

Infection of Wheat Embryos by *Pythium* Species During Seed Germination and the Influence of Seed Age and Soil Matric Potential

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ABSTRACT

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Pythium spp. (mainly *P. irregulare* and *P. ultimum* var. *sporangiiferum*) were isolated from the scutellum region of 30–55% of random winter wheat seedlings dug 3 wk after sowing (just emerged) from five sites, yet stand establishment was not a problem at any of the sites. The presence of *Pythium* spp. in the scutellum region was traced to embryo infections that occurred during the first 2 days after sowing. In pot experiments, infection of wheat embryos by *Pythium* spp. at 2 days after planting (20 C) occurred maximally (45%) at -0.1 bar matric potential and was essentially prevented at -0.4 to -1.2 bar. Seedlings produced from seeds pregerminated for 48 hr on moist filter paper in petri dishes then transplanted into *Pythium*-infested soil showed no evidence of leaf distortion or stunting and were identical to

those produced from seeds sown directly into *Pythium*-free (pasteurized) soil. The older the seed (e.g., 3–7 yr old), the greater the incidence of seed decay caused by *Pythium* spp. An exception was a 7-yr-old seedlot of cultivar Daws stored at a constant 5 C, which emerged 87.5% in *Pythium*-infested soil, in contrast to a portion of the same seedlot stored at the normal fluctuating summer/winter temperatures, which emerged 35% in *Pythium*-infested soil. Both seedlots emerged 100% in *Pythium*-free soil. Treatments of the old seed with carboxin and thiram, captan, or metalaxyl improved emergence, but the seedlings were still smaller than those produced from new seed.

Additional key word: soilborne pathogen.

Pythium root rot, caused by up to 10 species of *Pythium* (2), can be a major production constraint for winter wheat (*Triticum aestivum* L.) in areas of eastern Washington and northern Idaho receiving 40–45 cm of precipitation or more each year (5). Wheat yields are commonly greater by 15–25% where the population of *Pythium* species is reduced or nearly eliminated by treatment of the soil with solarization or fumigants (3,5,6). A 50–75% reduction in the population of *Pythium* spp. in only the top 5 cm of soil, by burning a layer of straw on the soil surface, resulted in a 15–20% greater yield of wheat (5). In greenhouse tests, seedlings typically emerged more slowly and showed obvious stunting and twisting of the first true leaves (but generally did not die) in heat-treated soil reinfested with *Pythium* (5).

Stand establishment usually is not a problem for wheat in *Pythium*-infested soil (3,5). However, the fact that most wheat seedlings emerge in the field (3,5) does not mean the seeds are not infected by *Pythium* during germination. Because seeds usually are planted 3 to 4 cm deep, the growth and yield response of wheat in soil with the population of *Pythium* reduced only in the top 5 cm could be explained by greater seedling vigor owing to less seed (embryo) infection. The incidence and severity of seed or embryo infections could also be affected by quality and age of the seed and soil moisture status. Aged soybean seeds are more leaky (lose more electrolytes when submerged in water) than new seeds (1,12), and aged corn seeds are more vulnerable to decay by *Pythium* (9). This paper reports results of studies designed to determine the occurrence and importance of seed infections for wheat and the relationship of these infections to soil moisture status and age of seed. A preliminary report has been published (4).

MATERIALS AND METHODS

Field studies. Seedlings of cultivar Hill-81 were dug 29 October 1985 (just emerging) near Rockford, WA (southern Spokane County; about 10 km from the Washington-Idaho border), from each of three sites in a field cropped earlier that year to spring wheat and from each of two sites in an adjacent field cropped earlier that year to lentils. The three sites in the first field had been, respectively, burned and then direct drilled (no tillage), spring-wheat stubble left standing and direct drilled, and stubble incorporated by tillage and the site seeded conventionally into a prepared seedbed. The two sites in the lentil field were, respectively, direct drilled and seeded conventionally into a prepared seedbed. All seeds and seedlings were removed from each of three, 30- to 40-cm lengths of row per drill strip, five drill strips per site. The plants from each drill strip (representing at least 90 cm of row) were bulked and washed, then 25 were selected at random for plating. The shoot, root, and seed piece (remnant endosperm) were removed with a scalpel, leaving the scutellum and a piece of tissue only 1 to 2 mm long (from the region of root-shoot transition) for plating on water agar amended with rifampin at 100 μ g/ml.

