Influence of Soil Temperature on Rhizoctonia Root Rot (*R. solani* AG-8 and *R. oryzae*) of Winter Wheat

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ABSTRACT

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Rhizoctonia solani AG-8 and *R. oryzae* are associated with Rhizoctonia root rot of cereals in the northwestern United States. These pathogens were evaluated in the greenhouse and field for effects on disease severity and growth, development, and yield of winter wheat. Experiments in the greenhouse were performed either with pasteurized soil mixture or intact cores of natural soil collected from the field. Soil temperatures were controlled at diurnal cycles of 27/16, 23/11, or 19/6 C, or experiments were performed at ambient temperatures of 28/15 C. Inocula of the *Rhizoctonia* species were also placed in a band below winter wheat seed in the field. *R. solani* caused moderate to severe disease and reduced plant growth and development in all six greenhouse and field tests. *R. solani* in natural soil caused more severe root rot at low than at high temperature. *R. oryzae* caused slight to moderate root rot in natural soil and severe root rot in pasteurized soil at high temperature, but never significantly ($P < 0.05$) suppressed plant growth or development. Grain yields for winter wheat growing in soil infested with *R. solani, R. oryzae,* or neither pathogen were 624, 8,724, and 9,444 kg/ha, respectively, during one field test. The yield component most closely associated with root rot during both field seasons was tiller development. We conclude that *R. solani* AG-8 is the principal incitant of Rhizoctonia root rot on winter wheat in the Pacific Northwest.

Additional keywords: barley, *Hordeum vulgare,* peas, *Pisum sativum, Thanatephorus cucumeris, Triticum aestivum, Waitea circinata.*

Rhizoctonia root rot is widespread and important on wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) in the northwestern United States (18,26). Rhizoctonia species associated with affected plants (15) include *R. solani* Kühn AG-8 (teleomorph: *Thanatephorus cucumeris* (Frank) Donk), other anastomosis groups of *R. solani,* and *R. oryzae* Ryker & Gooch (teleomorph: *Waitea circinata* Warcup et Talbot WAG-0). Burton et al (2) reported that *R. oryzae* was more damaging than *R. solani* AG-8 to barley seedlings at 26 C, equally damaging at 18 C, and did not cause damage at 12 C. Ogoshi et al (15) determined that anastomosis groups of *R. solani* other than AG-8 were avirulent to wheat and barley, and that *R. oryzae* was more virulent than *R. solani* AG-8 at 20 C and less virulent at 10 C. Ogoshi et al (15) concluded that "*R. solani* AG-8 and *R. oryzae* both are involved in Rhizoctonia root rot of wheat and barley in the Pacific Northwest." This determination is important because these fungi have different sensitivities to seed-treatment fungicides (3,7,24,25) and possibly to other disease control practices (12).

In low-rainfall (250–400 mm) regions of the Pacific Northwest, winter wheat is produced in a 2-yr rotation with summer fallow. In higher-rainfall regions, winter wheat is rotated with spring barley, green processing peas (*Pisum sativum* L.), or other crops. Most wheat in eastern Oregon is planted between 15 September and 30 October when soil is cooling rapidly. This has important epidemiological consequences. For example, at Pendleton, OR, the mean monthly soil temperature at 10 cm depth is 25 C during midsummer (July) and declines to 10 C during October. The average temperature is 2 C during midwinter (December and January) and increases to 15 C during mid-April and 20 C in late May. Harvest occurs during July and August. Root-zone soil therefore exceeds 10 C only during the first few weeks after early-sown winter wheat has been planted, and again during the last 3 mo of the 10-mo growing season. Whether soil temperatures are warm enough for *R. oryzae* to be an important pathogen of winter wheat in eastern Oregon is unclear.

