Biocontrol of Aphanomyces Root Rot and Pythium Damping-Off by *Pseudomonas cepacia* AMMD on Four Pea Cultivars

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ABSTRACT

King, E. B., and Parke, J. L. 1993. Biocontrol of Aphanomyces root rot and Pythium damping-off by *Pseudomonas cepacia* AMMD on four pea cultivars. Plant Dis. 77:1185-1188.

Pseudomonas cepacia strain AMMD applied as a seed treatment has been used for biocontrol of Pythium damping-off and Aphanomyces root rot of peas. We tested the biocontrol efficacy of this strain on four pea cultivars that differed in susceptibility to Aphanomyces root rot. In 1990 and 1991, seedling emergence, Aphanomyces root rot severity, and pea yield of biocontrol-treated and nontreated controls were compared in a field naturally infested with *Pythium* spp. and *Aphanomyces euteiches* f. sp. *pisi*. In 1991, the experiment also was conducted in an adjacent field with no history of pea cropping to evaluate the effect of the biocontrol agent in the absence of Aphanomyces root rot. Biocontrol efficacy was not limited to a single cultivar. Differential effects of biocontrol among cultivars were clearly related to the degree of susceptibility of each cultivar to *Pythium* and *Aphanomyces*. Seed treatment with *P. cepacia* AMMD significantly improved emergence of all four cultivars when disease was severe and improved emergence of two cultivars when disease was moderate. *P. cepacia* AMMD did not reduce symptoms of Aphanomyces root rot in either year. Bacterial seed treatment increased yield of three cultivars in the infested field in 1990 when compared with no treatment but did not increase yield of any of the cultivars in the same field in 1991. Bacterial seed treatment increased yield of one cultivar in the noninfested field. A metalaxyl seed treatment included in experiments in 1991 to control *Pythium* increased both emergence and yield.

Addtional keywords: biological control, *Pisum sativum*, soilborne diseases

Pythium spp. infect pea (*Pisum sativum* L.) seeds in the first few hours after planting and rot seeds before they can germinate unless they are protected by seed treatment with a fungicide such as captan or metalaxyl (8). A second soilborne disease, Aphanomyces root rot, caused by *Aphanomyces euteiches* Drechs. f. sp. *pisi* W.F. Pfender & D.J. Hagedorn, is the main factor limiting pea production in the Midwest (17). *Aphanomyces* can infect peas throughout the growing season, although infection usually occurs at the seedling stage. Damage to the root cortex prevents the roots from providing the shoot with adequate water. When weather is conducive to disease, root rot may cause 100% yield losses in infested fields (17). Because there is no commercially available control for Aphanomyces root rot, the disease is managed by avoidance of infested fields (19). Trifluralin and dinitramine herbicides may reduce disease severity (6), and incorporation of crucifer green manures reduces disease severity in successive pea crops (4,15). Hymexazol, marketed in Japan as Tachigaren for control of *Pythium* and *Aphanomyces* on sugar beets, reduces the severity of Aphanomyces root rot (J. Parke, *personal communication*), but this fungicide is not labeled for use on peas in the United States. The lack of a commercially available control for Aphanomyces root rot in the United States encouraged us to test rhizosphere bacteria from healthy pea plants grown in infested field soil for their biocontrol potential. One bacterial strain, AMMD of *Pseudomonas cepacia* (Burkholder) Palleroni and Holmes, increased yield of peas grown in infested fields in several locations and over several years (16).

Traditional biological control research has focused on the interaction between biocontrol agent and pathogen. Less attention has been paid to the role of the host plant in the interaction, yet the plant may affect the success of biocontrol through its ability to support the growth of individual biocontrol agents or through its influence on the development of rhizosphere communities. Several researchers have observed plant species-specific or cultivar-specific interactions with plant growth-promoting and deleterious rhizosphere bacteria. For example, only one of four bacterial strains that increased growth of radishes also increased growth of potatoes (10). Inoculation of citrus seedlings with strains of *Pseudomonas fluorescens* resulted in cultivar-specific growth stimulation or inhibition (5). Deleterious rhizosphere bacteria caused cultivar-specific changes in dry weights of different pea and wheat cultivars (1-3). Millet et al (14) found that yield response of wheat cultivars to strains of *Azospirillum brasilense* or other indigenous bacteria depended upon plant cultivar and the location of the field sites. In contrast, there was no interaction among several plant growth-promoting rhizosphere bacteria strains with host cultivar in a factorial experiment involving four potato cultivars and strains of *P. putida* and *P. fluorescens* (9).