To determine if *Pythium* infects the embryos of wheat seeds during germination in the field, we planted seeds of cultivar Hill-81 on each of three dates in replicate plots and then dug 1 and 7 days later (9 days in the case of the third planting date), and the embryos and endosperms were plated out separately. The plots were seeded with an HZ-type drill (hoe openers) in four-row plots about 4 cm deep in rows 40 cm apart on 16 September, 2 October, and 11 October 1985. Soil temperatures on the days of sowing were, respectively, 13/10 (max/min), 15/10, and 8/6 C. There were five replicates, and the rows were 5 m long in a randomized block design. The site was on the Washington State University Plant Pathology Farm and had been chemical fallowed (not cultivated;

all weed control by herbicides) the previous year. The population of *Pythium* was estimated at 160 propagules per gram in the top 15 cm of soil, determined by plate-counts as previously described (5). Rain began shortly after the plot was seeded on 16 September, and 24.5 mm was received as an intermittent drizzle over the next 48 hr. No rain fell for 12 days before and 5 days after the second sowing. About 9 mm of precipitation was received 7 October, but the next measurable rain (6.3 mm) did not occur until 12 days after the third planting. No fungicide treatment was applied with the seed.

One hundred swollen and germinated seeds (hereafter referred to as seedlings) were dug from random locations in four strips (totaling about 4 m) of row per plot, seeding date, and sampling time. The seedlings were separated from the soil by washing in the case of the first seeding date and by hand picking from the soil in the case of the second and third seeding dates, when the soil was drier. All seeds damaged or not germinated were discarded, and some seedlings were preserved for future microscopic examination. Only 50 of the 100 seedlings dug from each plot were processed further (250 per seeding date and sampling time); these were cleaned by spraying on a screen with a strong jet of water, washed in cheesecloth bags overnight in a stream of running tap water, given two brief rinsings in sterile water, then placed on an agar medium.

For the first planting date, 50 embryos and the corresponding 50 endosperms representing each replicate were placed on the MPVM *Pythium*-selective medium of Mircetich (11) amended with rifampin at 100 µg/ml. For the second and third planting dates, 50 embryos but only 20 endosperms were used per replicate plot. Embryos from the 2-day-old seedlings were easily removed with a sterile scalpel; they had usually swelled to an overall length of about 1 mm and came free without the scutellum. For an endosperm sample, about 1 mm³ of solid material was removed with the point of a scalpel from the central part of the seed. Embryos from 7-day-old seedlings had developed one or more roots, which were removed by cutting with a sterile scalpel, and a shoot up to 1 cm long, which was cut back to about 5 mm. At 7 and 9 days, the scutellum invariably remained attached to the embryo and was also placed on the MPVM. The endosperm was no longer solid at 7 and 9 days after planting, and it was therefore necessary to put part of the seed integument or testa lining the endosperm on the medium. The plates were incubated at 20 C for 48 hr, and the frequency of the pieces yielding *Pythium* then determined.

Identification of *Pythium* spp. Random isolates of *Pythium* obtained from seedlings in the field study were transferred as hyphal tips to Difco corn meal agar. These were maintained as stock cultures at 20 C for subsequent identification as described by Chamswang and Cook (2).

Greenhouse studies with known soil matric potentials. The influence of soil matric potential on embryo infection was studied in the greenhouse by using soil from the site near Rockford, WA, cropped to lentils that year (population of *Pythium* estimated at 650 propagules per gram). The soil was collected from the top 15 cm within a 10-m-diameter area of the field on 30 October 1985. Rain had fallen at the site 7 days earlier, and the top 30 cm was only slightly drier than field capacity (-0.45 bar) at the time of sampling.

