Aphanomyces euteiches f. sp. *phaseoli*, a Causal Agent of Bean Root and Hypocotyl Rot

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ABSTRACT

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A previously unrecognized strain of *Aphanomyces* was found that caused severe root and hypocotyl rot of snap beans (*Phaseolus vulgaris*). It is proposed that two formae speciales of *A. euteiches* be recognized: *A. euteiches* f. sp. *pisi*, which infects peas and beans, and *A. euteiches* f. sp. *phaseoli*, which infects beans but not peas. A sample of isolates of the former had radial growth rates on cornmeal agar of $\geq$10 mm/day at 32 C, and a difference between oogonium and oospore diameters of $\leq$6 μm, whereas the latter grew 1–3 mm/day at 32 C, and the respective diameter differences were $\geq$8 μm. *A. euteiches* f. sp. *phaseoli* causes more severe damage to beans than does *A. euteiches* f. sp. *pisi*. Both formae speciales infect alfalfa. Although all bean cultivars and breeding lines tested were susceptible to infection by *A. euteiches* f. sp. *phaseoli*, Wis. (RRR) 46 showed little damage, whereas all commercial cultivars tested were severely damaged by the pathogen.

Root rot is a major disease of snap beans. On the irrigated sandy soils of central Wisconsin, where over half of the state's snap bean acreage is located, losses due to root rot have become increasingly important in recent years.

Several pathogenic fungi incite root rot in beans. In the first report of bean root rot (2) *Fusarium martii* var. *phaseoli*, later renamed *F. solani* (Mart.) Appel & Wr. f. sp. *phaseoli* (Burk.) Snyd. & Hans., was identified as the causal agent. More recently, *Pythium* (Pringsh.) spp. also have been recognized as pathogens of bean roots in several areas (5,6,10). Both *Fusarium* (15) and *Pythium* spp. (5) have been reported to cause bean root rot in Wisconsin.

Aphanomyces euteiches Drechs. is an important pathogen of peas in Wisconsin and elsewhere in the midwestern United States. Although some studies (3,13) have indicated that *A. euteiches* can infect snap beans under laboratory conditions, *Aphanomyces* has not been reported as a pathogen of beans in the field. In isolations we made from field-grown beans in 1979-1980, however, an *Aphanomyces* sp. was frequently isolated from beans showing root and hypocotyl rot and was found to be pathogenic to beans (9). This fungus was compared with isolates of *Aphanomyces* obtained from peas to determine whether the two strains differ in host range and/or morphology. Host resistance to the strain of *Aphanomyces* from beans was also investigated.

MATERIALS AND METHODS

Pathogen isolates. Most of the isolates of *Aphanomyces* used in this study were recovered from field-grown beans and peas collected in central Wisconsin. Isolates of the bean strain of *Aphanomyces* were recovered from necrotic streaks on the hypocotyls of beans showing root rot symptoms. Most isolates of the pea strain of *Aphanomyces* were obtained from field-grown peas in central Wisconsin, but additional isolates were obtained from C. E. Windels, University of Minnesota, and from the American Type Culture Collection (ATCC #16409, originally deposited by J. L. Lockwood, Michigan State University). An *Aphanomyces* sp. isolated from alfalfa by McKeen (7) also was included in the study.

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Pathogenicity and host range. To test pathogenicity and host range of representative isolates of *Aphanomyces*, seeds of possible host species were planted in pasteurized soil (heated to 60 C for 30 min using aerated steam) infested with oospores of the pathogen. We produced oospores by growing the fungus for 3 wk in oatmeal broth, as described by Schneider (11). To separate oospores from the mycelium, it was comminuted in a blender with water, then further dispersed in a glass tissue grinder. The spore suspension was mixed into the soil with an air-powered spray gun to give a concentration of 200 oospores per gram of soil. The infested soil then was stored in closed plastic bags for 3 wk before being used in experiments. A separate batch of soil was prepared for each isolate of *Aphanomyces* that was used. Two isolates of the pea strain of *Aphanomyces* (P14 and S11) and two isolates of the bean strain of *Aphanomyces* (S2 and C1) were used in host range tests. Seeds of pea, alfalfa, beet, cabbage, oat, radish, and tomato, all known to be hosts of various *Aphanomyces* spp. (7,12,14), were planted in the infested soil. Beans and soybeans were also tested. Two 7.5-cm-diameter pots (replicates) were used for each combination of host species and isolate of *Aphanomyces*. Uninfested pasteurized soil was used for check treatments. The pots were placed in a greenhouse maintained at ~24 C and were watered lightly until the plants emerged. Thereafter, the soil was saturated daily until the end of the experiment. Three weeks after planting, roots were washed free of soil and examined microscopically for the presence of oospores in the tissue; those with no oospores were surface sterilized and plated on Bacto-water agar to determine whether infection had occurred. The experiment was repeated once.