Previous comparative pathogenicity studies with *R. solani* AG-8 and *R. oryzae* on cereals are incomplete in that they have been performed under conditions atypical of field environments. Studies in the United States (15) were conducted with 21- to 35-day-old seedlings grown in soil infested with 0.1% (w/w) millet seed colonized by the pathogen. In other studies (2), barley seedlings were grown in a sand+compost mixture infested with 1% (w/w) perlite+maize meal medium infested with the pathogen. Unpublished inoculum density-disease progress experiments with *R. solani* AG-8 in our greenhouse illustrated that maximum disease severity on wheat roots was achieved when a very low rate (3×10^{-3}%, w/w) of inoculum was added to intact columns of soil removed from the field and incubated with cyclic wetting and drying. Although this level of infestation is much lower than that used by previous investigators, the relationship between each of these levels and inoculum densities in natural soils is unknown. Phenologic growth stage and coronal root emergence probably differed among temperature treatments examined by Ogoshi et al (15). Mean emergence of winter wheat tillers (8) occurs at 250 (T_1), 300 (T_2), and 375 (T_3) growing-degree days (3 C base) from planting (19). The high (20 C) and low (10 C) temperature treatments of Ogoshi's study were sampled at approximately 360 and 245 growing-degree days, respectively. Tillering and coronal root development were presumably more advanced in the 20 C treatment than in the 10 C treatment. Therefore, apparent differences in virulence between *R. solani* and *R. oryzae* at 10 and 20 C were probably influenced by variable proportions of coronal and/or seminal roots and variable root morphology (6). Comparative tests with *R. solani* AG-8 and *R. oryzae* at low inoculum rates have not been performed at equivalent plant-growth stages with temperature as a variable, or natural soil environments in the greenhouse or in the field. Thus, the relative importances of *R.*

oryzae and *R. solani* AG-8 as pathogens causing Rhizoctonia root rot remains unclear.

The objectives of this study were to determine the relative importance of root rots caused by *R. solani* AG-8 and *R. oryzae* and to determine their respective effects on growth, development, and grain yield of winter wheat in semiarid eastern Oregon.

MATERIALS AND METHODS

Effects of *R. solani* AG-8 and *R. oryzae* on root rot, growth, development, and yield of winter wheat were examined in four greenhouse and two field experiments. Greenhouse experiments were used to study selected isolates of each pathogen, examine virulence in pasteurized soil mix at ambient temperatures, and compare virulence in pasteurized mix and natural soil at cyclic soil temperatures controlled independently of ambient air temperature. Virulence of the pathogens on six wheat cultivars and effects of soil temperature, as achieved by varying planting dates, were evaluated in field experiments.

Selection of *Rhizoctonia* isolates in ambient-temperature greenhouse experiments. An isolate of *R. solani* AG-8 with known virulence to wheat, barley, and pea was used. The isolate (CB-01) was selected from barley (22) near Pendleton, OR, during 1988 and has been characterized (G. C. MacNish, *personal communication*) as zymogram group ZG1-1 (14). Three *R. oryzae* isolates of unknown virulence were collected from root rot-affected barley for comparison with *R. solani* AG-8. The isolates (P-02, P-04A, an P-04B) were selected from the same field as isolate CB-01 of *R. solani*. Isolates P-02 and CB-01 were used in research reported previously (12,19–21).

A mixture containing peat, sand, loam, and #8 pumice (1:1:1:2 ratio, by volume) was pasteurized at 60 C for 75 min, cooled, and adjusted to pH 5.8 with lime. Inoculum of each pathogen was prepared by colonizing autoclaved millet seeds with *R. solani* or *R. oryzae* (13). Forty-eight square pots (17 and 13 cm sides on top and bottom, respectively; 15 cm high) were each filled with 1 kg of soil mix and then infested with one isolate (12 pots each for CB-01, P-02, P-04A, and P-04B) by inserting four pathogen-colonized millet seeds (0.03 mg of millet per kilogram of soil; 3×10^{-6}%, w/w) 5 cm deep at equidistant intervals 1 cm from the perimeter of each pot. Equal numbers of sterile millet seeds were placed in another 12 pots of soil mix to serve as noninfested controls. The pots were planted to Stephens wheat, Steptoe barley, or Dark Skin Perfection green pea by placing four seeds into each of four pots (replicates) for each of the five pathosystems. Seeds were placed midway between millet seeds (3 cm deep for pea and 1.5 cm deep for wheat and barley). Pots were watered as needed, and no fertilizer was applied. Air temperature in the greenhouse varied from 15 to 28 C during the experiment.