Biocontrol screening of *P. cepacia* AMMD has been conducted with a commercial pea cultivar, Perfection 8221, that is susceptible to Aphanomyces root rot (16). Perfection 8221 was chosen with the assumption that if a bacterial seed treatment reduced root rot severity on a susceptible cultivar, it should do the same when applied to less susceptible cultivars. For a biocontrol agent to be commercially acceptable it must be effective when applied to a wide range of cultivars.

We determined whether the biocontrol ability of *P. cepacia* AMMD was influenced by host cultivar. We evaluated emergence losses caused by Pythium seed rot, Aphanomyces root rot severity, and pea yield of four pea genotypes differing in degree of susceptibility to Aphanomyces root rot that were grown from nontreated seeds or from seeds treated with *P. cepacia* AMMD. A chemical seed treatment included in the second year of the 2-yr field experiment allowed us to estimate the importance of *Pythium* in yield loss.

MATERIALS AND METHODS

Choice of pea cultivars. Four pea cultivars or lines representing both canning and freezing cultivars were chosen for their differential response to Aphanomyces root rot and for their similarity in flowering time, since plant phenology may affect rhizosphere microflora (11-13, 18,20). The following were chosen: 1) Perfection 8221 (Nunhems Seeds, Inc.), a susceptible cultivar used for selection of the biocontrol bacterial strains (including *P. cepacia* AMMD) from Wisconsin field soils; 2) Dinos, a small-seeded pea that is highly susceptible to root rot (D. Webster, Asgrow Seed Co., *personal communication*); 3) Bolero (Asgrow Seed Co.), a large-seeded cultivar that is less susceptible to root rot; and 4) 8903 RR, a breeding line with resistance to Aphanomyces root rot (7) that had been screened for root rot resistance in the same field in which the current study was conducted.

Bacterial seed treatment. *P. cepacia* AMMD was isolated from pea roots grown in soil from the root rot nursery at the University of Wisconsin Exper-

Accepted for publication 6 August 1993.

iment Station, Arlington, and was identified by fatty acid analysis (16). Six 250-ml Erlenmeyer flasks, each containing 80 ml of nutrient broth plus yeast extract (NBY) (21), were inoculated from frozen stock cultures (−80 C in 10% dimethyl sulfoxide) of *P. cepacia* AMMD. Flasks were incubated at room temperature on a rotary shaker for 48 hr. Cultures from four flasks were pooled in a sterile 500-ml flask. Aliquots of 2.5 ml were plated on each of 88 NBY agar plates.

For each cultivar, bacterial growth from 22 plates was scraped into an aluminum pan. Seeds (450) were added and stirred until they were evenly coated. As a control treatment, 450 seeds of each cultivar were stirred with 36 ml of sterile distilled water. The amount of water was based on the wet weight of the bacteria added to treated seeds.

Chemical seed treatment. In 1991, an additional seed treatment was included. Seeds of each cultivar were coated with metalaxyl (Apron 25W) at the recommended rate of 2 oz/100 lb of seed, roughly 0.1 g in 10 ml of sterile distilled water per 450 seeds. Metalaxyl controls Pythium damping-off but has no effect on Aphanomyces root rot. All seeds were dried overnight at room temperature in a sterile laminar flow hood. Seeds were packaged and stored overnight at 4 C until planting.