In the first study, eight different water contents were tested in three consecutive experiments carried out over a 1-mo period using aliquots of the same soil. Each water content was achieved by placing the soil in 15-cm-diameter pots (about 1 kg of soil/pot) after different periods of air drying during November in a nonheated shed or by adding water after potting to obtain soils wetter than -0.45 bar. The eight water contents resulted in matric potentials of near zero (saturated), two samples each at -0.1 bar, and the other five at -0.075, -0.25, -0.45 (original matric potential), -1.25, and -1.5 bars, respectively. The matric potentials were determined with tensiometers placed in the soil and confirmed by a moisture release curve determined with a pressure-plate apparatus. Each pot was sown 2.5 cm deep with 30 seeds of cultivar Hill-81. To obtain the near-saturation treatment, soil at -0.45 bar was placed in the pots and watered immediately after sowing with an additional 110 ml of water per pot, applied at the

surface, and allowed to move as a wetting front through the soil. Five pots (replicates) were sown per moisture status and sampling time and were arranged on a greenhouse bench at 20 C in a completely randomized design for each experiment. Seeds were removed at 2, 4, and 6 days after planting, and isolations attempted from 20 embryos and corresponding 20 endosperms per replicate as described for the field study. Because the results were comparable, the three experiments are treated here as one.

A second study was conducted with soil from the same field near Rockford, WA, collected in April 1986, the morning after a rain, and placed immediately in 400-ml paper cups in preparation for sowing. The soil when placed in the cups had a water content that corresponded to about -0.1 bar matric potential, inferred from a drying-down curve determined with the pressure plate apparatus. Five replicate cups with soil at this initial matric potential were placed in a plastic bag to prevent further drying. The remaining cups were placed on a greenhouse bench and the soil allowed to air dry from the surface for different lengths of time to produce matric potentials (at the depth of sowing) of approximately -0.3 to -0.5, -0.7 to -0.8, and -1.0 to -1.2 bars. Seeds were placed 1.5 cm deep and removed 48 hr later together with soil at the seed depth for determination of the water content. These water contents were then used to infer the matric potentials more precisely from the moisture-release curve.

Pregermination of seeds to avoid embryo infections. Evidence for the significance of embryo infections during the first 24-48 hr after sowing to seedling vigor was obtained by pregerminating wheat seeds on wet filter paper in petri dishes for 24 and 48 hr at 15 C and then transplanting them into *Pythium*-infested and *Pythium*-free (treated with moist heat at 60 C/30 min [5]) soils. The checks were seeds planted into the respective soils without pregermination. Two experiments were conducted, each with four replicates and four 4-cm × 21-cm tubes (Ray Leach Cone-tainer Co., Canby, OR) for each seed × soil treatment and replicate. Two seeds were planted per tube. Incubation during seedling emergence was at 15 C.

Experiments with seeds of different ages. Four different seedlots for each of the cultivars Daws and Nugaines and harvested, respectively, in 1985, 1984, 1983, and 1981, were tested in 1986 to determine the relationship between age of the seed and damage by *Pythium* to emerging seedlings. Two other lots of Daws, from the same 1979 harvest but stored for 7 yr at either a constant 5 C or at more typical uncontrolled summer and winter temperatures, were also compared in 1986. Seeds of each lot were sown in *Pythium*-free (pasteurized) soil and also in pasteurized soil reinfested with a mixture of oospores of *P. ultimum* Trow var. *sporangiiferum* Drechs. and *P. irregulare* Buisman at about 500 propagules per gram of soil. All seedlots were tested in a 7-day blotter test conducted independently by the Washington State University Seed Laboratory. Seeds for each cultivar and age were sown without treatment into the pasteurized and *Pythium*-infested soils contained in the tubes. In other tests, 1981 and 1985 Nugaines seeds treated with either a mixture of 17% carboxin and 17% thiram (= Vitavax 200), captan, metalaxyl, or left untreated were compared by sowing into the pasteurized and *Pythium*-infested soils. Each seedlot × soil × seed treatment was replicated four times, with four tubes and two seeds per tube per replicate. Emergence was measured at 5 and 10 days, and shoot length was measured at 14 days after sowing.

RESULTS

Quantitative recovery of *Pythium* from seedlings at emergence.

When the small fragments representing the scutellum and transitional tissue between root and shoot were plated on water agar amended with rifampin, *Pythium* was recovered from 50-55% (average for 125 plants for each site) of the 3-wk-old seedlings dug from the two sites direct-drilled into lentil and standing wheat stubble (not burned), respectively, 45% of the seedlings dug from the site direct-drilled into burned stubble and 30-35% of the seedlings from each of the two sites tilled and seeded conventionally.

