Influence of Soil Treatments on Growth and Yield of Wheat and Implications for Control of Pythium Root Rot

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Cooperative research, the U. S. Department of Agriculture, Agricultural Research Service, and the Washington State University College of Agriculture and Home Economics Research Center, Pullman. College of Agriculture and Home Economics Research Center Scientific Paper 7490.

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Accepted for publication 6 February 1987 (submitted for electronic processing).

ABSTRACT

Cook, R. J., Sitton, J. W., and Haglund, W. A. 1987. Influence of soil treatments on growth and yield of wheat and implications for control of Pythium root rot. Phytopathology 77:1192-1198.

The population of *Pythium* spp. (based on plate counts) was more than 300 propagules per gram of soil in 33 of 39 wheat fields sampled in eastern Washington and northern Idaho during 1983–1986, and none had less than 100 propagules per gram of soil in the top 15 cm. Treatment of plots with either methyl bromide, chloropicrin, or 1-3, dichloropropene and 17% chloropicrin eliminated 95–99% of the inoculum and resulted in adult wheat plants that were 3–10 cm taller than those grown in nontreated soil. Solarization and burning a layer of straw (10–12 t/ha) on the soil surface before sowing eliminated 80–90 and 40–50% of the *Pythium* inoculum, respectively, and likewise resulted in taller adult wheat plants. The correlation (r^2) between population of *Pythium* before sowing and adult-plant heights was −0.54, significant at $P = 0.001$. Wheat yields were 13–36% greater in response to fumigation in fields where wheat was grown every other year, 3–12% greater where wheat was grown every third year, and 19 and 14% greater, respectively, in response to solarization and burning straw. The greater yield of wheat in response to soil treatments resulted mainly from more heads per plant rather than more plants. In the greenhouse, heat treatment of soil at 45 C/20 min eliminated *Pythium* and resulted in seedlings up to 25% taller than those in untreated soil; the reestablishment of *Pythium ultimum* var. *sporangiiferum* at 500 propagules per gram in heat-treated soil again resulted in stunted seedlings. Treatment of seed with metalaxyl resulted in taller seedlings in natural soils and treated soils reinfested with *Pythium*, but not in soil free of *Pythium*. Roots were commonly stripped of root hairs as well as fine rootlets in the top 15 cm of soil in nontreated plots, and *Pythium*-like hyphae were observed in the root hairs from the field. The results indicate that *Pythium* is an important pathogen of Pacific Northwest wheat in areas receiving 40–45 cm of precipitation annually.

Additional key words: root disease, soilborne pathogen.

A previous study (8) with soil fumigation revealed that existing cultivars of winter wheat (*Triticum aestivum* L.) in annual-cropped areas of eastern Washington and adjacent northern Idaho with 40–45 cm of annual precipitation have the potential to yield 15–25% more than presently achieved by growers without adding more fertilizer or water. Neither the flush of mineral nitrogen that occurred in the top 20 cm of soil after fumigation nor the delay in nitrification of ammonium in fumigated soils could account for the yield response (8). For example, 1-3, dichloropropene (Telone II) and 1-3, dichloropropene and 17% chloropicrin (Telone II C 17) each caused the equivalent flushes (10–15 kg/ha) of mineral nitrogen when applied at 240 L/ha, and each delayed nitrification to about the same extent, but only Telone C resulted in a growth and yield response in the crop. Telone C, but not Telone, at the rates used, was fungicidal to *Pythium* spp. in soil. Moreover, metalaxyl resulted in yields 1 to 2 t/ha greater than the untreated checks, equal in some cases to the response of wheat to methyl bromide fumigation (8,9). Other researchers (1,2,12,13,19) have also implicated the elimination of *Pythium* spp. as an explanation for the response of crop plants to soil fumigation.

Earlier work on Pythium root rot of cereals dealt with spring-grown barley (2) and wheat (16,17) in the north-central states and prairies of Canada. Little prior work exists on the importance of Pythium root rot of winter wheat. At least 10 species of *Pythium* occur in roots of wheat in eastern Washington and northern Idaho; all are pathogenic to wheat to some extent (6). The present study was conducted to determine more fully the role of *Pythium* control in the response of wheat to soil fumigation and the significance of Pythium root rot as a production constraint to Pacific Northwest wheat.

MATERIALS AND METHODS

Fumigated plots and their cropping histories. Ten field experiments with soil fumigation were carried out with winter wheat during the 1982, 1983, 1984, 1985, and 1986 crop years (crop year = year of harvest, actually planted the previous fall). All sites had been planted to peas or lentils the previous year and either winter wheat (2-yr rotation) or spring barley (3-yr rotation) the year before that. All 10 sites were in commercial fields in eastern Washington with conventional tillage provided by the growers.

Methyl bromide was applied under a clear plastic tarp at about 400 kg/ha in the only experiment in 1982 and in one of three experiments in 1983. Telone II C17 (Tel C) at 480 L/ha was used in all other experiments. Chloropicrin at 220 kg/ha and ethazol (5-ethyoxy-3-trichoromethyl-1,2,4-thiadizole) at 10 kg a.i./ha were also included as treatments in experiments conducted in 1983 and 1984. Fumigants were injected 15 cm deep through shanks spaced 30 cm apart, and the soil was immediately mixed to a depth of 5–8 cm and roller-sealed using a modified Lely Rotera to prevent loss of fumigant (8). Ethazol was applied as a water suspension to the soil surface and immediately incorporated with the Rotera. Checks received the same Lely Rotera treatment but no chemical. Each plot was approximately 2.7 × 6.5 m arranged in a randomized complete block design with five replicates. All treatments were applied in mid-September for the respective crop-harvest years.