Field sites. In 1990, this experiment was conducted in the pea root rot nursery at the University of Wisconsin Experiment Station in Arlington (Plano silt loam: Typic Argiudoll, fine silty mixed mesic). This field has been planted with peas each season for the last 20 yr. It supports a high population of *Pythium* spp. and *A. e. pisi* (16) and will be referred to as the "infested" field. In 1991, the experiment was repeated in another part of the same field and also in an adjacent field with no recent history of pea cropping ("noninfested" field). Peas grown in this soil under conditions ideal for Aphanomyces root rot development in a growth chamber assay (16) did not develop disease symptoms.

Experimental design. A factorial design was employed with two bacterial treatments (with or without *P. cepacia* AMMD) and four pea cultivars. The experiment was arranged as a randomized complete block with seven replicates of each treatment by cultivar combination. Replicates consisted of two 0.76-m rows of each treatment each planted with 30 seeds at 5.1-cm intervals. Rows were spaced 0.91 m apart. The vinyl gloves worn by the planters were changed between treatments to prevent cross-contamination.

Evaluation criteria. Biocontrol efficacy was evaluated in three ways. Weekly stand counts tracked seedling emergence losses caused by Pythium damping-off and plant mortality caused by Aphanomyces root rot. Stand counts were expressed as percentage of the total number of planted peas. Disease severity ratings indicated damage to roots caused by Aphanomyces root rot. Pea yield was measured at the end of the growing season.

Roots were rated to assess the severity of Aphanomyces root rot according to the scale developed by Sherwood and Hagedorn (19) as modified for field use. At first flower, all plants in one of the two rows of peas of each treatment in a block were excavated. The roots were washed to remove soil. Plants were evaluated visually and assigned a rating on a five-point scale based on the overall appearance of the root system and on the color and firmness of the epicotyl (0 = healthy plant, 1 = plant with slightly honey-colored roots and epicotyl, 2 = plant with obvious root discoloration and pruning and a soft epicotyl, 3 = living plant with a collapsed epicotyl and a heavily discolored/pruned root system, 4 = dead plant).

Plants were harvested at the commercial processing stage. All of the plants in the remaining row were counted and pulled, and the pods were picked by hand. The peas were removed with a small electric podder. Unopened pods were split by hand. Fresh weight of the peas was determined.

Data analysis. Stand counts, Aphanomyces root rot disease severity ratings (means from each block), and yield of fresh peas were each analyzed with a two-factor analysis of variance (ANOVA) (Statisitical Analysis Systems, version 6.07, SAS Institute, Cary, NC). Separate analyses of variance also were performed for the data from each cultivar. Comparisons among main effects means or among treatments within a cultivar were made with Fisher's protected LSD ($P = 0.05$).

RESULTS

Pythium damping-off was more severe in 1990 than in 1991 (Table 1). In 1990, the mean percent emergence for nontreated seedlings (all cultivars combined) was 47.4% as compared with 80.1% in the same field in 1991. Emergence was similar in both the field infested with Aphanomyces and the noninfested field in 1991. Emergence among nontreated seedlings differed among the four cultivars. In 1990, emergence of nontreated 8903 RR and of Perfection 8221 was less than emergence of Bolero and Dinos. In both fields in 1991, emergence of nontreated Perfection 8221 was less than that of the other three cultivars.

It was in this context of variable disease incidence among experiments and variable response to disease among cultivars that we tested for differential responses to seed treatment with *P. cepacia* AMMD and metalaxyl (Table 1). In 1990, when emergence was low overall, seed treatment significantly improved emergence for all four cultivars compared with no seed treatment. However, the magnitude of the increase in emergence resulting from seed treatment with *P. cepacia* depended upon the pea cultivar. This significant interaction between seed treatment and cultivar ($P = 0.0154$) in the initial two-way ANOVA necessitated pairwise comparisons of seed treatment effects within each cultivar in 1990. In both fields in 1991, seed treatment significantly improved emergence of Perfection 8221. There was a statistically significant interaction between seed treatment and cultivar in the noninfested field ($P = 0.0001$) but not in the infested field ($P = 0.0847$). Bacterial seed treatment significantly improved emergence of cultivar 8903 RR in the infested field and of both 8903 RR and Dinos in the noninfested field. Seed treatment with metalaxyl to control