Additional isolates of *Aphanomyces* were tested only for pathogenicity to peas and beans. These tests were performed by dipping roots of 7-day-old seedlings in a suspension of zoospores for ~2 min before transplanting to vermiculite. Zoospores were produced by the method of Mitchell and Yang (8), and the concentration was adjusted to ~1×10^5 zoospores per milliliter for use as inoculum. After inoculation, the plants were grown for 14 days at ~24 C, harvested, and evaluated for infection and damage.

Cultural and morphological characteristics. To determine radial growth rates of the isolates of *Aphanomyces*, a 7-mm plug was taken from the edge of an actively growing colony and transferred to a plate of cornmeal agar. Inoculated plates were incubated in the dark at the desired temperatures. Colonies were examined and the diameter (average of two measurements per plate) of each colony was measured every day for 7 days or until the plate was covered by growth. Rate of increase in colony radius was determined, taking the colony size at 24 hr after inoculation as the starting point. There were two replicate plates per treatment, and each experiment was

repeated at least once.

Morphological characters, including sizes of oogonia and oospores, were determined on cultures grown for 15–20 days on cornmeal agar at 20 C in the dark. Fifty spores of each isolate were measured.

Testing bean lines for resistance to *Aphanomyces*. Field experiments to screen bean lines for resistance to root rot caused in part by *Aphanomyces* were conducted in a naturally infested field containing *Pythium* spp. as well as *Aphanomyces* pathogenic to beans. Twenty-five commercial cultivars and 15 breeding lines were planted in replicated plots. Ratings of root rot severity were made 9 wk after planting. Ratings were on a 0–4 scale (0 = no disease, 4 = maximum severity), based on amount of root pruning and the extent of discoloration and flaccidity of roots and hypocotyls.

Lines that performed well in the field trial were tested for resistance to *Aphanomyces* in the greenhouse. Ten captan-treated seeds of each test line were planted in flats of pasteurized soil containing 150 oospores of the S2 isolate of *Aphanomyces* per gram of soil. Flats were watered lightly until plants emerged, then watered daily to saturation until plants were evaluated 3 wk after planting. Root and shoot disease severity was rated on a 0–4 scale. The experiment was repeated once.

Because testing of bean lines with oospore-infested soil is time-consuming, a quicker method of inoculating with zoospores was evaluated. For this test, zoospores of the S2 and C1 isolates of *Aphanomyces* were produced as above, and a dilution series of zoospore suspensions was prepared, providing concentrations of 10^2, 10^3, 10^4, and 10^5 zoospores per milliliter. Eight-day-old seedlings of three different bean lines were dipped in the zoospore inoculum for 2 min, then transplanted to vermiculite. The plants were placed in a greenhouse at ~24 C and watered daily for 2 wk. Roots and hypocotyls were then rated for disease severity.

RESULTS

Symptoms of naturally occurring root rot, including root destruction and necrotic streaking of the hypocotyl, were reproduced on beans grown in pasteurized soil artificially infested with oospores of isolates of *Aphanomyces* obtained from beans. *Aphanomyces* was reisolated from infected tissue, confirming its role as a pathogen.