Field experiments using solarization and burning straw. Two field experiments were carried out on the Washington State University Plant Pathology Farm to determine the effects of solarization and burning straw on populations of *Pythium* and the subsequent growth and yield of wheat. Both experiments used land that had been in fallow but not tilled (chemical fallowed) the previous year. For the first experiment, soil was treated in five replicate plots in the autumn of 1983, either by solarization beneath a clear plastic tarp (10) or by burning a layer of straw on the soil surface. For solarization, the plastic tarp was left in place for about 5 wk, from late July through August 1983. No precipitation fell during this period, and, hence, differences in evaporation were the only differences in soil moisture availability between tarped and nontarped plots. Temperatures monitored 5 cm deep reached 45–50 C for 3 to 4 hr on each of about 15 days during the 5-wk period; cloud cover limited the effect of the treatment on the other days. To treat by burning, clean, bright straw was loosely piled about 75 cm deep (12–15 t/ha) and burned on each of the five replicate blocks 5 × 5 m. The ash was then distributed as uniformly as possible over both the respective burned and adjacent nonburned (check) plots to test whether ash alone on the soil surface promoted wheat growth. A randomized block design was used for each treatment except for ash-only, which was randomized only to the extent that it occurred on one of four sides of a burned plot. For the second experiment, four replicate plots were established as a latin square with straw at 0, 3, 6, and 12 t/ha applied in the fall of 1984, burned immediately, and the site was seeded 2 wk later.

Estimation of the population of *Pythium*. The *Pythium* population was estimated for soil in each of 39 wheat fields in eastern Washington and adjacent northern Idaho during 1983–1986 and also for plots after the various soil treatments. For the fields, five soil cores were taken in a radius of 2 to 3 m at each of five locations per field. The cores were taken to a depth of 15 cm with a 2.5-cm-diameter Hoffer soil sampler and bulked for each of the five locations. For the field experiments, nine cores were taken per plot, depth (15 cm), and sampling time (2 days, 1 mo, and 8 mo after treatment) with the Hoffer soil sampler and bulked as one composite sample for that treatment, time, and replicate. All soil samples were allowed to air dry slowly in open paper bags and were then crumbled as necessary by hand and sieved. Chamswarng (5) showed that the highest estimates of the population were obtained from the fraction that passed through a 0.5-mm-mesh sieve (35 mesh) but collected on a 0.25-mm-mesh sieve (60 mesh). All samples were processed in this manner before a 10-g subsample was taken from each composite, suspended in 0.2% water agar, and dilution-plated at both 1:50 and 1:100 on the MPVM selective medium of Mircetich (12). Three plates were made per subsample and dilution (30 plates per field or soil treatment). Colonies were marked after 24 hr at 25 C and each plate checked twice again, after 48 and 72 hr of incubation, before the final inoculum density was estimated.

Sowing, plant growth assessments, and harvest of wheat. Wheat cultivar Daws was sown in 1982 (one experiment) and 1983 (all three experiments); Stephens in one experiment and a 1:1 mixture of Daws and Stephens in the other experiment in 1984; and Hill-81 in the two experiments conducted in each of 1985 and 1986. In addition, Daws, Dusty, Hill-81, and Stephens all were tested in 1985 and again in 1986 in paired plots of fumigated (Tel C at 480 L/ha) and nonfumigated soil. There was no cultivation or other soil disturbance between the time of soil treatment and sowing. All experiments with soil fumigation were sown with a double-disk-type seeder with openers spaced either 30 or 17.5 cm apart. The two experiments with solarization and burning of straw were seeded with a four-row plot seeder fitted with John Deere HZ-type hoe openers and split packer wheels with rows 40 cm apart. Plots were seeded each year between 1 and 7 October. All sites received 90–110 kg of N per hectare either as liquid ammonia (the 10 commercial fields) or dry ammonium sulfate/ammonium nitrate (Plant Pathology Farm) in the fall and an additional 30–40 kg of N per hectare as dry ammonium nitrate top dressed in early spring. All plots were sprayed with triadimefon and/or benomyl in late spring or early summer (except in 1985 and 1986, both dry years) to protect against rusts (mainly those caused by *Puccinia striiformis* and *P. recondita*) and Pseudocercosporella foot rot (*P. herpotrichoides*), respectively.

Emergence and tillering were determined for the paired plots of Daws, Dusty, Stephens, and Hill-81 in both 1985 and 1986 by counting the number of emerged seedlings (about 2 wk after sowing) and the number of tillers with heads (just before maturity) per 0.5-m of row in each of five or six randomly selected places in the center rows of each plot. In addition, the percentage of headed tillers was estimated at least three times during a 1-wk period when heads were emerging most rapidly. The estimate was subjective and based on the observer's judgment of the proportion of heads fully emerged from the boot. Plant height was determined in all experiments beginning in 1983 and was based on measurements to the top of the spike just before maturity in each of nine locations per plot. Yields were measured for each experiment, either by bundling the two center rows of each plot and then threshing the heads in a stationery Vogel thresher (1982–1984) or by machine harvesting with a Wintersteiger Nurserymaster combine (1985 and 1986).