The experimental design for each crop species was a completely randomized design. Each of the five pathogen treatments was replicated with four pots for each crop species.

At 300 growing-degree days (GDD, with 0 C base; 4) after plant emergence (14 days), the soil mixture was washed from roots. Rhizoctonia root-rot severity on the upper 5 cm of seminal roots was assessed on a scale of 0 = no lesions, 1 = lesions on <25% of first-order and <50% of second-order lateral branches, 2 = lesions on 25–50% of first-order and >50% second-order lateral branches, 3 = lesions on >50% of first-order lateral branches, 4 = lesions or severed roots on 1–2 main axes, and 5 = lesions on 3 or more main axes. This scale represents intensities and specific locations of root damage that are progressively more damaging to the health of the plant. Randomly selected roots were washed and, without surface disinfestation, placed onto 2% water agar amended with 50 μg of rifampicin/ml. Emerging fungi were transferred onto 0.5-strength potato-dextrose agar for further growth and identification.

Plant growth and development characteristics were determined on the same seedlings rated for severity of root rot. The Haun development stage (4,9) for each wheat and barley plant was estimated on the mainstem (e.g., Haun 2.8 indicates that three leaves are present, with the third leaf 80% as long as the second). The length of the longest mainstem leaf was measured to 1 mm accuracy. Presence or absence of tillers was recorded for each tiller position (9); T_0 = coleoptilar tiller, T_1 = tiller in the axil of the first leaf of the main stem, etc. Root axes of seminal and coronal roots (the primary axis and first- or second-order branches of each) crossing a horizontal plane 3- and 5-cm below the caryopsis were counted by floating washed root systems in water over a white background that had intersection lines scaled at the appropriate positions. Shoots were then cut at the soil surface position, dried in an oven, and weighed. Data for each crop were analyzed individually by analysis of variance. One isolate (P-02) of *R. oryzae* was selected for use in all subsequent experiments.

Virulence in natural soil. Soil was collected from a fallow field at the Columbia Basin Agricultural Research Center near Pendleton. Wheat plants produced previously on the field were not known to have been affected by Rhizoctonia root rot, as ascertained by inspections of roots in a plant breeding nursery located at the collection site. Nevertheless, a low level of disease was present during subsequent studies with this soil in the greenhouse, and both species of Rhizoctonia were isolated from damaged roots. The soil was a well-drained Walla Walla silt loam (coarse-silty mesic Typic Haploxeroll) with surface pH (in 0.01M $CaCl_2$) of 5.3–5.6. Undisturbed soil columns contained in 8-cm-diameter × 13-cm-high plastic cylinders were collected with a soil sampler (23) in which cylinders made from plastic drain tile are inserted into the sampling tube prior to collection. A plastic plate was placed under each soil column to retard evaporative water loss from the bottom.

Forty-eight soil columns were incubated for 4 wk at 20–28 C on a bench in the greenhouse. The soil was moistened to approximately −100 J/kg matric potential for 2 wk, and then 16 columns were infested with *R. solani* AG-8 (no. CB-01), *R. oryzae* (no. P-02), or neither pathogen. Four millet seeds of a single isolate, or noncolonized seed, were inserted into each soil column, as described previously. Soils were incubated for another 3 wk, and then four seeds of Stephens wheat were placed in each pot according to the pattern and depth described earlier. Eight replicate pots of each treatment were prepared for sampling after 300 and 600 GDD (14 and 29 days, respectively). Watering was performed as needed to create a cyclic matric potential between −100 and −1,000 J/kg. Watering was based on the soil water desorption characteristic curve for the soil, known weight of each pot and soil at the beginning of the experiment, periodic (2- to 4-day interval) weighing of each pot, and watering pots with individually calculated volumes of water (to 5-ml accuracy) when the potential approached −1,000 J/kg. No fertilizer was applied. Air temperature in the greenhouse varied from 15 to 28 C during the experiment. Sampling for root rot and plant growth and development was as described in the previous experiment. Data within each sampling period were evaluated by analysis of variance.