Host range studies. As indicated by results shown in Table 1, bean isolates of *Aphanomyces* infected beans and alfalfa, but they did not infect any cultivar of peas tested. On the other hand, pea isolates of *Aphanomyces* infected peas (all cultivars), beans, and alfalfa. Appearance of beans and peas exposed to the two strains of *Aphanomyces* is shown in Figs. 1 and 2. Although beans exposed to the pea isolates were infected, the severity of root and hypocotyl rot was much less than in beans exposed to the bean isolates. There was no evidence of infection in peas exposed to the bean isolates, and attempts to isolate *Aphanomyces* from them were unsuccessful. Results (Table 1) show that alfalfa was more severely affected by the pea isolates than by the bean isolates. Radish, beet, and cabbage were only rarely infected by the pea isolates, with a restricted lesion at the collar of a small number of plants; oospores were produced in very low numbers. Soybean, oat, and tomato were apparently not infected by any isolate tested.

Cultural and morphological characteristics. Measurements of radial growth rate for the four isolates used in host range tests showed that the isolates of *Aphanomyces* from pea (P14 and S11)

TABLE 1. Host range of pea and bean isolates of *Aphanomyces*[y]

		Infection by *Aphanomyces euteiches*			
		f. sp. *pisi*		f. sp. *phaseoli*	
Host	Cultivar	P14	S11	S2	C1
Bean	Early Gallatin	+[z]	+	++	++
Alfalfa	Apollo	++	++	+	+
Pea	8221 Perfection	+++	+++	0	0
	Dark Skin Perfection	+++	+++	0	0
	Alaska 14a	+++	+++	0	0
	Early Sweet A45	+++	+++	0	0
	036A	+++	+++	0	0
Soybean	Marshall	0	0	0	0
Radish	Champion	(+)	(+)	0	0
Beet	Great Western	(+)	(+)	0	0
Cabbage	Golden Acre	(+)	(+)	0	0
Oat	Lodi	0	0	0	0
Tomato	Bonny Best	0	0	0	0

[y]Test conducted by planting seeds in pasteurized soil infested with oospores of the various isolates at the rate of 200 oospores per gram of soil.

[z]Infection ratings: +++ = plants killed; ++ = moderate to severe root damage, many oospores produced in tissue; + = slight root damage, oospores present; (+) = restricted lesions on small number of plants, oospores rare; and 0 = no infection, *Aphanomyces* could not be reisolated from tissue.

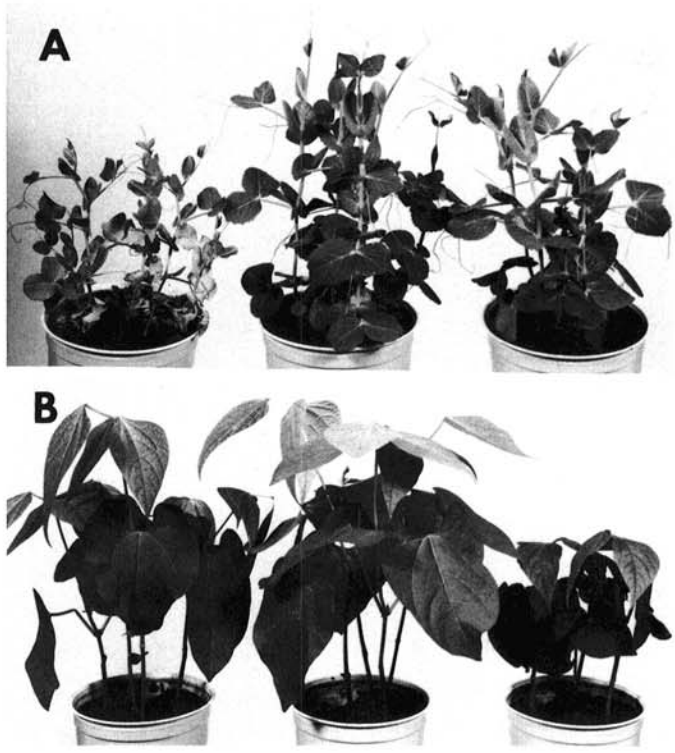

Fig. 1. Appearance of **A,** peas and **B,** beans grown for 3 wk in soil containing: left, oospores of *Aphanomyces* pea isolate P14; center, no inoculum; right, oospores of *Aphanomyces* bean isolate S2.