Verification of root infections by *Pythium*. Plants were dug from plots in each of two experiments beginning in the two-leaf stage (early November 1983) and at intervals thereafter until they were fully headed (mid-June 1984). Each plant was removed with an intact core of soil. Each core was 10–20 cm in diameter (depending on the size of the plant) and at least 15 cm deep. Each soil core and accompanying plant were placed in a plastic container and transported to the laboratory without further disturbance. Soil was separated from the roots by soaking the cores in water, then gently agitating the root system in the water. Final washing of the roots was accomplished under a running tap while the roots were suspended on a fine-mesh screen. It was necessary to rub or brush some roots during the final wash to remove tightly bound soil, but this treatment was minimized to avoid the breakage and loss of fine lateral roots and root hairs. Microscopic observations were limited to the lateral roots (usually 100–200 μm in diameter), which were broken free from the main roots with a forceps, placed on a glass slide in 0.1% acid fuchsin in lactophenol, and covered with a 50-mm-long cover slip. The slides were heated briefly to help clear the roots and facilitate deeper staining before examination. Representative rootlets and root hairs were plated on water agar for isolation of *Pythium* species. Similar but less detailed observations of roots and isolation of *Pythium* species were carried out in the experiments sown in the fall of 1984.

Greenhouse studies with heat-treated soil and metalaxyl-treated seed. The influence of *Pythium* on wheat seedlings was studied in the greenhouse using soil naturally infested with *Pythium* at about 500 propagules per gram, the same soil heat treated (2) at 60 C/30 min, and soil heat treated and then reinfested with *Pythium ultimum* Trow var. *sporangiiferum* Drechsler at about 500 oospores per gram. The oospores were produced by growing the fungus in petri dishes on a thin layer of liquid medium made of extract from potatoes and carrots (6). Seeds of cultivar Daws were sown in each of these soils and nontreated (check) soil with and without seed treatment with metalaxyl at about 1 g a.i./kg of seed. These six treatments (three soils × two seed treatments) were replicated four times with seven 4-cm-diameter (21-cm-long) plastic tubes (Ray Leach Cone-tainer, Canby, OR), two seeds per tube for each replicate and treatment. Height and length of the first true leaf were measured for each plant (8). In a second experiment, soil was used without heat treatment or was heat-treated at 45, 53, and 55 C/20 min. The populations of *Pythium* were estimated by dilution-plate counts for each treated soil and the check and wheat seedling growth then compared in each soil.

RESULTS

Populations of *Pythium* in wheat-field soils. All of the 39 wheat fields sampled in eastern Washington and northern Idaho had populations of *Pythium* spp. estimated at more than 100 propagules per gram; 14 (36%) had 300–400 propagules per gram, four had 400–500 propagules per gram, three had 500–600, three had between 600 and 700, and nine fields had between 700 and 1,000 propagules per gram (Fig. 1).

Effects of soil treatments on the *Pythium* population. Results for effects of the fumigants and ethazol were virtually identical in the two trials in 1983 and two more in 1984, and thus only data for 1983 are presented. Chloropicrin at 220 kg/ha and Tel C at 480 L/ha each reduced the population of *Pythium* by 95% or more (Table 1). Ethazol, at the rate used, had no effect on the *Pythium* population.

Treating the soil by burning straw in the autumn of 1983 eliminated about 75% of the inoculum of *Pythium* in the top 5 cm of soil relative to ash only but had no effect on the population at 5–10 or 10–15 cm deep (Table 2). Treatment by solarization eliminated 90% of the inoculum from the 0–5 cm depth relative to ash only, 50% from the 5–10 cm depth, but had no detectable effect below 10 cm. Burning straw applied to the soil surface at 3 t/ha in the fall of 1984 had no detectable effect on the *Pythium* population but burning 6 and 12 t/ha eliminated about 50% of the population of *Pythium* down to 10 cm depth (Table 2).

Effect of soil treatments on growth and yield of wheat. Plants were significantly taller than the checks in every treatment where soil was fumigated, solarized, or straw burned on the soil surface but not where treated with ethazol or ash only (Table 3). Significant negative correlations occurred between the *Pythium* populations in the fall (data for populations 2 days after fumigation, i.e., before sowing) and heights of adult plants 8 to 9 mo later (just before maturity). Combining all data for the four fumigation (and ethazol) trials in 1983 and 1984 and the solarization and burn experiment in 1984 (total of 17 comparisons) the value of r^2 for *Pythium* populations before sowing and adult-plant height 8 to 9 mo later was -0.54, significant at $P = 0.001$ (Fig. 2). The values of r^2 were: -0.79 for the nonfumigated plots only (checks and ethazol-treated) in the four 1983 and 1984 experiments; -0.83 and -0.93, respectively, for the two 1983 fumigation (and ethazol) experiments; -0.94 for the combined data of the 1984 fumigation (and ethazol) experiments; and -0.76 for the 1983 solarization/burn experiment.

All four cultivars averaged 10–20% more tillers with heads in fumigated than in the adjacent (paired) nonfumigated plots; the differences were significant at $P = 0.05$ for Dusty, Daws, and Hill-81 but not for Stephens (Table 4). Only Hill-81 averaged numerically more emerged seedlings per unit-length of row in fumigated than in nonfumigated plots, but none of the differences in stand counts were significant (Table 4). All four cultivars headed 4 to 5 days earlier in fumigated than in nonfumigated plots in 1985 (data not shown) and 1–3 days earlier in fumigated than in nonfumigated plots in 1986 (Table 4).

TABLE 1. Populations of *Pythium* species as estimated by dilution-plate counts at times after chemical treatment of the soil

Soil treatment[z]	*Pythium* population per time and test (propagules per gram)[y]					
	1983-1			1983-2		
	2 day	1 mo	8 mo	2 day	1 mo	8 mo
Check	335	230	410	575	683	213
CP	0	0	45	0	15	tr
Tel C	tr	25	95	tr	50	20
Ethazol	235	185	...	674	470	...