Incidence of embryo and endosperm infection in the field. *Pythium* was recovered from 12% of the embryos and less than 1% of the endosperms of seeds dug 2 days after the first planting date (Table 1). By 7 days, the percentage of infected embryos was unchanged, but more endosperms had become infected (Table 1). In contrast, *Pythium* was recovered from only 1% or fewer of the embryos and endosperms of seeds dug from the drier soil 2 and 7 (or 9) days after the second and third planting dates (Table 1).

Identity of *Pythium* spp. About 90% of the isolates obtained at random from the seedlings were fast-growing types and were identified as either *P. ultimum* var. *sporangiferum* or *P. irregulare*. The remaining slow-growing types were not identified.

Influence of soil matric potential on embryo and endosperm infections. The highest percentage of embryo infections (about 45%) occurred at about -0.1 bar matric potential in the soil obtained in late October 1985, from the lentil field near Rockford (Fig. 1). This incidence of embryo infection was slightly higher than that attained with the same soil watered immediately after sowing (near or at saturation during the early stages of seed germination). Very little infection of embryos occurred in soil drier than -0.4 to -0.5 bar. Virtually identical results of maximal infection at -0.1 bar, slightly less than maximal in saturated soil, and little infection in soil drier than -0.4 to -0.5 bar were obtained when the experiment was repeated with soil obtained from the same field in April 1986.

Influence of pregermination of seeds on emergence and seedling vigor. Seeds planted directly (no pregermination) into *Pythium*-infested soil produced seedlings that were shorter and of more variable heights compared with those in *Pythium*-free soil (Fig. 2). This difference in emergence and appearance of the seedlings was less apparent if the seeds were pregerminated for 24 hr before

planting and nonexistent if the seeds were pregerminated for 48 hr before planting (Fig. 2).

Relationship of seed age and seed treatment to *Pythium* damage. All seedlots, regardless of cultivar and age, rated 92-99% "strong sprout" in the blotter test performed by the Washington State University Seed Testing Laboratory, and 93.7-100% emerged as seedlings within 7 days (at 13-15 C) after sowing in pasteurized soil (Fig. 3; Table 2). In contrast, there was an inverse relationship between age of the seed and seedling emergence in the nontreated soil, with the highest percentages of emergence recorded for seeds 1 to 2 yr old and the lowest for seeds 3, 5, and 7 yr old (Fig. 3; Table 2). An exception was the Daws seed stored for 7 yr at 5 C, which emerged about as well as 1-yr-old Daws seed when planted in *Pythium*-infested soil. Another exception was the 3-yr-old Daws, which produced fewer seedlings than the 5-yr-old Daws seed. Treatment of the 5- and 1-yr-old Nugaines seeds with any of the three fungicides, carboxin and thiram, captan, or metalaxyl again resulted in over 90% emergence regardless of age (Fig. 4), although the seedlings produced with the 5-yr-old seed were generally of smaller stature.

DISCUSSION

Wheat seeds become infected in the embryo region during the first 2 days after sowing in suitably moist soil but still produce seedlings that emerge under field conditions. Such "nonlethal infections" can account for why *Pythium* spp. were recovered from the scutellum region of 30-55% of random seedlings dug from commercial fields near Rockford, WA, 3 wk after sowing. In the plots at Pullman, an average of 12.4% of embryos were infected by

TABLE 1. Incidence of wheat seed embryo and endosperm infections by *Pythium* species at three dates of sowing in a field plot near Pullman, WA, at 2 and 7 (or 9) days after sowing in 1985

Date of sowing	Days after sowing	Rainfall ^b (mm)	Infection per seed part ^a	
			Embryo (%)	Endosperm (%)
16 Sept	2	13.8	12.4	0.4
	7	24.5	14.4	4.8
2 Oct	2	0	0.4	0
	7	0	1.6	1.0
11 Oct	2	1.3	0	0
	9	0	2.4	0

^a Each value is the average for 50 embryos and 20 endosperms (50 endosperms for wheat seeded 16 September) for each of five replicate plots per seeding and sampling date.

^b Cumulative rainfall during the 2 or 7 (9) days after sowing, as recorded from the hour of sowing.