Controlled soil temperature experiments. These experiments were similar to the previously described ambient-temperature experiments with the following exceptions: 1) three soil-temperature ranges were used, 2) parallel and simultaneous studies were performed in natural soil and pasteurized soil mix, 3) samples were collected only at 650 GDD for the foliar canopy (35–38 days), 4) each inoculum treatment consisted of 10 replicate pots, 5) each temperature treatment consisted of two replicates (two "runs" in the same chambers, separated by a 1-yr interval), and 6) root rot of seminal and coronal roots were rated separately. Therefore, the experimental design consisted of a factorial of three temperature and three pathogen treatments, with 10 pots for each combination during each of two temperature runs. The experiment was performed for two soils (natural and potting). The potting mixture was used to evaluate virulence of *R. solani* and *R. oryzae* at different soil temperatures without the high level of microbial interactions inherent with soil collected from the field.

Soil temperature in the greenhouse was controlled by conductive heating and cooling in two cabinets (Environmental Growth Chambers, Chagrin Falls, OH; Root Zone Cabinet Model R-1). Pots of soil (drain tile cylinders described previously) collected

from the field were inserted into close-fitting holes drilled through insulated top plates on each cabinet. The top of each pot was level with the top plate of the cabinet. Each cabinet had a capacity for 60 pots and was operated at diurnal cycles to coincide with 12-h lighting cycles provided by high-pressure sodium lamps. Cabinets were separated by 1 m, and a table of equal height was placed between them for incubation of additional pots at ambient greenhouse temperature. Foliage of all plants was at ambient temperatures.

Cyclical day/night root temperatures of 27/16 C, 19/6 C, and ambient were selected to produce different root and shoot growth patterns (1,6,27). Ambient air temperature at pot height ranged from 23 to 11 C during the first run in 1990, and 25 to 12 C for the second run in 1991. Copper-constantan thermocouples were used to monitor temperatures hourly in circulating air at pot level inside each cabinet, in the center of one soil column and at foliage height above each pathogen × soil × temperature treatment, and 1 m above each of the three soil temperature treatments. Data were recorded by a CR5 Digital Recorder with 10-channel scanner and CR53 Printer (Campbell Scientific, Inc., Logan, UT). Day/night cycles for both lights and soil-temperature control cabinets were set at 12 h, with the high soil-temperature period offset from the daylight cycle by a delay of 1 h. Cabinets operated within 1 C of target temperatures, and equilibration of soil to a new temperature occurred in less than 1 h.

Photon flux densities at plant height during the light period were 120–180 μmol/m^2/s. Watering was performed as described earlier to cycle the matric potential between approximately −100 and −1,000 J/kg. No fertilizer was applied. Seminal root rot was rated on a 0–5 scale as described previously. Ratings for crown roots were based on percentages of main root axes with lesions: 0 = none, 1 = <25%, 2 = 26–50%, 3 = 51–75%, and 4 = >76%. Data consisted of means for two replicates (runs) of the experiment. Data for each pathogen × temperature treatment were analyzed separately for each soil, by analysis of variance according to a randomized complete block design (pathogen = main plot, temperature = subplot).

Field experiments. Experiments with winter wheat were conducted during 1987–1988 and 1991–1992 at the Columbia Basin Agricultural Research Center. The fields were in a 430-mm annual precipitation zone and used for winter wheat in rotation with summer fallow. The Walla Walla silt loam was moderately deep (>100 cm to hardpan) and well drained, with a surface horizon pH (in 0.01 M $CaCl_2$) of 5.3–5.6.

Experimental areas were fertilized by a broadcast application of 90 kg N/ha and 5 kg S/ha during the fallow period. Weeds in the fallow were controlled with a mechanical rod weeder. Weeds were removed manually during the 1987–1988 crop year and were controlled chemically in the 1991–1992 crop. Herbicides applied during the spring of 1992 included bromoxynil plus 2-methyl-4-chlorophenoxyacetic acid (each at 375 g active ingredient/ha, as Bronate; Rhône-Poulenc Ag Co., Research Triangle Park, NC), dicamba (125 g active ingredient/ha, as Banvel; Sandoz Crop Protection Corp., Des Plaines, IL), and triameturon-methyl plus related compound (28 g active ingredient/ha, as Harmony Extra; E.I. Du Pont de Nemours and Co., Wilmington, DE).

