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Host range of a deleterious rhizobacterium for biological control of downy brome

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Pseudomonas fluorescens strain D7 (*P. f.* D7; NRRL B-18293) is a root-colonizing bacterium that inhibits downy brome (*Bromus tectorum* L. BROTE) growth. Before commercialization as a biological control agent, strain D7 must be tested for host plant specificity. Agar plate bioassays in the laboratory and plant–soil bioassays in a growth chamber were used to determine the influence of *P. f.* D7 on germination and root growth of 42 selected weed, cultivated or native plant species common in the western and midwestern United States. In the agar plate bioassay, all accessions of downy brome were inhibited by *P. f.* D7. Root growth of seven *Bromus* spp. was inhibited an average of 87% compared with that of controls in the agar plate bioassay. Root growth of non-*Bromus* monocots was reduced by 0 to 86%, and only 6 out of 17 plant species were inhibited 40% or greater. Among all plant species, only downy brome root growth from two accessions was significantly inhibited by *P. f.* D7 in plant–soil bioassays (42 and 64%). *P. f.* D7 inhibited root growth and germination in agar plate bioassays more than in plant–soil bioassays. Inhibition in plant–soil bioassays was limited to downy brome, indicating promise for *P. f.* D7 as a biocontrol agent that will not harm nontarget species.

Nomenclature: Downy brome; *Bromus tectorum* L. BROTE; rhizobacterium; *Pseudomonas fluorescens.*

Key words: Bioassay, germination, rhizosphere.

Downy brome is a winter annual grass weed widely distributed in North American croplands and rangelands (Morrow and Stahlman 1984; Thill et al. 1984). Several characteristics make it a problem in small grains. It germinates in the autumn and overwinters in a semidormant state (Klemmedson and Smith 1964), and can thus accumulate root mass through autumn and early winter. In the spring, downy brome resumes root growth before winter wheat (*Triticum aestivum* L.), giving it a competitive advantage for limited soil moisture (Thill et al. 1984). Current downy brome control methods include herbicides, tillage, and crop rotation (Peeper 1984). Herbicides reduce yield losses, but may injure the crop and contaminate groundwater, whereas tillage can expose soil to water and wind erosion (Peeper 1984). As a potential new management tool, selected bacteria are being evaluated as biological control agents for growth suppression of downy brome. Many bacteria found on root surfaces can decrease seed germination or root growth of barley (*Hordeum vulgare* L.) (Harper and Lynch 1980), sugar beet (*Beta vulgaris* L.) (Suslow and Schroth 1982), potato (*Solanum tuberosum* L.) (Loper et al. 1985), and wheat (Alstrom 1987; Cherrington and Elliott 1987; Fredrickson and Elliott 1985). In particular, *Pseudomonas fluorescens* strain D7 (*P. f.* D7; NRRL B-18293), isolated from winter wheat roots in eastern Washington, inhibited downy brome growth in laboratory bioassays (Kennedy et al. 1991) and field trials (Kennedy et al. 1991). The strain is an aggressive colonizer of downy brome roots (Kennedy et al. 1991) and produces a plant-suppressive compound that effectively inhibits downy brome in hydroponic systems in the absence of the bacterium (Tranel et al. 1993). The plant-suppressive compound has been isolated and partially purified, while maintaining inhibitory activity against downy brome and the plant pathogenic fungus *Gaeumannomyces graminis* var. *tritici* (Gurusiddaiah et al. 1994).

A successful biocontrol agent must not affect the growth and development of nontarget plants (Boyetchko 1997; Caesar et al. 1999; Kennedy and Kremer 1996; Stanley and Julien 1999; Wapshere 1974). Because deleterious rhizobacteria can profoundly affect the growth of certain plant species in the field (Alstrom 1987; Cherrington and Elliott 1987; Fredrickson and Elliott 1985; Loper et al. 1985; Suslow and Schroth 1982), the specificity of the plant-suppressive compounds must be determined on a wide range of species prior to commercialization of a microorganism such as *P. f.* D7. Our objective was to determine the influence of *P. f.* D7 on seed germination and root growth of representative agronomic crops, rangeland forage grasses, commercial turfgrasses, and weeds that grow in the Pacific Northwest and midwestern United States.