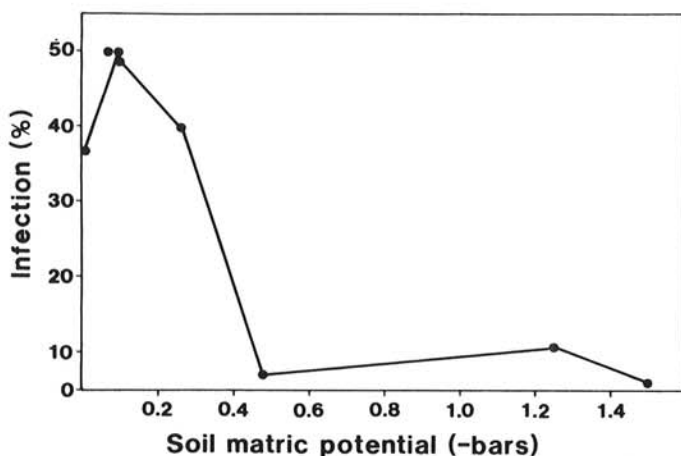


Fig. 1. Relationship between soil matric potential in pots of soil and percentage of infection of embryos of wheat seeds by *Pythium* spp. 2 days after sowing in the soils at the indicated matric potentials maintained at 20 C in the greenhouse.

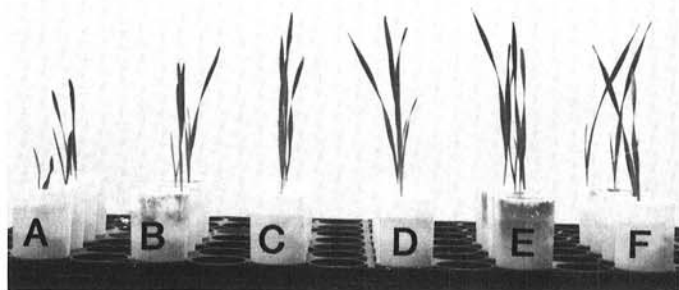


Fig. 2A-F. Seedlings of Daws wheat grown from 1-yr-old seed in *Pythium*-infested (A-C) and *Pythium*-free (D-F) soil. The seeds were sown directly (A and D) or after incubation (pregermination treatment) for 24 (B and E) and 48 hr (C and F) on wet filter paper in petri dishes.

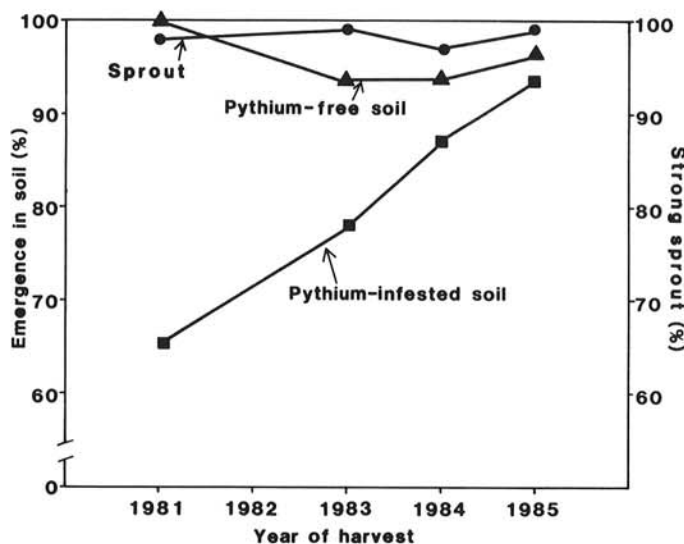


Fig. 3. Wheat seedling emergence in soil infested with *Pythium ultimum* var. *sporangiferum* and *P. irregulare* combined at 600 propagules per gram of (*Pythium*-infested) soil and in pasteurized (*Pythium*-free soil) and germinability of the same seed lots in a blotter test (strong sprout, percent).