Table 1. Means for 1990 and 1991 field experiments on the effects of pea cultivar and seed treatment on seedling emergence

Experiment Seed treatment	Percent emergence[a] per cultivar Perfection 8221	Dinos	8903 RR	Bolero
Infested field 1990				
None	39.3	66.7	30.5	53.1
Pseudomonas cepacia AMMD	81.0	91.7	59.5	84.8
LSD[b]	3.8	7.9	11.7	3.8
Infested field 1991				
None	68.3	84.8	86.9	80.5
P. cepacia AMMD	84.1	90.2	92.9	87.9
Metalaxyl	86.4	94.5	97.5	92.6
LSD	9.2	5.8	2.8	6.1
Noninfested field 1991				
None	60.5	82.9	81.7	81.9
P. cepacia AMMD	76.4	90.5	93.1	81.4
Metalaxyl	86.4	93.3	94.4	92.1
LSD	5.3	6.2	5.0	7.2

[a] Based on number of seedlings that emerged from 60 seeds planted in each block.
[b] Fisher's protected LSD ($P = 0.05$) for within-cultivar comparisons.

Pythium significantly improved emergence of all cultivars in both the infested and the noninfested field.

The severity of Aphanomyces root rot also varied among seasons and fields (Table 2). In the field infested with *Aphanomyces*, root rot was more severe in 1990 (mean disease severity rating = 2.7) than in 1991 (mean rating = 2.2). Plants in the noninfested field were asymptomatic (mean rating = 0.1). Regardless of the level of disease, neither *P. cepacia* AMMD nor metalaxyl seed treatment affected Aphanomyces root rot severity compared with nontreated controls in any of the three experiments. In the infested field in 1990, the most severe test, root rot symptoms were least severe for 8903 RR and most severe for Dinos. In the same field in 1991, 8903 RR again showed fewer symptoms than the other three cultivars.

Each of the four cultivars had a unique yield potential in the absence of disease, as evidenced by the yields from the noninfested field (Table 3). Yield data from the infested field reflect both intrinsic cultivar-specific yield differences and differential susceptibility to Pythium damping-off and Aphanomyces root rot. Seed treatment with *P. cepacia* AMMD appeared to increase yield of all cultivars in both 1990 and 1991, but the within-treatment variability was so great that many of these differences were not statistically significant. Seed treatment resulted in significantly greater yields for three of the four cultivars and a significant interaction between seed treatment and cultivar ($P = 0.0051$) in 1990 when both Pythium damping-off and Aphanomyces root rot were severe. In 1991, under less severe disease conditions, seed treatment resulted in greater yield only for cultivar 8903 RR in the noninfested field. There was no effect of bacterial seed treatment on yield in the infested field. Seed treatment with metalaxyl resulted in greater yields only for cultivar 8903 RR in the infested and noninfested fields in 1991.

DISCUSSION

When both Pythium damping-off and Aphanomyces root rot were severe, *P. cepacia* AMMD significantly increased emergence of all cultivars and yield of three of the four cultivars. This suggests that although we used only a single cultivar, Perfection 8221, in previous studies, *P. cepacia* AMMD will also be an effective biocontrol agent on other pea cultivars. However, we would expect the degree of biocontrol to differ among cultivars.

Substantial increases in emergence and yield as a result of seed treatment with *P. cepacia* strain AMMD were most likely attributable to control of Pythium seed rot and damping-off rather than to control of Aphanomyces root rot, in that bacterial seed treatment did not reduce root rot symptoms. Indirect evidence for this is the observation that emergence was increased similarly by seed treatment with the biocontrol agent and by metalaxyl, a fungicide effective against *Pythium* spp. Furthermore, the increase in emergence resulting from seed treatment with the biocontrol agent occurred even in the absence of *Aphanomyces* (in the noninfested field in 1990). In relation to emergence of nontreated seeds, bacterial seed treatment was most effective when Pythium damping-off was severe, further evidence that *Pythium* was the target of biocontrol.