Materials and Methods

Inoculum Preparation

Isolates of *P. f.* D7 were stored at −80 C in 6.8 M glycerol. Cultures from cryostorage were plated onto Sands and Rovira (Sands and Rovira 1970) agar and grown for 48 h before being transferred to *Pseudomonas* minimal salts broth (Bolton et al. 1989). After growth at 22 C for 32 h, cultures were centrifuged (8,800 × *g;* 15 min), and the supernatant, which contained less than 10^6 cells per milliliter, was used in agar plate bioassays. For use as a soil inoculant, the strain was cultured and centrifuged as above, the supernatant was discarded, and the cells were resuspended in 7.0 mM $CaSO_4$. The supernatant alone was used in the agar plate

TABLE 1. Scientific and common names and WSSA-approved computer codes of species tested for inhibition by *Pseudomonas fluorescens* strain D7.

Scientific name	Habitat[a]	Common name	Code
Monocots			
Aegilops cylindrica Host	W	Jointed goatgrass	AEGCY
Elytrigia elongata (Host) Nevski	F	Tall wheatgrass	AGREL
Agropyron spicatum Scribn.	F	Bluebunch wheatgrass	
Agrostis gigantea Roth	W, F	Redtop	AGSGI
Alopecurus pratensis L.	W, F	Meadow foxtail	ALOPR
Avena fatua L.	W, F	Wild oat	AVAFA
Bromus catharticus Vahl	W	Rescuegrass	BROCA
Bromus inermis Leyss.	W	Smooth brome	BROIN
Bromus japonicus Thunb. ex Murr.	W	Japanese brome	BROJA
Bromus mollis L.	W	Soft brome	BROMO
Bromus diandrus Roth	W	Ripgut brome	BRODI
Bromus secalinus L.	W	Cheat	BROSE
Bromus tectorum L.	W	Downy brome	BROTE
Dactylis glomerata L.	W, F	Orchardgrass	DACGL
Festuca arundinacea Schreb.	W, F, T	Tall fescue	FESAR
Festuca pratensis Huds.	F	Meadow fescue	FESPR
Hordeum vulgare L.	C	Barley	HORVX
Lolium multiflorum Lam.	W, F, T	Italian ryegrass	LOLMU
Lolium perenne L.	F, T	Perennial ryegrass	LOLPE
Phalaris arundinacea L.	W, F	Reed canarygrass	TYPAR
Phleum pratense L.	W, F, T	Timothy	PHLPR
Poa pratensis L.	W, F, T	Kentucky bluegrass	POAPR
Psathyrostachys juncea (Fischer) Nevski	W	Russian wild rye	
Triticum aestivum L.	C	Wheat	
Dicotyledons			
Aeschynomene sp. L.	W	Jointvetch	
Amaranthus retroflexus L.	W	Redroot pigweed	AMARE
Anthemis cotula L.	W	Mayweed chamomile	ANTCO
Brassica napus L.	C	Rapeseed	
Carthamus tinctorius L.	C	Safflower	
Chenopodium album L.	W	Common lambsquarters	CHEAL
Chondrilla juncea L.	W	Rush skeletonweed	CHOJU
Cucumis sativus L.	C	Cucumber	
Eryngium yuccifolium Michx.	W	Button snakeroot	
Galium boreale L.	W	Northern bedstraw	GALBO
Lactuca sativa L.	C	Lettuce	
Lens culinaris Medik.	C	Lentil	
Lesquerella kingii (S. Watson)	W	Bladderpod	
Medicago sativa L.	C	Alfalfa	
Pastinaca sativa L.	W	Wild parsnip	PAVSA
Pisum sativum L.	C	Pea	
Sisymbrium altissimum L.	W	Tumble mustard	SSYAL
Vicia sativa L.	W	Common vetch	VICSA

[a] Habitat denotes a crop (C), weed (W), forage grass (F) or turf grass (T).

bioassay because we were interested in the activity of the secondary metabolites produced by *P. f.* D7 in inhibiting seed germination and root growth and not in causing infection of the seeds or roots (Fredrickson and Elliott 1985). Whole cells were used in the plant–soil bioassay to permit the bacteria to colonize plant roots. It is possible that if the supernatant alone were applied to soil, the plant-suppressive compound would be degraded or would not migrate in the soil to infect the roots.

