well developed among grasses. On the average, perennial grasses were 1.6-times more responsive to VAM inoculation than annuals at lower P levels (perennials: 2.08 versus annuals: 1.32) and 1.3-times more responsive at higher P levels (perennials: 1.27 versus annuals: 0.97). Perennial grasses were as responsive to VAM infection at higher P as annuals were at lower P, and the annuals surveyed exhibited, as a group, little response at all to VAM infection at higher P levels.

A survey such as that presented in Table 2 has a number of inherent weaknesses. It combines studies done under different environmental conditions, at different values of "high" and "low" P, with different response parameters, and with species with greatly different evolutionary histories and current ranges. Such inherently problematic comparisons have led authors such as Newman and Reddell (1987) to suggest that differentiating degrees of responsiveness and dependency at family or even generic levels may be invalid. In the experiments presented here, I have sought to avoid those pitfalls by comparing only sympatric, congeneric species under a common set of conditions. The results of those experiments closely parallel those derived from the broader survey (Table 2). This suggests that the pattern present among the limited number of taxa tested here may be a generalization appropriate to the larger assemblage of strongly mycotrophic species.

These results have implications for understanding successional change in ecosystems dominated by grasses. The successional replacement of pioneering annual grasses by later successional perennial grasses occurs as soil nutrient availability decreases and as competitive pressures increase. The greater responsiveness and dependency range of perennial grasses allow them to benefit from mycorrhizal associations at lower soil nutrient levels more than the less responsive annuals. These differences in responsiveness must be considered as significant within the suite of life history traits used to erect hypotheses concerning successional replacement patterns in communities dominated by strongly mycotrophic species.

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