Interactions between seed treatment and cultivar may reflect differences among cultivars in seed quality and in susceptibility to Pythium damping-off. Emergence of 8903 RR was poor in 1990. Seeds of this breeding line were hand-collected and had the lowest germination rate of all cultivars when surface-sterilized and germinated on sterile filter paper. The significant increase in emergence resulting from bacterial seed treatment for this cultivar in 1990 may be explained by its greater susceptibility to damping-off. In 1991, the percent increase in emergence associated with seed treatment with either *P. cepacia* AMMD or metalaxyl was greatest for Perfection 8221, which had the lowest emergence among nontreated cultivars.

Seed treatment with both *P. cepacia* AMMD and metalaxyl failed to reduce symptoms of Aphanomyces root rot for any of the cultivars compared with no seed treatment in the infested field in both 1990 and 1991. *P. cepacia* AMMD may have failed to control *Aphanomyces*, or disease suppression may not have been accurately reflected by the rating system. Aphanomyces root rot severity is difficult to measure. Roots are rated when the plants first begin to flower. At this stage, belowground symptoms are evident but aboveground symptoms are not yet apparent. Even when differences in disease severity are very clear at first flower, they may not predict differences in yield. The weather during the period between root rating and harvest is critical in determining the outcome of the disease. If the fields stay wet and evapotranspiration is moderate, even

Table 2. Means for 1990 and 1991 field experiments on the effects of pea cultivar and seed treatment on Aphanomyces root rot severity

Experiment Seed treatment	Aphanomyces root rot severity ratings[a] per cultivar			
	Perfection 8221	Dinos	8903 RR	Bolero
Infested field 1990				
None	3.0	3.0	2.2	3.0
Pseudomonas cepacia AMMD	2.9	3.1	2.1	2.7
Infested field 1991				
None	2.4	2.4	1.6	2.2
P. cepacia AMMD	2.5	2.2	1.5	2.3
Metalaxyl	2.2	2.6	1.7	2.1
Noninfested field 1991				
None	0.1	0.2	0.1	0.1
P. cepacia AMMD	0.1	0.2	0.1	0.2
Metalaxyl	0.1	0.1	0.1	0.2

[a] Rated on a scale where 0 = healthy plant and 4 = dead plant.

Table 3. Means for 1990 and 1991 field experiments on the effects of pea cultivar and seed treatment on fresh weight of peas at processing stage

Experiment Seed treatment	Fresh pea yield[a] per cultivar			
	Perfection 8221	Dinos	8903 RR	Bolero
Infested field 1990				
None	26.8	10.1	39.6	34.4
Pseudomonas cepacia AMMD	43.1	26.9	106.6	67.6
LSD[b]	26.8	8.2	32.4	25.8
Infested field 1991				
None	107.0	51.1	207.6	184.6
P. cepacia AMMD	132.6	81.4	234.9	277.9
Metalaxyl	141.8	52.2	284.3	247.8
LSD	39.7	36.7	50.8	81.0
Noninfested field 1991				
None	218.7	219.7	275.7	408.4
P. cepacia AMMD	229.1	217.9	317.9	410.0
Metalaxyl	242.0	205.4	324.6	404.9
LSD	67.9	71.4	41.5	99.8

[a] Pea fresh weight (g) per row.
[b] Fisher's protected LSD ($P = 0.05$) for within-cultivar comparisons.

damaged roots may be able to support the plant. If the weather is hot and dry, yield differences may correspond more closely to differences in root ratings.

The root rating system also is more accurate when disease symptoms are absent or severe than when the rating is in the middle range, when determinations are more subjective. It is interesting that there were statistically significant differences among root ratings for cultivars in the noninfested field, where the average disease severity was only 0.1. A difference of several hundredths of a unit on a scale of zero to four is probably not biologically meaningful.