Agar Plate Bioassays

This bioassay was modified from Kennedy et al. (1991). One milliliter of supernatant was dispensed onto 18 ml of cooled 1.0% (v/v) water agar that had been poured the previous day into 100- by 15-mm petri plates. One milliliter of sterile uninoculated *Pseudomonas* minimal salts broth was added to the control plates. Over 3 to 4 h, the supernatant absorbed into the agar. The plant species selected were taxonomically diverse and represented broad phylogenetic categories as suggested by Wapshere (1974). The weed species closely related to downy brome were tested first, followed by crop and weed species progressively less similar to downy brome. The environments in which the plant species are most commonly found (Table 1) were determined from numerous sources (Madison 1971; McVicker 1974; Turgeon 1980; Vallentine 1971). Eight to twelve seeds were placed on the agar surface and incubated in the dark at 15 C. The variability in the number of seeds used depended upon seed size and availability of seed supply. After 5 to 8 d, the seed germination percentage was determined and the length of the longest root from each seed measured. Three replicate

plates per treatment were used and each bioassay was conducted at least twice. Data presented are the means from two bioassay experiments.

Plant–Soil Bioassays

Air-dried Ritzville silt loam (coarse-silty, mixed, mesic Calciorthidic Haploxerolls, pH 6.5; 1.0% organic matter) was passed through a 2-mm sieve, mixed with acid-washed silica sand (4:1, v/v, soil–sand), and amended with 9.0 g NH_4NO_3, 2.5 g $ZnSO_4$, and 1.7 g $Ca_3(PO_4)_2$ per 10 kg soil. The nonsterile soil mix was brought to 25% moisture (− 0.03 MPa) with sterile distilled water and placed in 140-ml plastic pots (6-cm diameter). Four to eight seeds of each species were placed on the soil surface. One milliliter of bacterial suspension (approximately 5×10^6 cells) or 7.0 mM $CaSO_4$ was pipetted directly onto the seeds in each pot. The soil surface was covered with 3 mm of sand to reduce evaporation. Pots were incubated in a chamber with 14- and 10-h light and dark periods, respectively (day and night temperatures of 18 and 13 C, respectively), and a photon flux of 500 to 550 μmol photon m^{-2} s^{-1} at the surface of the canopy. Although these conditions may not be optimum for germination and root growth of some of the plant species tested, the control or uninoculated pots would take these differences into account. Pots were weighed at the start of each experiment, and at 2-d intervals. Distilled water was applied to the soil surface to replace loss caused by evaporation. Four replicate pots for each treatment were used, and each species was tested at least twice. Ten days after shoot emergence, plants were removed from the pots, and roots were washed with water to remove the adhering soil. Roots were severed from shoots, dried at 60 C for 18 h, and weighed.

Statistical Analyses

Both experiments were set up as a completely randomized design. Statistics were conducted on mean root lengths for each agar bioassay plate and on each individual pot for the plant–soil bioassay. Data were analyzed by analysis of variance and transformed to percent of control after statistical analyses. Actual root lengths and root weights are not presented here for ease of reading, and because each plant species has a different growth rate, making comparisons in root length and root weight among species is irrelevant. Treatment means were compared with controls using Fisher's Protected LSD method (Steel et al. 1997).

Results and Discussion

Agar Bioassay

In agar plate bioassays, supernatant of *P. f.* D7 cultures consistently reduced root lengths of downy brome accessions by an average of 97% (Table 2). The bacterial supernatant reduced the root length of all *Bromus* spp. by 71 to 100% compared with the control root lengths (Table 2). Seed germination of downy brome accessions was consistently inhibited 61% or more. Seed germination of the other *Bromus* spp. was reduced by 38 to 90% compared with the controls. The supernatant of *P. f.* D7 reduced the root lengths of non-*Bromus* grasses in the agar bioassay by 10 to 86% (Table 2). The 12 to 31% reduction in germination of *Lolium* spp. was attributed to variability in the germination rates of the seed stock. Variable seed germination may have affected the results with these species in the soil assays and the bioassay.

In the original screening process, only one cultivar of winter wheat was used to identify potential weed-suppressive bacteria (Kennedy et al. 1991). This cultivar, 'Daws', showed the least reduction in root growth of the wheat cultivars tested in this study. In the bioassay, susceptibility of wheat to the plant-suppressive compounds depended on variety, with seedling root growth being reduced by an average of 44%. Seed germination was not significantly reduced for any of the non-*Bromus* monocots.

Dicotyledonous seedling root growth and germination on agar plates were not significantly reduced by *P. f.* D7 supernatant compared with the control treatments (data not shown). Overall, the monocots were more susceptible to the supernatant than the dicots, with the grand mean root length reduction for monocots twice as great as that for dicots.