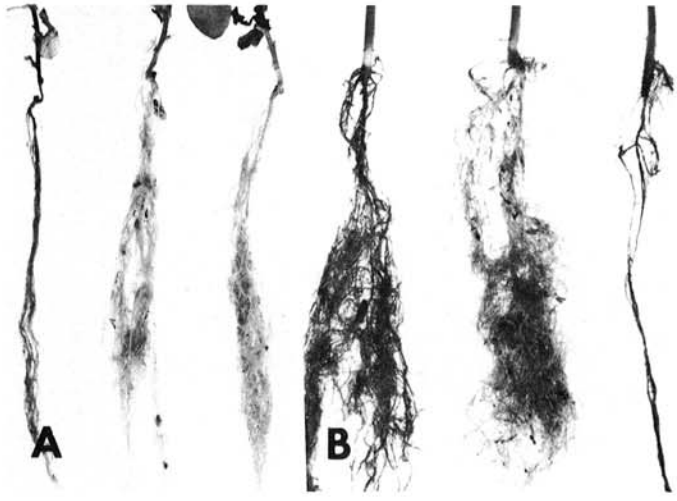

Fig. 2. Appearance of the roots of **A,** peas and **B,** beans grown for 3 wk in soil containing: left, oospores of *Aphanomyces* pea isolate P14; center, no inoculum; right, oospores of *Aphanomyces* bean isolate S2.

generally grew at a slightly greater rate than did the isolates from bean (C1 and S2). Average values for the pea isolates and bean isolates are compared in Fig. 3. All isolates showed maximum growth rate at 28 C and no growth at 35 C. The greatest difference between the two strains was evident at 32 C, where pea isolates grew at least five times as fast as bean isolates.

Morphological characteristics of the bean isolates C1 and S2 are as follows. Hyphal diameters range from 4 to 12 μm. Antheridia are generally diclinous, with monoclinous antheridia very rarely present. The number of antheridia per oogonium varies from one to four, with most oogonia having two or three antheridia attached. Oogonial diameters of isolates C1 and S2 range from 23 to 44 μm, averaging 31.8 and 32.7 μm, respectively. The mature oogonial wall shows a sinuous inner contour. Oospore diameters in isolates C1 and S2 range from 17 to 28 μm, averaging 22.4 and 23 μm, respectively. These characteristics differ from those of the pea isolates (P14 and S11) only in that the oogonia of the latter are slightly smaller than those of the bean isolates (C1 and S2). Oospore sizes, however, are not markedly different among these four isolates. Therefore, the oospores of the isolates of *Aphanomyces* from bean are more markedly aplerotic than those of the isolates from pea.

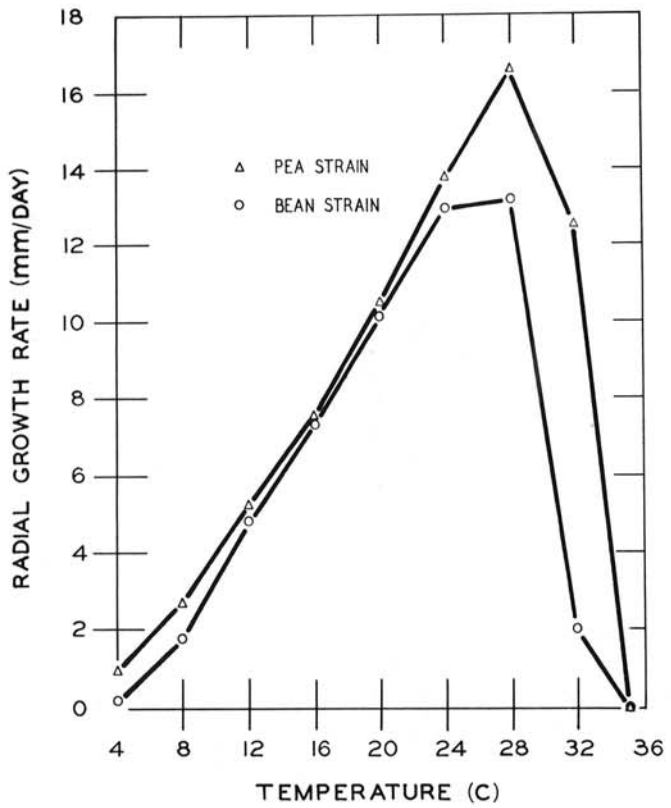

Fig. 3. Growth rates of pea and bean strains of *Aphanomyces euteiches* on cornmeal agar at various temperatures. Differences between strains are significant ($P = 0.05$) at 4, 8, 28, and 32 C. Values for pea strain are averages for isolates P14 and S11; values for bean strain are averages for isolates S2 and C1. Four replicates were used for each isolate at each temperature.