[y] Each population estimate is based on dilution-plate counts of a composite soil sample from each of five replicates, two dilutions (1:50 and 1:100) per composite sample, and three plates per dilution (30 plates per value). The two tests were conducted, respectively, in fields cropped the previous 3 yr to winter wheat/spring barley/peas (1983-1) and winter wheat/spring barley/lentils (1983-2). The years refer to year of harvest (to be consistent with test); treatments were applied in September 1982, and populations estimated at indicated times thereafter. Virtually identical results were obtained in response to these same treatments in each of two experiments completed in 1984.

[z] Tel C = Telone II C17 applied at 480 L/ha; CP = chloropicrin applied at 220 kg/ha; ethazol applied at 10 kg a.i./ha, all incorporated with a Lely Rotera.

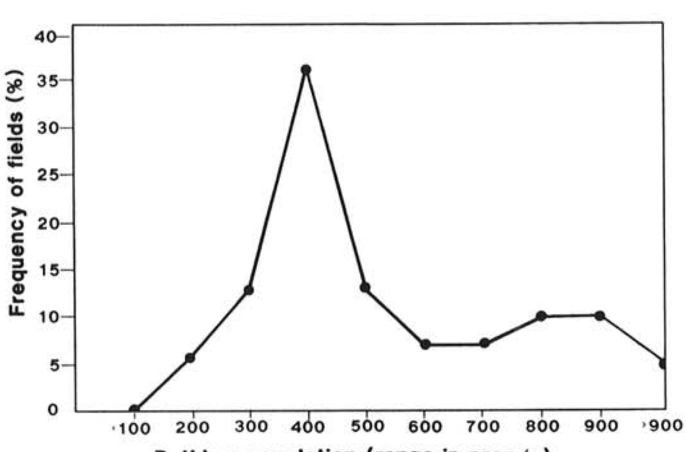

Fig. 1. The range of population (propagules per gram) of *Pythium* species as estimated by dilution-plate counts for soil samples taken from each of 39 wheat fields in eastern Washington and adjacent northern Idaho between 1983 and 1986. The values for the *Pythium* population indicate the maximum average population, i.e., from left to right, < 100 = less than 100 propagules per gram, 200 = more than 100 but less than 200 propagules per gram, 300 = more than 200 but less than 300 propagules per gram, etc.

TABLE 2. Influence of treatments applied at the soil surface on *Pythium* populations and wheat growth and yield responses in two fields in the 1984 and 1985 crop years, respectively

Soil treatment[y]	Pythium population (prop/g) per soil depth (cm)			Wheat response[x]	
	0–5	5–10	10–15	Height (cm)	Yield (t/ha)
1984					
Check	...[z]	...	...	92.2 c	5.7 c
Burn (12–15 t)	83	190	57	97.0 a	6.5 ab
Ash	350	160	65	94.4 bc	5.7 c
Solarized	13	43	57	96.2 ab	6.8 a
1985					
Check	262	450	...	74.4 c	5.1 b
Burn (3 t)	573	367	...	78.0 b	5.8 ba
Burn (6 t)	121	234	...	79.0 b	5.9 a
Burn (12 t)	109	262	...	78.7 b	6.2 a

[x] Height data analyzed by analysis of variance and yield by general linear model. Means followed by the same letter are not significantly different at $P = 0.05$ by Duncan's multiple range test.

[y] For Burn, clean, bright wheat straw was placed as a layer on the soil surface at the indicated rates (t/ha) and burned. In 1984, ash from each burned plot was distributed uniformly onto an adjacent equal-sized block as a check. For Solarized, clear plastic sheeting was sealed into the top 10 cm of soil around the periphery of each plot area for about 5 wk before sowing.

[z] Not determined.

TABLE 3. Heights of adult wheat-plant cultivars Daws and Stephens as influenced by treatment of soil with fumigants or ethazol about 2 wk before seeding in each of two tests conducted in two different years

Soil treatment[z]	Adult plant height per test (cm)[x,y]			
	Daws		Stephens	
	1983-1	1983-2	1984-1	1984-2
Check	96 c	90 b	93 d	96 d
CP	105 ab	94 a	104 ab	103 c
Tel C	109 a	96 a	103 a	104 c
Ethazol	94 c	90 b	96 cd	96 d

[x] Each value is the mean of nine measurements in each of five replicate plots per experiment and analyzed by general linear model. Values followed by the same letter are not significantly different at $P = 0.05$ according to Duncan's multiple range test.

[y] Rotations for the four test sites were: 1981-1 and 1984-2, wheat/spring barley/peas/wheat; 1981-2, wheat/peas/wheat; and 1984-1, wheat/spring barley/lentils/wheat.

[z] Tel C = Telone II C17 applied at 480 L/ha; CP = chloropicrin applied at 220 kg/ha; ethazol applied at 10 kg a.i./ha, all incorporated with a Lely Rotera.

Yields were greater by 0.7–1.9 t/ha (Fig. 3) in response to one or more fumigation treatments in the five trials conducted in fields where wheat was grown every other year (2-yr rotation). These values were 13–36% greater than the checks and were significant by the Student's t test at $P = 0.05$ or $P = 0.01$, depending on the experiment. Yields were greater by only 0.1–0.9 t/ha in five trials conducted in fields where wheat had been grown every third year (3-yr rotation). These differences were significant in only two of the five experiments and both were in response to treatment with chloropicrin but not to treatment with Tel C (Fig. 3).