Plant–Soil Bioassay

In soil in the growth chamber, only downy brome root growth was reduced significantly (Table 3). Response depended on accession, with two of the three downy brome accessions being significantly inhibited by the bacterium. In contrast to the results of the agar bioassay, *P. f.* D7 did not significantly reduce root growth of wheat and barley varieties, jointed goatgrass [*Aegilops cylindrica* (L.) Host], and redtop (*Agrostis gigantea* Roth) in the plant–soil bioassay. Perennial ryegrass (*Lolium perenne* L.) germination, but not root growth, was significantly reduced by the bacterial suspension in the plant–soil bioassay.

The roots of one dicot, rapeseed (*Brassica napus* L.), were stimulated by bacterial inoculation. The observed stimulation of root growth suggests that *P. f.* D7 may have plant growth–promoting properties, similar to the plant growth promotion of potatoes, lettuce (*Lactuca sativa* L.), cucumber (*Cucumis sativa* L.), and tomatoes (*Lycopersicon esculentum* L.), described in a previous report by VanPeer and Schippers (1989). The mechanism of such growth-promoting activity has not been resolved, but may include the production of organochelators or antimicrobial metabolites (Kloepper and Schroth 1981; Weller 1988).

Root response to *P. f.* D7 in agar plates or soil was not consistent within a plant family. For example, among Leguminosae species, root responses in agar plates differed up to 10-fold (data not shown), whereas the difference was about fivefold in the plant–soil bioassay (Table 3). Plant responses to *P. f.* D7 supernatant in the agar plate bioassay did not correlate with the responses observed in the plant–soil bioassay ($R^2 = 0.18$). Root inhibition in the agar bioassay was always greater than in soil. This is expected because the agar bioassay only tested for the production of plant-suppressive compounds and not the competitive or colonizing ability of a bacterium in the rhizosphere.

Inhibition of root growth was not only greater, but occurred in a greater number of species in the agar plate bioassay than in the plant–soil bioassay, and there may be several reasons for the lack of inhibition in soil. The biological control agent must be able to survive and compete in soil, and must colonize the seed and root (Kennedy and Kremer

TABLE 2. Influence of *Pseudomonas fluorescens* D7 cell-free supernatant on root lengths and seed germination of monocotyledons germinated for 5 d on agar plates.

Scientific name	Reduction	
	Root length[a]	Seed germination[b]
	%	
Aegilops cylindrica Host	42*	−7
Agropyron spicatum Scribn.	58*	−27
Agrostis gigantea Roth	45*	−34
Alopecurus pratensis L.	24	13
Avena fatua L.	14	−40
Bromus catharticus Vahl	81*	51*
Bromus inermis Leyss.	71*	38
Bromus japonicus Thunb. ex Murr.	100*	82*
Bromus mollis L.	99*	90*
Bromus diandrus Roth	80*	63*
Bromus secalinus L.	81*	51*
Bromus tectorum L.		
Ellis, OK, accession	100*	99*
Fort Collins, CO, accession	94*	61*
Fort Hays, KS, accession	99*	88*
Pendleton, OR, accession	92*	65*
Pullman, WA, accession	98*	87*
Dactylis glomerata L.	33	9
Elytrigia elongata (Host) Nevski	65*	−9
Festuca arundinacea Schreb.	13	0
Festuca pratensis Huds.	30	−17
Hordeum vulgare L.		
var. 'Luke'	25	0
var. 'Paha'	40	0
var. 'Steptoe'	49*	0
Lolium multiflorum Lam.	86*	12
Lolium perenne L.	0	31
Phalaris arundinacea L.	14	0
Phleum pratense L.	34	−23
Poa pratensis L.	14	−12
Psathyrostachys juncea (Fischer) Nevski	27	−8
Triticum aestivum L.		
var. 'Daws'	10	0
var. 'Hill 81'	30	0
var. 'Stephens'	60*	4
var. 'Moro'	76*	4

[a] * = significantly different from control at $P < 0.05$.
[b] Negative values indicate growth promotion.