Despite the inherent difficulties of assessing disease severity, significant differences in root rot ratings were observed among cultivars. This was especially apparent in 1990 when disease was severe. The breeding line resistant to *Aphanomyces*, 8903 RR, showed the least severe symptoms, followed by Bolero, Perfection 8221, and Dinos. In the following season, 8903 RR again showed the lowest disease severity. The fact that root ratings distinguished resistant from susceptible cultivars suggested that root ratings were a valid measure of disease severity and indicated that both *P. cepacia* AMMD and metalaxyl did not control Aphanomyces root rot.

Yield is the most complex indicator of differential effects of *P. cepacia* AMMD among cultivars because each cultivar has a unique yield potential in the absence of disease and because yield integrates both emergence losses, caused primarily by *Pythium* spp., and losses later in the season resulting from Aphanomyces root rot in the infested field. Significant increases in emergence were reflected in increased yield in 1990. However, not all of the yield increases could be explained by control of *Pythium*. For example, yield of Dinos in the infested field in 1991 was 59% greater following seed treatment with *P. cepacia* AMMD even though emergence was similar among treated and nontreated peas. In addition to biocontrol of *Pythium* spp., perhaps *P. cepacia* AMMD stimulates or accelerates root development, so that infected plants better tolerate damage by *Aphanomyces*. This would explain the increase in yield despite no reduction in disease severity ratings.

In 1991, despite significant emergence effects caused by seed treatment with *P. cepacia* AMMD or metalaxyl for several cultivars, only cultivar 8903 RR in the noninfested field had significantly greater yield. Because seed treatment with metalaxyl also resulted in greatest yield for this cultivar only, it is likely that the yield response of 8903 RR in the infested field was associated with its genetic resistance to *Aphanomyces*. Apparently, Aphanomyces root rot substantially reduced any initial advantage of increased emergence for the three susceptible cultivars.

Conclusions from these experiments were greatly strengthened by the addition of the chemical seed treatment to control *Pythium* in the second field season and by the decision to conduct the experiment both in a field where Aphanomyces root rot was severe and in a field where root rot has had little or no effect. While the intent of the experiment was to look for interactions between the bacterial biocontrol agent and several pea cultivars, the addition of these controls allowed a greater understanding of the effects of this particular biocontrol agent in a system that includes both pathogens.

Many of the reports of successful biocontrol of plant pathogens are based on a comparison of the biocontrol treatment with no treatment. It would be more meaningful if yield increases caused by biocontrol also were expressed as a proportion of yield in the absence of disease. This would give a better indication of the degree of advantage conferred by disease control. For example, Dinos showed a 166% yield increase over no treatment as a result of bacterial seed treatment in 1990 but had a final yield of only 27 g, one-eighth of the yield in the noninfested field.

Although we can determine whether there are cultivar-specific effects of biocontrol with this system, other model systems would be necessary to elucidate the effect of disease resistance genes on biocontrol efficacy. The resistance of peas to Pythium seed rot and to Aphanomyces root rot is not simply inherited, nor is it well characterized. Determination of the mechanisms of interactions between introduced bacterial strains, pathogens, and their plant hosts would involve comparisons of isogenic plants with single gene differences.

These results are significant from a practical standpoint because all cultivars benefited from bacterial seed treatment when disease was severe. This suggests that the conclusions of our previous efficacy tests with Perfection 8221 predict the success of biocontrol in combination with other host cultivars. Some bacteria/cultivar combinations may have even greater disease-reduction potential. In two of three tests, the combination of the biocontrol agent with the root rot-resistant breeding line 8903 RR gave the highest percentage yield increase over no treatment. Ultimately, integrated pest management strategies involving the combination of biocontrol and host genetic resistance could be used to further improve crop performance in infested fields.

ACKNOWLEDGMENTS

We thank the Midwest Food Processors Association for their financial support; Earl Gritton, Asgrow Seed Company, and Nunhems Seeds, Inc., for contributing pea seed; and Bob Rand for technical assistance.