The two experiments (1985 and 1986) involving paired plots (fumigated/nonfumigated) of Daws, Dusty, Stephens, and Hill-81 were both in fields in 3-yr rotations. Whereas all four cultivars showed the typical growth responses to Tel C (Table 4), yields of the four cultivars were only slightly but generally not significantly greater in fumigated than in nonfumigated plots in both years. The 1985 experiment was conducted on a 15–20° slope, typical of most fields in the rolling Palouse of eastern Washington and northern Idaho. Precipitation was about 3.5 cm below normal for the 1984–1985 crop year (September 1984–October 1985) and below normal by about this same amount in the 1986 crop year. To test the possibility that available water and not root disease was the yield-limiting factor (7) in this experiment, the five replicate-pairs of each cultivar blocked by the position on the contour in the 1985 trial were analyzed as treatments, and the plots seeded to each cultivar on the contour were analyzed as the replicates. By this arrangement, the response to fumigation was highly significant (23%) at the lowest position on the contour but was not significant at any of the other four positions higher up the slope (Fig. 4). The

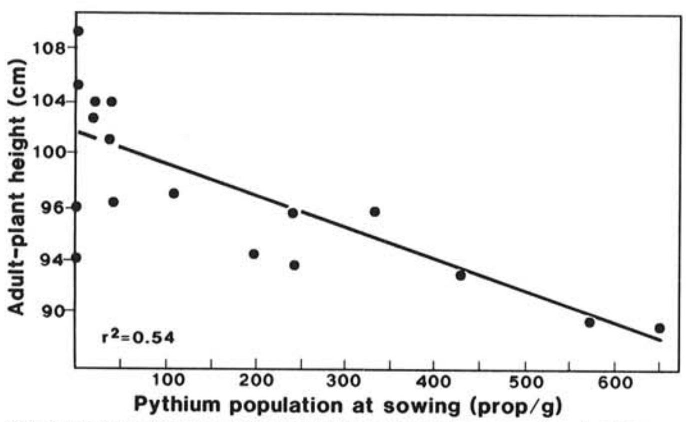

Fig. 2. The relationship of the population of *Pythium* spp. estimated 2 days after soil treatment in the fall (10–14 days before sowing) and average heights of adult wheat plants in response to those same treatments (measured 8 to 9 mo later).

TABLE 4. Response of four cultivars of winter wheat to treatment of soil with Telone II C17 before sowing

Cultivar	Tel C[v]	Stand[w] (no/m)	Headed[x] (%) 6/12	6/13	6/16	Tillers[y] (no/m)	Yield[z] (t/ha)
Hill-81	−	25	5	10	90	135	7.2
	+	33	20	30	95	153*	7.8
Stephens	−	28	70	90	97	167	7.4
	+	27	95	95	150	189	7.2
Daws	−	22	35	60	95	168	6.8
	+	27	70	75	100	201*	7.4**
Dusty	−	36	5	15	80	194	6.7
	+	37	20	45	95	215*	6.7

[v] Telone II C17 (+) applied at 480 L/ha, shank-injected, and incorporated with a Lely Rotera. Checks (−) received the same Lely Rotera treatment.
[w] Based on number of plants emerged 3 wk after sowing. Each value is an average of the number counted in six 0.5-m lengths of row in each of five replicate plots.
[x] Estimated to the nearest 5% based on full extension of the heads above the flag leaf on three dates in June. Values rounded to the nearest 5%.
[y] Based on number of tillers with heads in each of five 0.5-m lengths of row in each of five replicate plots. Values marked with an * are significantly different from the untreated check at $P = 0.05$ by the Student's t test.
[z] Based on harvest of the center four rows (out of eight) from each of the five replicate plots. The value marked with ** is significantly different from the untreated check at $P = 0.01$ by the Student's t test.

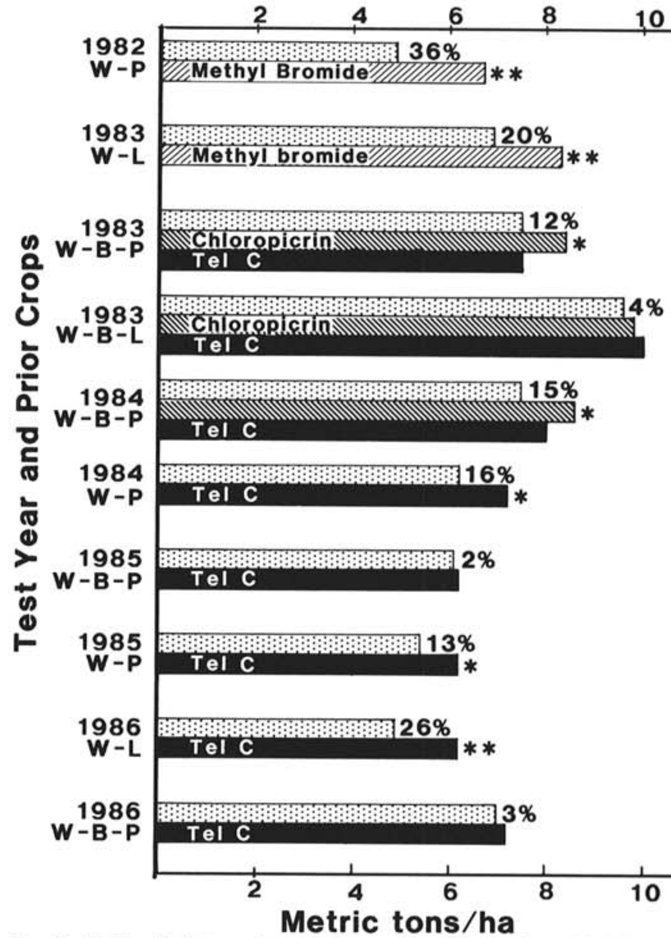

Fig. 3. Yields of winter wheat in nontreated (bars without labels) and fumigated plots for 10 experiments carried out during 1982–1986 in fields in eastern Washington where the previous crops in the fields involved 2-yr rotations of either winter wheat and then peas (W-P), winter wheat and then lentils (W-L), or 3-yr rotations of winter wheat/spring barley/peas (W-B-P) or winter wheat/spring barley/lentils (W-B-L).