1996). Root surfaces favor other Gram⁻ rods, and thus many diverse bacteria would be present to compete with *P. f.* D7 for carbon, energy, and nutrients in the unsterilized soil medium (Alexander 1977). The bacterium is also confronted with other soil microfaunal groups and competition with indigenous flora for the available substrates (Compeau et al. 1988; Marumoto et al. 1982; Watrud et al. 1985). Second, root exudate quality and quantity, soil physical and chemical properties, and, in a field situation, cropping history will affect the competitiveness of the bacterial species (Brock 1985; Loper et al. 1985; Lynch 1979; Scher et al. 1988). Thus, colonization rates of *P. f.* D7 on the plant species tested could vary markedly in different situations. Thirdly, the plant-suppressive compounds may not be produced in biologically significant quantities in the soil solution compared with the liquid growth medium. Also, the bacteria and the plant-suppressive compounds may not be as mobile in the soil solution as on an agar plate.

Plant responses in both bioassays were variable, and root length reductions of up to 40% were not significant (Table 2). Many field-pollinated seedlots were used that may express high intraspecies variability in germination rate. Preimbibition of seed and culling of those seeds that did not germinate prior to supernatant addition was not practical, because of contamination and desiccation of agar during the preincubation period.

While the *P. f.* D7 supernatant caused root inhibition in some species of monocots and dicots in agar plate bioassays, the extent of inhibition in all species was not as great as that observed for *Bromus* spp., and suppression of non-*Bromus* spp. did not occur in the soil system (Tables 2 and 3). The root-suppressive capability of *P. f.* D7 was specific to *Bromus* spp. in the plant–soil bioassay. Whereas inhibition of plant growth by *P. f.* D7 occurred more readily in the agar plate bioassay than in the plant–soil bioassay, both methods are important in the screening process for developing microorganisms for biological weed control. The agar plate bioassay is the first step in the screening process for potential biological control organisms, and isolates that inhibit germination and root growth are further screened in

TABLE 3. Root mass and seed germination reduction of monocotyledons and dicotyledons inoculated with *Pseudomonas fluorescens* D7 (5×10^6 cells/pot) and grown for 14 to 21 d in a Ritzville silt loam in the growth chamber.

Scientific name	Reduction	
	Root mass[a,b]	Seed germination
	%	
Monocots		
Aegilops cylindrica Host	30	0
Elytrigia elongata (Host) Nevski	6	−22
Agrostis gigantea Roth	30	−25
Avena fatua L.	2	−8
Bromus japonicus Thunb. ex Murr.	35	0
Bromus tectorum L.		
Fort Hays, KS, accession	13	4
Pendleton, OR, accession	64*	0
Pullman, WA, accession	42*	0
Dactylis glomerata L.	30	−12
Festuca arundinacea Schreb.	0	7
Hordeum vulgare L. var. 'Steptoe'	11	4
Lolium perenne L.	22	46*
Phleum pratense L.	0	−25
Triticum aestivum L. var. 'Hill 81'	0	3
Triticum aestivum L. var. 'Daws'	0	0
Triticum aestivum L. var. 'Stephens'	0	0
Triticum aestivum L. var. 'Moro'	0	0
Dicotyledons		
Amaranthus retroflexus L.	1	−26
Brassica rapa L. var. 'Humus'	−44*	0
Carthamus tinctorius L.	32	−40
Chenopodium album L.	7	−29
Lens culinaris Medik. var. 'Crimson'	17	0
Medicago sativa L. var. 'Ladak'	17	0
Pisum sativum L. var. 'Alaska'	3	−6

[a] * = significantly different from control $P < 0.05$.
[b] Negative values indicate growth promotion.

the soil–plant bioassay. Some differences in the susceptibility of accessions may exist and need to be studied further. Other researchers have shown that susceptibility to a plant-suppressive compound differs among weed accessions from different regions (Vogelgsang et al. 1999). *P. f.* D7 may be developed as a selective biocidal agent against *Bromus* spp. in much the same way as selective herbicides that may control a particular group of plants while having a lesser or negligible effect on desirable vegetation (Willis 1990). In an overview of concerns with mycoherbicides, TeBeest and Templeton (1985) advised that nontarget specificity will not present a safety problem provided susceptible plants are not in the application area, and if the biocontrol agent does not persist or disseminate. It has been shown that *P. f.* D7 does not persist under hot, dry conditions and, therefore, would not present an environmental risk (Kremer and Kennedy 1996). *Pseudomonas fluorescens* does not sporulate (Krieg 1984), and thus may not disperse in the manner of many fungal pathogens. *P. f.* D7 specifically inhibits downy brome and will be of little ecological risk to nontarget plants.

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