To determine whether the bean strain of *Aphanomyces* could be consistently differentiated from the pea strain by oogonial size and growth rate in culture at 32 C, measurements taken on seven isolates of *Aphanomyces* from field-grown beans were compared with those taken on six Wisconsin isolates of *Aphanomyces* from field-grown peas. Isolates of *A. euteiches* obtained from Minnesota and Michigan (isolates A9 and ATCC 16409, respectively), as well as an isolate of *Aphanomyces* from infected alfalfa in Ontario (7), were also included. Pathogenicity of the isolates to peas and beans was assessed by the zoospore dip inoculation procedure.

All *Aphanomyces* cultures isolated from bean hypocotyls were similar in their pathogenicity pattern and distinct from the other isolates in being nonpathogenic to peas (Table 2). Isolates of *Aphanomyces* from beans were also consistent in their low rate of growth at 32 C compared to that of the pea isolates. There was no consistent distinction between the two groups of isolates with regard to diameter of oospores or oogonia. However, an analysis of the difference in diameter between oogonium and oospore (aplerotic zone) showed that this zone was significantly larger in the bean strain than in the pea strain (Table 2). This larger aplerotic zone was easily distinguishable, even without measurement, in the case of some of the isolates. But in the case of others, measurement was necessary to verify the larger aplerotic zone of the bean isolates. Isolate 460, obtained from alfalfa (7), was pathogenic to peas, but not as virulent as the *A. euteiches* pea isolates tested.

Testing bean lines for resistance to *Aphanomyces*. Isolations from diseased beans in the field test showed that plants were infected by both *Aphanomyces* and *Pythium* spp. Although all commercial bean cultivars tested in the field were severely damaged by these pathogens, three breeding lines, Wis. (RRR) 36, Wis. (RRR) 46 (4), and State Half Runner, showed less damage than the others (Table 3). These three lines, as well as several cultivars that were severely diseased in the field plot, were tested in oospore-

TABLE 2. Pathological, cultural, and morphological characteristics of bean and pea strains of *Aphanomyces euteiches*

Isolate	Host source	Geographic source	Pathogenicity[w]		Growth at 32 C (mm/day)	Spore diameters (μm)[x,y]		
			Bean	Pea		Oogonium	Oospore	Aplerotic zone[z]
S7	Bean	Hancock, WI	+	0	1.3	32.0 a	22.3 bc	9.7 a
S2	Bean	Hancock, WI	+	0	1.9	32.7 a	23.0 cd	9.7 a
C1	Bean	Nekoosa, WI	+	0	2.2	31.8 a	22.4 bc	9.4 ab
Ad-A	Bean	Nekoosa, WI	+	0	2.2	28.5 b	20.5 a	8.0 b
KB	Bean	River Falls, WI	+	0	1.9	29.5 b	21.2 ab	8.4 b
FL	Bean	Nekoosa, WI	+	0	2.9	29.7 b	21.7 b	8.0 b
VE4	Bean	Nekoosa, WI	+	0	1.2	29.6 b	21.6 b	8.0 b
N2	Pea	Nekoosa, WI	+	+	13.2	29.9 b	23.9 de	6.0 c
L29	Pea	Nekoosa, WI	+	+	10.6	29.1 b	23.6 de	5.5 cd
A9	Pea	Minnesota	+	+	18.5	28.5 b	23.2 cd	5.3 cde
S11	Pea	Hancock, WI	+	+	12.7	26.7 c	21.4 ab	5.3 cde
AR1	Pea	Arlington, WI	+	+	15.4	29.4 b	24.3 b	5.1 cde
P14	Pea	Plainfield, WI	+	+	13.7	26.9 c	22.1 bc	4.8 de
AR2	Pea	Arlington, WI	+	+	13.7	28.8 b	24.0 de	4.8 de
16409	Pea	Michigan	0	+	13.2	30.0 b	25.9 f	4.1 e
460	Alfalfa	Ontario	+	+	10.1	29.1 b	24.2 e	4.9 de

[w] Pathogenicity determined by dipping roots of 7-day-old seedlings in a suspension containing 10^5 zoospores per milliliter, then growing plants for 14 days before assessing infection.