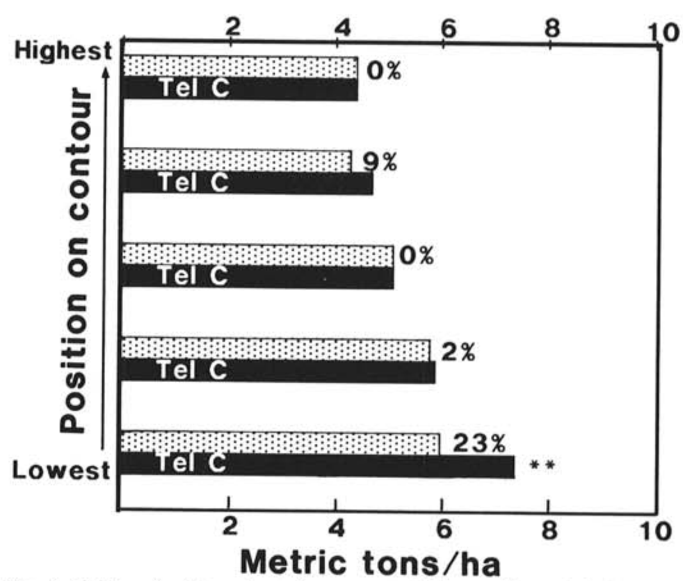

Fig. 4. Yields of winter wheat in nontreated (bars without labels) and fumigated (Telone II C17) plots on the contour at increasing distances up a 15–20° slope.

average yield in the fumigated plots was progressively less with increasing distance up the slope.

Yields were greater by 1.1 and 0.8 t/ha, respectively, in response to solarization and burning in 1984, and were pregressively greater in response to increasing amounts of straw burned on the soil surface in 1985 (Table 2).

Condition of roots from fumigated compared with nonfumigated soils. The first microscopic evidence for the occurrence of *Pythium* as a root pathogen was obtained with seedlings dug in the two- to three-leaf stage in November and early December. Coenocytic hyphae typical of *Pythium* species occurred in abundance in the root hairs and outer cell layers of the fine rootlets (Fig. 5A). When plated on water agar amended with rifampicin, *Pythium* was recovered, including from root hairs. Oospores were not observed in the rootlets until March or April (spring), by which time roots and rootlets recovered from the top 10–15 cm of nonfumigated soil were yellowish-brown and visually stripped of root hairs (Fig. 5B). In contrast, roots and rootlets recovered from fumigated soil were white and dense with hairs as late as June of the harvest year (Fig. 5C).

Influence of *Pythium* and metalaxyl on seedling vigor in pasteurized and natural soil. Wheat seedlings grown in heat-treated (45, 53, 55 or 60 C/20 min) Palouse silt loam obtained from a field in a typical pea-wheat rotation emerged faster and had longer first true leaves than wheat grown in the same soil not treated (Table 5). No *Pythium* was detectable by plate counts of the heat-treated soils. Similarly, wheat seedlings grown from metalaxyl-treated seed emerged faster and had longer leaves than wheat grown from untreated seed, except in heat-treated (pathogen-free) soil (Table 6, Fig. 6). Untreated seed grown in heat-treated soil reinfested with *P. ultimum* var. *sporangiiferum* (at about 500 propagules per gram) were identical in stature and appearance to those in the nontreated soil, unless the seed was treated with metalaxyl (Table 6, Fig. 6).

DISCUSSION

The increased growth and yield responses of winter wheat to soil fumigation, solarization, or burning straw on the soil surface can be explained partly or largely as a response of wheat to the reduction of *Pythium* inoculum from the soil. Treatments effective in reducing the *Pythium* population were the same treatments effective in producing the increased growth and yield responses. Ethazol as a soil treatment unexpectedly had no effect on the *Pythium* population, possibly because the rate of application was too low, but likewise had no effect on plant growth and was thus equivalent to another check. Highly significant negative correlations ($r^2 = -0.94$ for one set of comparisons, and -0.54 for the combined data of five experiments in 2 yr) occurred between the population of *Pythium* before sowing (2 days after the soil treatment) and heights of adult plants the following year.

TABLE 5. Influence of treating soil with moist heat on the population of *Pythium* species and response of wheat seedlings

Treatment[z]	*Pythium* (prop/g)	Emergence[y] 5 days	Emergence[y] 14 days	First leaf[y] (cm)
Check	583	22	90	7.8 b
45 C/20 min	0	100	100	10.2 a
53 C/20 min	0	95	100	10.3 a
55 C/20 min	0	88	96	9.6 ab

[y] Soil treated with most heat using a steam-air mixture (2).
[z] Each value is based on four replicates with seven tubes each sown with two seeds per replicate and treatment. Analyzed by analysis of variance. Values for first leaf measurements with the same letter are not significantly different at $P = 0.05$ by Duncan's multiple range test.