Wheat cultivar experiment: 1987–1988. On 25 September, an 11-row double-disk drill with a partitioned seed box was used to place air-dried millet seed colonized by *R. solani* (CB-01), *R. oryzae* (P-02), or neither into the field. The center drill row was not used, resulting in pairs of 5-row plots for each drill strip. Rows of inocula (main plots) were 60 m long and placed into moist soil 8 cm deep with 25-cm row spacing. Five treatments (main-plot rows) consisted of each pathogen delivered at inoculum rates of 18 or 42 infested millet seeds per meter (millet density = 200 seeds/g) or noninfested millet seed delivered at the high rate. The lower inoculum rate was achieved by mixing infested and noninfested millet together in the drill so that equal quantities of millet seed were dispensed in each row. Inocula in each compartment of the seed drill were rerandomized between each of three drill strips. Main plots were replicated six times.

On 27 October, all main plot rows were divided into six 8-m segments separated by 1-m alleys. Subplots consisted of six winter wheat selections planted randomly into one 8-m segment of each main plot (row). Test plants included two soft-white common cultivars (Stephens and Dusty), two soft-white club types (Tres and OR 855), and two hard-red types (Batum and Hoff). Wheat (42 seeds/m of row) was planted into dry soil at 3 cm depth (5 cm above the millet seed) with a single-row planter. Rainfall occurred on 1 November and seedling emergence occurred within 7 days. Minimum and maximum soil temperatures at 10-cm depth were recorded by an automated weather station.

Samplings were made at 300 and 600 GDD from planting (15 March and 22 April, respectively). On each date, 10 plants were removed from each subplot for plant growth and disease assessments. Measurements included disease severity index for Rhizoctonia root rot on seminal roots, number of seminal and coronal roots/plant in a plane 5 cm below the caryopsis, plant height, tillers/plant, and shoot weight. The incidence or severity of other root and shoot diseases was quantified if present and routine isolations of fungi were made from symptomatic roots as described earlier.

Grain yields were measured by threshing each subplot row individually with a single-row plot combine. Data were analyzed as a split-plot analysis of variance.

Planting date experiment: 1991–1992. Six planting dates were selected to determine effects of soil temperature on root rots of wheat caused by *R. solani* and *R. oryzae*. Planting dates (main plots) for Stephens wheat were at 15-day intervals from 1 September to 15 November 1991. Subplots included inocula of the two pathogens or noninfested millet seed placed into soil 10 days before each main plot was planted. All treatments were replicated six times.

Inoculum was placed 8 cm deep into moist soil by a six-row double-disk plot drill. The drill was equipped with a compartmented distribution system for placing individual inocula in each row. Rows were 6 m long and 30 cm apart. Inoculum subplots consisted of paired rows treated with millet seeds infested with *R. solani* AG-8, *R. oryzae,* or neither pathogen. The position of each pair of rows within the six-row subplots was rerandomized for each replicate. Inoculum was delivered at the rate of 170 millet seeds/m of row (28 kg/ha).

Stephens wheat (85 kg/ha) was planted 2–3 cm deep 10 days after infestation of each main plot. Seeds were planted with a single-row drill directly over the rows of inoculum. The field had been managed as a standard wheat-summer fallow rotation (4) prepared by chisel plow (20 cm deep) and multiple passes of a rod weeder at 5–7 cm depth. This system preserves soil moisture below the rod weeder depth and a dry, fluffy soil and straw mulch above the sharply delimited moisture line. Inoculum placed 8 cm deep was in moist soil and wheat planted 2–3 cm deep was in dry mulch. Each main plot was therefore watered by sprinkler only to wet the surface 7–8 cm so that seedling emergence was assured during an early-autumn drought. Main plots (2 m wide) were separated by a 2-m buffer planting of wheat to avoid wetting soil in adjacent main plots before they were treated with inoculum or planted to wheat. Plots were irrigated on the day of planting and at 3- to 5-day intervals for 10–15 days, until a total of 3.7 cm of water had been applied for plantings on 1 September, 15 September, and 1 October. The watering rate was 2.3 cm for the 15 October planting, at which time autumn rains began. Plantings on 1 and 15 November were not irrigated. This sequence of irrigations and rains provided approximately equivalent moisture conditions for emergence of wheat at each planting date. Temperature was the primary environmental variable across planting dates.