[x] Measurements taken on 50 spores of each isolate grown on cornmeal agar in the dark for 15–20 days at 20 C.

[y] Values within a column followed by the same letter do not differ as determined by Duncan's new multiple range test, $P = 0.05$.

[z] Difference between oogonial and oospore diameters.

TABLE 3. Disease severity of bean lines and cultivars in field and greenhouse root rot tests

Bean line or cultivar	Disease severity rating[w]	
	Field trial[x]	Greenhouse test[y]
Wis (RRR) 46	1.2 a[z]	1.1 a
Wis (RRR) 36	1.3 a	1.7 a
State Half Runner	1.2 a	2.5 bc
Montcalm (kidney bean)	···	3.2 c
Torrent	2.2 b	3.4 c
Bush Blue Lake 94	2.3 bc	3.7 c
Lancer	2.9 c	3.8 c
Early Gallatin	2.5 c	3.9 c

[w] Disease severity ratings are averages of root and hypocotyl ratings; 0 = no disease and 4 = maximum severity.
[x] Field trial was conducted in a naturally infested field containing both *Pythium* spp. and *Aphanomyces*; values are means of four replicates, 20 plants per replicate.
[y] Greenhouse test: plants grown for 3 wk in pasteurized soil artificially infested with oospores of *Aphanomyces* (isolate S2) at 150 oospores per gram of soil. Values are means of two replicates, 10 plants per replicate.
[z] Values within a column followed by the same letter do not differ as determined by Duncan's new multiple range test, $P = 0.05$.

infested, pasteurized soil to assess their reaction to the bean strain of *Aphanomyces* (isolates C1 and S2) alone. In these tests, Wis. (RRR) 46 and Wis. (RRR) 36 showed much less damage than any other line or cultivar tested (Table 3 and Fig. 4). State Half Runner showed an intermediate amount of damage, and the commercial lines Torrent, Lancer, Early Gallatin, and Bush Blue Lake 94 all showed severe damage. Kidney bean cultivar Montcalm also was severely affected.

Inoculation of Wis. (RRR) 36, State Half Runner, and Early Gallatin with zoospore inoculum gave results similar to those in oospore-infested soil (Table 4) in that Wis. (RRR) 36 showed slight, State Half Runner intermediate, and Early Gallatin severe damage. The concentration which resulted in the best separation of host reactions was 10^3 zoospores per milliliter.

DISCUSSION

The strain of *Aphanomyces* associated with the root rot complex of snap beans in Wisconsin is an important and destructive pathogen on this crop, inciting root and hypocotyl rot. It is also pathogenic to alfalfa, but does not infect peas.

Although all commercial cultivars of beans tested were susceptible to the bean strain of *Aphanomyces,* the breeding lines Wis. (RRR) 36 and Wis. (RRR) 46 were resistant to the disease in the field and greenhouse. Although these lines were susceptible to infection by the pathogen, they showed little necrosis of root or hypocotyl. These lines were developed through field testing in central Wisconsin and were probably exposed to inoculum of the bean strain of *Aphanomyces* during the breeding program.

Taxonomic placement of the bean strain of *Aphanomyces* is problematical. Morphologically the strain is closest to *A. euteiches,* according to the characters used by Scott (12). However, there are slight cultural and morphological differences that distinguish it from the isolates of *A. euteiches* from peas that we studied. Perhaps of more importance is the fact that the bean isolates do not infect peas. Infection of and severe damage to peas is, functionally, the key species character of *A. euteiches* for most workers and is also a key character in Scott's Key (12).