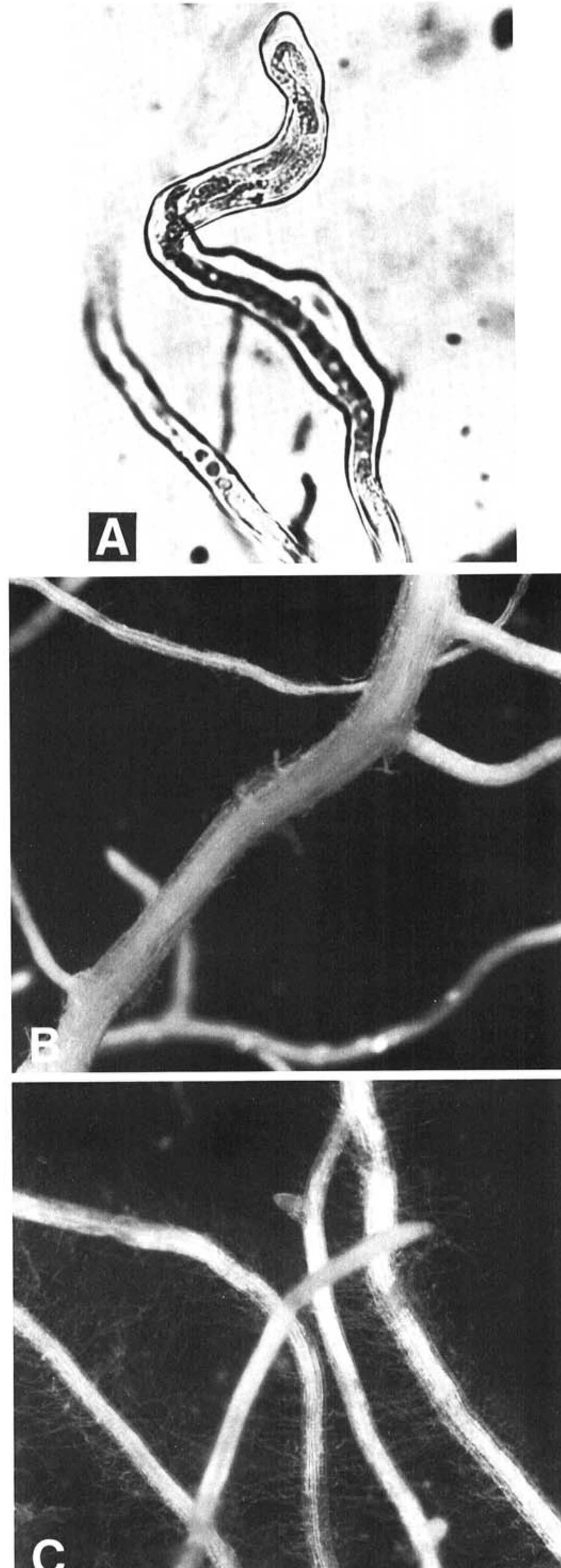

Fig. 5. Wheat roots recovered from the top 15 cm of field plots. **A,** *Pythium*-like hyphae in a root hair of wheat in the two-leaf stage recovered from the field; **B,** Roots from natural soil; and **C,** Roots from soil fumigated with Telone C17 at about 480 L/ha before seeding.

In the greenhouse, treatment of the soil with moist heat at 45 C/20 min eliminated the *Pythium* population, and seedlings emerged faster and were taller in response to this same treatment. Baker and Cummings (3) found that moist-heat treatment at 45 C/20 min was also sufficient to eliminate *Pythium* from planting material of *Aloe variegata* L. Heat-treatment probably accounts for the elimination of *Pythium* spores by solarization and burning straw in the field plots. The symptoms of *Pythium* damage on wheat seedlings were reproduced by adding oospores of *P. ultimum* var. *sporangiiferum* back to the heat-treated soil. Finally, treatment of seed with metalaxyl corrected the problem of stunted seedlings in both the natural and *Pythium*-infested pasteurized soil in the greenhouse study.

Earlier (8), we showed that chloropicrin but not Tel C reduced the population of *Fusarium* spp. in soil, but because both fumigants caused a wheat growth and yield response, *Fusarium* control cannot account for the effect. In the present study, chloropicrin appeared superior to Tel C in two trials, but Tel C never failed to reduce the *Pythium population* and produce a growth response evident as taller plants. Telone by itself produced no growth or yield response in any of five experiments conducted at five locations in our earlier study (8); because Telone is a nematicide, the control of plant parasitic nematodes cannot likely account for the growth and yield response of wheat to soil fumigation in eastern Washington. Take-all, caused by *Gaeumannomyces graminis* (Sacc.) Arx & Oliv. var. *tritici* Walker, is controlled in the Pacific Northwest by a single year to a nonhost crop (7); because our trials were conducted in fields rotated to peas or lentils the previous year, control of this disease cannot likely account for the response. Benomyl was applied to all plots in the present study to control and, hence, rule out foot rot caused by *Pseudocercosporella herpotrichoides* (Fron.) Dei. as a factor. Cephalosporium stripe, caused by *Cephalosporium gramineum* Nis. & Ika., occurs in the 2-yr but not in the 3-yr

TABLE 6. Influence of pasteurization, *Pythium ultimum* var. *sporangiiferum* added back to pasteurized soil, and metalaxyl seed treatment on growth of wheat seedlings

Soil treatment[z]	Seed treatment	Emergence (%)[y] 7 days	Emergence (%)[y] 14 days	First leaf (cm)[y]
Check	Check	0	94	8.9 b
	Metalaxyl	61	100	9.7 ab
Pasteurized	Check	96	100	10.3 a
	Metalaxyl	95	98	10.2 a
Pasteurized reinfested	Check	20	93	8.7 b
	Metalaxyl	59	100	10.1 a

[y] Each value is based on four replicates with seven tubes each sown with two seeds per replicate and treatment. Values for first leaf measurements analyzed by analysis of variance. Values followed by the same letter are not significantly different at $P = 0.05$ by Duncan's multiple range test.
[z] Pasteurization involved moist heat treatment with a steam-air mixture at 60 C/30 min (2).