A data acquisition system (CR-21X Micrologger, Campbell Scientific, Inc., Logan, UT) monitored soil temperature at 10 cm depth in each main plot. Temperature data collected by six thermisters (CS-107B, Campbell Scientific) were used to determine hourly mean soil temperature. Plants were collected for sampling at leaf stages 4 to 6. Plantings on 1 and 15 September were sampled on 17 and 29 October, respectively, and all six plantings were sampled on 11 March 1992. On each date, 15 plants were removed

from each planting date × pathogen subplot for plant growth and disease assessments as described for the earlier field experiment. Plants were harvested manually on 1 July. Measurements included plant height, shoot weight, heads per meter of row, grain yield (kg/ha and g/head), and 1,000-kernel weight. Data for the three pathogen subplots within each planting date were analyzed by analysis of variance. Effects of six planting dates, three pathogens, and their interactions on plant growth and disease variables were also examined by analysis of variance according to a split-plot design, with planting date as main plots and inoculum type as subplots.

RESULTS

Selection of *Rhizoctonia* isolates. *R. solani* AG-8 (CB-01) and *R. oryzae* were both highly virulent to wheat, barley, and pea in a pasteurized soil mix (Table 1). There were no differences in virulence among the three isolates of *R. oryzae;* data for only one isolate (P-02) are reported in Table 1. Isolate P-02 was the only *R. oryzae* used for all subsequent experiments.

Ambient temperature experiment. *R. solani* was much more virulent than *R. oryzae* when placed into intact columns of soil collected from the field (Table 2). At 300 GDD and temperatures fluctuating from 15 to 28 C, *R. solani* suppressed plant growth (weight), numbers of roots at 5-cm depth, root length, and plant development. In contrast, *R. oryzae* suppressed only root length. Root rot severity was inversely correlated ($P < 0.05$) with all growth variables except plant height. Natural inoculum of *R. solani* caused a minor "background" level of root rot in the non-inoculated controls, and small black lesions on 0–5% of roots indicated the occurrence of take-all caused by *Gaeumannomyces graminis* var. *tritici.*

Pathogen effects on wheat growth at 600 GDD were identical to those at 300 GDD except that plant height was not affected by *R. solani* at the later sampling time, and *R. oryzae* increased root rot severity but did not suppress plant growth at 600 GGD. The disease index for all treatments at 600 GDD was correlated inversely with all growth variables except plant height.

Soil temperature control experiment with natural soil. Ambient air temperatures (11–23 C) for this experiment were 4–5 C lower than for the previous experiment. Both pathogens increased root rot ratings on seminal roots in the ambient treatment, but ratings for roots affected by *R. solani* were much higher ($P < 0.05$) than those affected by *R. oryzae* (Table 3). *R. solani* was the only pathogen that increased the rotting of coronal roots and suppressed plant height growth development stage, and number of roots at 5-cm depth. Results were therefore similar for comparable treatments in this and the previous experiment (Tables 2 and 3).

At low soil temperature (6–19 C), the results were nearly identical to those at ambient (11–23 C) air temperature. When the soil temperature was high (16–27 C), *R. solani* was damaging

TABLE 1. Relative virulence of *Rhizoctonia solani* AG-8 (isolate CB-01) and *R. oryzae* (isolate P-02) to seedlings of winter wheat, spring barley, and pea grown in the greenhouse in a pasteurized soil mixture at 15–28 C for 300 postemergence growing-degree days