TABLE 2. Wheat seedling emergence and height in soil infested with *Pythium ultimum* var. *sporangiferum* and *P. irregulare* combined at 600 propagules per gram (+P) and in pasteurized soil (-P) and the relationship to age and germinability of the seeds in a blotter test (strong sprout, present)

Cultivar	Seed age ^z	Strong (%)	Seedling response ^y			
			Emergence (%)		Height (cm)	
			+P	-P	+P	-P
Experiment 1						
Daws	1985	94	84.4 a	100.0 a	21.7 a	22.8 a
	1984	95	87.5 a	100.0 a	20.5 ab	21.8 ab
	1983	92	65.6 b	96.9 a	18.2 b	20.5 c
	1981	98	84.4 a	100.0 a	20.3 ab	21.0 bc
Experiment 2						
Daws	1985	...	90.0 a	97.5 a	15.7 a	18.0 a
	1981	...	90.0 a	91.0 a	13.9 abc	17.2 a
	1979	...	35.0 b	100.0 a	11.5 bcd	16.1 a
	1979-5C	...	87.5 a	100.0 a	15.3 a	17.1 a

^yEach value is the average for five replicates, eight seeds (four tubes with two seeds sown per tube) planted per replicate. Data analyzed by analysis of variance. Values within each column followed by the same letter are not significantly different by Duncan's multiple range test at $P = 0.05$.

^zIndicates year of harvest. 1979-5C was the same lot originally as 1979, but was stored at 5 C.

only 2 days after planting on 16 September and when rain fell during most of the 2-day germination period. A maximum of 45% of the embryos were infected by 2 days after sowing in field soil contained in pots (or cups) on a greenhouse bench at 20 C, which agrees with the 30-55% of scutellum infections in the same field from which the soil was obtained. The three- to fourfold higher incidence of scutellum (or embryo) infection in the fields (or soil removed from one of the fields) near Rockford than in the plots at Pullman may be the result of the much higher population of *Pythium* at the Rockford (650 propagules per gram of soil) than at the Pullman (160 propagules per gram) site. The major species at the two sites were *P. ultimum* var. *sporangiferum* and *P. irregulare*; both were shown previously (2) to infect seeds as well as roots of wheat seedlings.

Previous studies (3,5) have failed to demonstrate a significant or consistent loss of stand for winter wheat caused by *Pythium* under Pacific Northwest conditions. This situation holds true in spite of the ubiquitous and generally high populations of this pathogen complex in wheat-field soils of the region (5). However, while generally not a factor to stand establishment (plant density), embryo infections by *Pythium* may have a major effect on early seedling vigor. The variable stunting of seedlings and especially the abnormally short and twisted first true leaves of seedlings produced in *Pythium*-infested soil (3,5) apparently is the result of early embryo infections; seeds pregerminated for only 2 days on moist filter paper then transplanted to soil infested with *Pythium* showed none of these symptoms and were indistinguishable from the healthy seedlings produced in *Pythium*-free soil. The reduced seedling vigor caused by embryo infections together with subsequent destruction by *Pythium* of rootlets and root hairs (5) can account for shorter stature of adult plants, lack of tillering, and lower yield of winter wheat when *Pythium* is not controlled.

The only significant incidence of embryo infection in the field plots at Pullman occurred with the first planting date when rain fell during most of the 48-hr period after sowing. Soils were not cooler until the third planting date at Pullman, hence temperature cannot account for the near-failure of embryo infections in these later planting dates. Moreover, D. Ingram (*personal communication*) has shown that *P. ultimum* var. *sporangiferum* and *P. irregulare* both infect wheat embryos down to 5 C, and that the incidence of embryo infection by these two fungi is the same between 5 and 25 C when temperature is expressed as degree days using a base of 0 C. In the greenhouse at 20 C, embryo infection by 2 days (40 degree days) occurred maximally in soils at -0.1 bar matric potential but was essentially prevented in soils drier than -0.4 to -0.5 bar. The results of the Pullman field trial indicate further that while matric potential may be too low for embryo infections at some planting