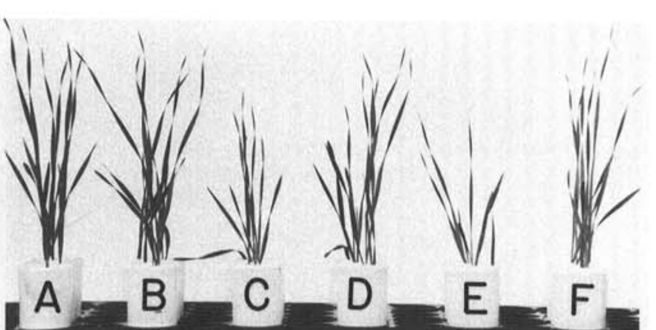

Fig. 6. Growth of wheat seedlings in pasteurized (60 C/30 min) soil (A and B), pasteurized soil reinfested with *Pythium ultimum* var. *sporangiiferum* (C and D), and natural soil (E and F) when grown from seed treated with metalaxyl (B,D,F) or not treated (A,C,E).

rotations, and the fumigation response in our present study was generally greater in fields managed by a 2-yr than in those in a 3-yr rotation. However, seeding in October (as in our study) should have controlled this disease (7). Moreover, close inspection of our check plots failed to reveal even one plant of this easy-to-recognize disease. Root rot of wheat caused by *Rhizoctonia solani* Kühn (mainly AG-8?) is associated with reduced or no tillage (18), but conceivably could have been subclinical on wheat in our studies. Except for this pathogen, however, *Pythium* spp. are the only known root pathogens of wheat that can account for the general stunting, restricted tillering, and slight or occasional loss of stand in late seedings and which can be controlled by the soil treatments used.

The response of wheat plants to soil fumigation or to heat treatment is evident mainly as taller plants, more tillers per plant, and a darker green color to the foliage. These responses are typical of the responses of plants to improved fertility of the soil. However, the additional 10–20 kg of N per hectare detected in fumigated soil (8), in addition to the 120–150 kg of N per hectare applied as fertilizer, cannot account for the additional grain produced by the plants grown in the fumigated soil. Moreover, the additional nitrogen occurred in response to fumigation with Telone alone, yet this chemical had no effect on wheat growth (8). In the present study, nutrients in the straw ash were not responsible for the increased growth response because ash alone had no effect on wheat growth and yield. Even more significantly, wheat headed up to 5 days earlier in fumigated compared with nonfumigated plots, a response not likely explained by nitrogen because this nutrient tends to delay maturity. Bruehl (4), Vanderpool and Simmonds (16), and Vanderpool and Truscott (17) each showed with spring cereals that Pythium root rot delayed heading and maturity.

Pythium-like hyphae were observed in the root hairs of seedlings in only the two- to three-leaf stage, evidence that loss of root hairs begins early in the life of the plant. Bruehl (4) working with barley, Kraft et al (11) working with grasses, Nemec (14) working with citrus, and probably others have observed that *Pythium* is a colonist of root hairs as well as the cortical tissues of roots. The loss of rootlets and root hairs from roots in the top 10–15 cm of soil could account, in part, for the generally shorter stature and lower yields of wheat plants in the natural soil compared with those in treated soil. Conversely, the healthier roots and greater density of root hairs associated with *Pythium* control could result in greater uptake in nutrients and hence plants that appear better fertilized (1,4,12,15,19). Because *Pythium* species apparently are ubiquitous inhabitants of the wheat field soils in the Pacific Northwest, being detected at populations greater than 100 propagules per gram in all fields sampled, their debilitating effect on wheat probably is also ubiquitous. This can explain why plants grew better in response to soil fumigation in every field where fumigation or the heat treatments were applied.

The greater yield responses after soil fumigation in fields in 2-yr rather than in 3-yr rotations suggest that *Pythium* damage may be more important where wheat is grown every second than where grown every third year. With at least 10 species of *Pythium* present in soils of this region (6), and with some significantly more pathogenic than others on wheat, it is conceivable that growing wheat favors a species mixture more destructive to wheat. More fields in 3- and 2-yr rotations must be compared to verify that *Pythium* damage can be regulated by length of the crop rotation.

Ten years ago, we (*unpublished*) discontinued trials with soil fumigation in the low to intermediate rainfall area (25–40 cm annual precipitation) because the increased growth response in these areas was not accompanied by a yield response. Apparently, wheat is capable of yielding to the limits of the available water in these areas in spite of *Pythium* damage (7). Indeed, wheat in fumigated plots sometimes grew too well, producing more vegetative growth than could be supported to maturity by the available water; the result was shriveled grain (low volumetric grain weight) and lower rather than higher yields than in adjacent nonfumigated plots. Our 1985 results with the four cultivars grown on a slope suggest that for eastern Washington, 5.5–6.0 t/ha is the lower limit of yield potential where a yield response to fumigation can be expected. This yield or greater can be expected in areas having more than 35–40 cm of water available to the crop over the growing season (7). Near Pullman, and in years of normal precipitation, about 50–55 cm of water will be available for the crop, sufficient to produce 8.3–8.5 t/ha. Actual yields with this much water are more commonly 6.5–7.0 t/ha, sometimes lower. We estimate that *Pythium* spp. together with any other factor(s) responsible for the damage to wheat eliminated by our treatments, commonly limits wheat yields to only 75–80% of the potential set by available water in the Pullman area in years of normal or above normal precipitation.

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