	Inoculum				
	R. solani	*R. oryzae*	Control	LSD $P = 0.05$	$P > F$[a]
Wheat					
Root-rot index (0–5)[b]	4.8	3.7	0.3	0.4	<0.001
Root axis no./plant (5-cm depth)	1.8	2.9	3.2	0.3	<0.001
Plant height (cm)	12.5	18.1	17.3	3.7	0.009
Plant growth stage	3.7	4.4	4.4	0.4	0.013
Plant weight (mg)	57	108	116	28	<0.001
Barley					
Root-rot index (0–5)[b]	5.0	4.9	0.3	0.4	<0.001
Root axis no./plant (5-cm depth)	1.7	3.3	3.9	0.7	<0.001
Plant height (cm)	13.9	20.8	18.5	4.2	0.004
Plant growth stage	3.9	4.4	4.5	0.4	0.036
Plant weight (mg)	53	97	121	42	<0.001
Pea					
Root-rot index (0–5)[b]	4.9	4.0	0.6	0.5	<0.001
Root axis no./plant (5-cm depth)	2.6	3.3	3.8	1.1	0.001
Plant height (cm)	13.9	18.3	21.5	4.3	0.003
Plant weight (mg)	192	197	320	66	<0.001

[a] The probability of obtaining a larger value of F for the effect of inoculum in an analysis of variance.
[b] Root-rot severity index for seminal roots: 0 = lesions on <25% of first-order and <50% of second-order lateral branches, 2 = lesions on 25–50% of first-order and >50% second-order lateral branches, 3 = lesions on >50% of first-order lateral branches, 4 = lesions on 1–2 main axes, and 5 = lesions on three or more main axes.

TABLE 2. Influence of *Rhizoctonia solani* AG-8 and *R. oryzae* on root rot, growth, and development of winter wheat at two phenological ages in columns of natural soil maintained in the greenhouse at 15–28 C for 300 and 600 postemergence growing-degree days

	300 Growing-degree days					600 Growing-degree days				
	Inoculum					Inoculum				
	R. solani	*R. oryzae*	Control	LSD $P = 0.05$	$P > F$[a]	*R. solani*	*R. oryzae*	Control	LSD $P = 0.05$	$P > F$
Root-rot index (0–5)[b]	4.5	1.3	0.7	1.1	<0.001	4.8	2.1	0.7	0.8	<0.001
Root axis no./plant (5-cm depth)	10	25	27	9	0.004	13	30	28	7	0.013
Plant height (cm)	18	24	22	5	0.035	25	34	38	10	0.332
Plant growth stage	2.5	3.0	2.9	0.2	<0.001	4.0	4.4	4.5	0.2	0.002
Plant weight (mg)	28	45	46	12	0.008	93	214	192	67	0.004
Root length (cm)	10	14	17	3	0.001	14	20	20	3	0.001

[a] The probability of obtaining a larger value of F for the effect of inoculum in an analysis of variance.
[b] Root-rot severity index for seminal roots: 0 = no lesions, 1 = lesions on <25% of first-order and <50% of second-order lateral branches, 2 = lesions on 25–50% of first-order and >50% second-order lateral branches, 3 = lesions on >50% of first-order lateral branches, 4 = lesions on 1–2 main axes, and 5 = lesions on three or more main axes.

to roots but significantly less than in the cooler soils. *R. oryzae* caused significant root rot of seminal roots at high temperature but did not suppress plant growth.

Temperature effects were significant for all parameters measured on plants inoculated with *R. solani*. This pathogen was more virulent and damaging to plant growth and development at the low and ambient temperatures than at a high soil temperature. In contrast, *R. oryzae* was more virulent at the highest soil temperature, as indicated by root disease ratings, but did not suppress plant growth at high or low temperature. Significant inoculum × temperature interactions were present for root rot ratings and plant height. A small percentage (0–5%) of roots exhibited symptoms of take-all; Pythium root rot (brown root lesions by *Pythium* spp.), and common root rot (black lesions on subcrown internodes, caused by *Cochliobolus sativus*) were also present but none differed significantly ($P < 0.05$) among treatments and none was correlated with plant growth or Rhizoctonia root rot.