Since the bean strain is similar to the pea strain of *A. euteiches,* but differs from it in host range, we propose that this strain should be referred to as a forma specialis (special form) of *A. euteiches.* Forma specialis is defined as follows by Ainsworth (1): "an intraspecific category for taxa characterized from a physiological standpoint (esp. host adaptation) but scarcely or not at all from a morphological (Bot. Code, Art. 4)." The relationship of the bean strain to the pea strain of *Aphanomyces euteiches* seems well described by this forma specialis designation. The usefulness of the forma specialis designation is in recognizing distinct populations of

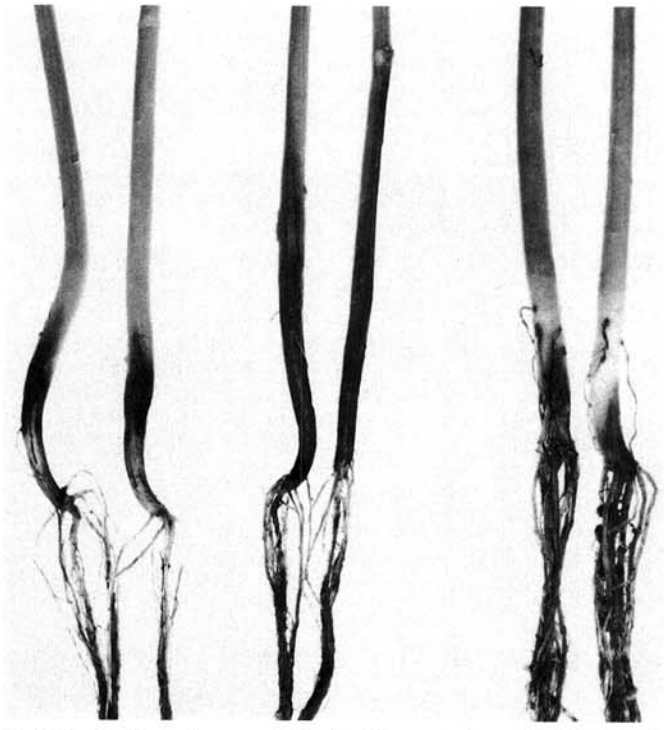

Fig. 4. Roots of bean lines grown for 3 wk in pasteurized soil infested with oospores of the bean strain of *Aphanomyces.* Cultivars: left, State Half Runner; center, Early Gallatin; and right, Wis. (RRR) 36.

TABLE 4. Reaction of bean lines to inoculation with zoospores of *Aphanomyces euteiches* f. sp. *phaseoli* isolates S2 and C1

Bean line or cultivar	Disease severity ratings[y] after inoculation at indicated zoospore concentration			
	10^2/ml	10^3/ml	10^4/ml	10^5/ml
Wis (RRR) 36	0.4 a[z]	0.7 a	1.2 a	1.3 a
State Half Runner	1.4 b	2.1 b	2.0 b	2.5 b
Early Gallatin	3.0 c	3.3 c	3.6 c	3.6 c

[y] Severity values are averages of root and hypocotyl ratings (0–4); data from two trials, 10 plants per treatment per trial.
[z] Values within a column followed by the same letter do not differ as determined by Duncan's new multiple range test, $P = 0.05$.

an organism which, although morphologically similar, are physiologically distinct in a way which is important to those working with the organism. We propose that the morphological species *A. euteiches* be separated into two formae speciales as follows: *A. euteiches* Drechs. f. sp. *pisi* Pfend. & Hag., to include those isolates which infect and cause severe damage to *Pisum sativum* L. and which may also infect and cause slight damage to roots of *Phaseolus vulgaris* L.; and *A. euteiches* Drechs. f. sp. *phaseoli* Pfend. & Hag., to include those isolates that do not infect *Pisum sativum* but which do infect and cause severe damage to *Phaseolus vulgaris.* In the study reported here, isolates of *A. euteiches* f. sp. *phaseoli* were also distinct from isolates of *A. euteiches* f. sp. *pisi* in having slower radial growth rates in culture at 32 C, as well as oospores which have a slightly larger aplerotic zone than those of *A. euteiches* f. sp. *pisi.*

We hope that recognition of formae speciales in *A. euteiches* will be useful to pathologists who work with this species and may spur additional investigations into the nature of the differences in populations among and within what are presently defined as species of this important genus.

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