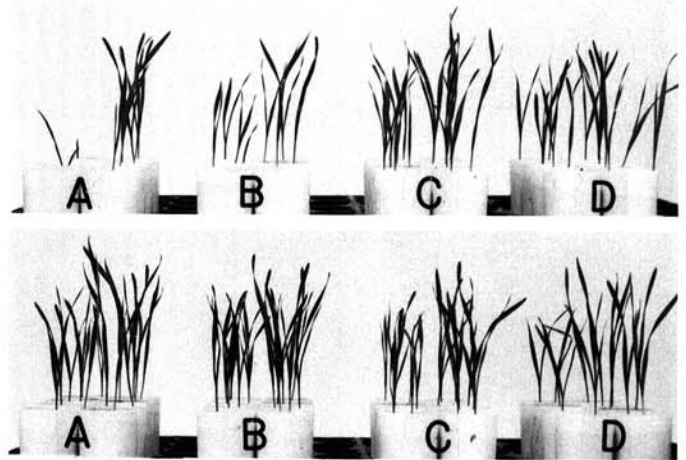


Fig. 4A-D. Seedlings of Nugaines wheat grown from 5-yr-old (left side of each pair) and 1-yr-old seed in *Pythium*-infested (top) and *Pythium*-free soil (bottom). The seeds were not treated (A) or treated with captan (B), metalaxyl (C), or a mixture of 17% carboxin and 17% thiram (D).

dates, wheat seeds may still germinate in such soil. One method to minimize embryo infections is, therefore, to plant when the soil is still likely to be moist enough for seed germination but too dry for infections by *Pythium*. The wettest soil in our field trial occurred with the earliest planting date, but, more commonly in the Inland Pacific Northwest, growers can expect well-drained seedbeds in September but not in October.

In general, the older the seed the lower the percentage of seedling emergence in the *Pythium*-infested soil, yet 92-99% of the seeds were rated as "strong sprout" by the WSU Seed Laboratory, and about this same percentage of seeds produced seedlings in the pasteurized soil. Koehler (9) showed for corn that emergence was 85, 55, and 40% for seeds 0.5, 1.5, and 2.5 years old, respectively, and 100, 99, and 98% for the same lots treated with thiram. Treatment of the 1981 and 1985 Nugaines seeds with either carboxin and thiram, captan, or metalaxyl resulted in relatively good seedling emergence for both ages. This finding is further evidence that the failure of the older seeds to emerge in natural soil is due to infections by *Pythium*. This finding also indicates the importance of using a seed treatment fungicide if older seed is to be planted. However, the results reveal just as clearly that using new wheat seed with or without a seed treatment fungicide may provide as good or better control of *Pythium* damage than old seed treated with fungicide.

Possibly, the seeds of all lots become embryo-infected at about the same frequency, but older seed is less vigorous, has a slower rate of germination, or is more sensitive to embryo infections. Alternatively, seeds are known to release (leak) more electrolytes as they age (1), and *Pythium* species cause more seed decay if the seeds are leaky (13). Viability of soybean seeds was not affected by aging, but seedling vigor, as measured by the length of the radicle, was inversely proportional to the amount of leakage (12). In our study, emergence was good in the pasteurized soil, but the older the seed the shorter the seedling at the one-leaf stage, suggesting that seed reserves were progressively less available to the seedling as the seed aged.

Factors other than age of the seed also affect vulnerability of the seed and seedling to *Pythium*. For example, the percentage of emergence was lower for the 3-yr-old Daws seed than for 5-yr-old Daws seed, possibly because of different storage conditions or different field conditions under which the seeds were formed. Seedling emergence was markedly better for 7-yr-old Daws stored at 5 C for the entire 7 yr than seed from the same lot stored under conditions typical of commercial storage, i.e., a shed with neither heat in the winter nor cooling in the summer. The embryos of cereal seeds also may be exposed to infections by cracks in the seed coat (8,10). Much more work is needed on conditions of harvesting and storage as they affect vulnerability of the seeds to infection by *Pythium* to account for the variations in damage from *Pythium*

among seedlots of a given age.

Traditionally, wheat growers and seedsmen in the Pacific Northwest have preferred seed 1 or 2 yr old to avoid seed dormancy (7). However, dormancy in new wheat seed is expressed mainly or exclusively in warm soils such as encountered when seeding in August-September in the wheat-fallow area of east central Washington. Growers in the higher rainfall (40-45 cm or more annual precipitation), annual-cropped areas of the Inland Pacific Northwest of the United States, where *Pythium* is most important, seed in late September and October. Soils are usually wet and cool by this time, and seed dormancy is no longer a problem. Growers and seedsmen should begin to use current-year seed more generally for these later seedings to minimize seedling damage from *Pythium*.

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