LITERATURE CITED

1. Astrom, B. 1991. Intra- and interspecific variation in plant response to inoculation with deleterious rhizosphere pseudomonads. J. Phytopathol. 131:184-192.
2. Astrom, B., and Gerhardson, B. 1988. Differential reactions of wheat and pea genotypes to root inoculation with growth-affecting rhizosphere bacteria. Plant Soil 109:263-269.
3. Astrom, B., and Gerhardson, B. 1989. Wheat cultivar reactions to deleterious rhizosphere bacteria under gnotobiotic conditions. Plant Soil 117:157-165.
4. Chan, M. K. Y., and Close, R. C. 1987. Aphanomyces root rot of peas 3. Control by the use of cruciferous amendments. N.Z. J. Agric. Res. 30:225-233.
5. Gardner, J. M., Chandler, J. L., and Feldman, A. W. 1984. Growth promotion and inhibition by antibiotic-producing fluorescent pseudomonads on citrus roots. Plant Soil 77:103-113.
6. Grau, C. R., and Reiling, T. P. 1977. Effect of trifluralin and dinitramine on Aphanomyces root rot of pea. Phytopathology 67:273-276.
7. Gritton, E. T. 1990. Registration of five root rot resistant germplasm lines of processing pea. Crop Sci. 30:1166-1167.
8. Harman, G. E. 1984. Diseases caused by *Pythium* spp. Pages 5-6 in: Compendium of Pea Diseases. D. J. Hagedorn, ed. American Phytopathological Society, St. Paul, MN.
9. Howie, W. J., and Echandi, E. 1983. Rhizobacteria: Influence of cultivar and soil type on plant growth and yield of potato. Soil Biol. Biochem. 15:127-132.
10. Kloepper, J. W., Schroth, M. N., and Miller, T. D. 1980. Effects of rhizosphere colonization by plant growth-promoting rhizobacteria on potato plant development and yield. Phytopathology 70:1078-1082.
11. Lambert, B., Leyns, F., van Rooyen, L., Gossele, F., Papon, Y., and Swings, J. 1987. Rhizobacteria of maize and their antifungal activities. Appl. Environ. Microbiol. 53:1866-1871.
12. Lambert, B., Meire, P., Joos, H., Lens, P., and Swings, J. 1990. Fast-growing, aerobic, heterotrophic bacteria from the rhizosphere of young sugar beet plants. Appl. Environ. Microbiol. 56:3375-3381.
13. Martin, J. K. 1971. Influence of plant species and age on the rhizosphere microflora. Aust. J. Biol. Sci. 24:1143-1150.
14. Millet, E., Avivi, Y., and Feldman, M. 1985. Effects of rhizospheric bacteria on wheat yield under field conditions. Plant Soil 86:347-355.
15. Muehlchen, A. M., Rand, R. E., and Parke, J. L. 1990. Evaluation of crucifer green manures for controlling Aphanomyces root rot of peas. Plant Dis. 74:651-654.
16. Parke, J. L., Rand, R. E., Joy, A. E., and King, E. B. 1991. Biological control of Pythium damping-off and Aphanomyces root rot of peas by application of *Pseudomonas cepacia* or *P. fluorescens* to seed. Plant Dis. 75:987-992.
17. Pfender, W. F. 1984. Aphanomyces root rot. Pages 25-28 in: Compendium of Pea Diseases. D. J. Hagedorn, ed. American Phytopathological Society, St. Paul, MN.
18. Rovira, A. D. 1965. Interactions between plant roots and soil microorganisms. Annu. Rev. Microbiol. 19:241-266.
19. Sherwood, R. T., and Hagedorn, D. J. 1958. Determining the common root rot potential of pea fields. Wis. Agric. Exp. Stn. Bull. 12 pp.
20. Starkey, R. L. 1929. Some influences of the development of higher plants upon the microorganisms in the soil: I. History and introductory. Soil Sci. 27:319-334.
21. Vidaver, A. K. 1967. Synthetic and complex media for rapid detection of fluorescence of phytopathogenic pseudomonads. Effects of carbon source. Appl. Microbiol. 15:1523-1527.