Soil temperature control experiment with pasteurized soil mix. Both pathogens caused severe necrosis of roots at the high soil temperature in the potting mixture (Table 3). At the lower temperatures, the virulence of *R. solani* remained high but that of *R. oryzae* declined. *R. solani* suppressed plant growth at all temperatures and had a much stronger negative effect at low temperature than at high and ambient soil temperatures. *R. oryzae* had a negative influence on number of roots at 5-cm depth at all three temperatures, but did not suppress plant height, weight, or development stage at any temperature. Root rot indices for both coronal and seminal roots in this experiment were correlated ($P < 0.001$) inversely with all plant growth variables.

Wheat cultivar experiment (1987–1988). Minimum and maximum soil temperatures at 10-cm depth on 1, 10, 20, and 30 November were 11/14, 6/9, 2/4, and 2/3 C, respectively. Soil remained cold through the winter. Minimum and maximum soil temperatures at 10-cm depth on 1 and 15 March, 1 and 15 April, 1 and 15 May, and on 1 June 1988 were 4/11, 3/7, 3/12, 12/17, 7/13, 13/22, and 9/18 C, respectively. The warmest soil (17/26 C) during this period occurred on 22 May.

Little or no difference in root rot or plant growth occurred among the six wheat cultivars at either sampling date. Plant growth and disease also were similar for the high and low inoculum rates of each pathogen. Further analysis was performed after grouping data for all cultivars and deleting data for the high rate of inoculum.

R. solani caused severe root rot and strongly suppressed plant growth at 300 and 600 GDD (Table 4 and Fig. 1, respectively) and grain yield (Table 4). There was never any evidence that *R. solani* had any effect on plants growing in adjacent rows separated from the inoculum by 25 cm (Fig. 1). *R. oryzae* caused root rot but did not significantly suppress plant growth or grain yield.

Planting date experiment (1991–1992). Mean soil temperature for the six planting dates declined from 23 C on 1 September to 5 C on 1 November (Fig. 2). The winter during the 1991–1992 wheat season was considered very mild with respect to normal for the region. Mean temperatures were generally below 5 C during December and January and then increased to 13 C by 1 May and 28 C by late June.

Seedling emergence periods lengthened as soils cooled. Days between planting and emergence were 5, 6, 5, 13, 21, and 42 for plantings made on 1 and 15 September, 1 and 15 October, and 1 and 15 November, respectively. Plant development stages for each planting were evaluated on 6 February. Tiller numbers present during the six respective plantings were 7-8, 5-7, 3-6, 0-1 (two to four leaves), 0 (one to three leaves), and 0 (one to three leaves).

Rhizoctonia root rot from native inocula was always present at low levels in noninfested control treatments (Table 5). Natural inocula caused seminal root rot ratings to be greater ($P < 0.05$) for plantings in September than in October or November. Coronal roots were affected equally by native inocula for all planting dates. *R. solani* was highly virulent to seminal roots during all planting dates but became less capable of rotting coronal roots as soil temperature declined. *R. oryzae* was moderately virulent to seminal roots of wheat planted during September but not during October or November, or to coronal roots of wheat planted at any time.

Numbers of roots that crossed a horizontal plane 3- or 5-cm below the caryopsis were decreased by *R. solani* for all six planting dates (Table 5). *R. oryzae* never suppressed root numbers at 3 cm depth but caused slight suppression in root number at 5 cm depth for plantings made on 1 September and 1 October.

TABLE 3. Influence of *Rhizoctonia solani* AG-8 and *R. oryzae* on root rot, growth, and development of winter wheat in columns of natural soil incubated at three day/night soil temperatures (results of two experiments combined)

	High[a] (27/16 C)				Ambient (23/11 C)				Low (19/6 C)				$P > F$[b]		
	R. solani	*R. oryzae*	Control	LSD $P = 0.05$	*R. solani*	*R. oryzae*	Control	LSD $P = 0.05$	*R. solani*	*R. oryzae*	Control	LSD $P = 0.05$	Rhiz.	Soil Temp.	R × T
Natural soil															
Root-rot index															
Seminal roots (0–5)[c]	3.8	3.4	1.9	0.6	4.2	2.0	1.2	0.7	4.5	1.5	1.0	0.8	<0.001	0.048	0.005
Coronal roots (0–4)[d]	1.6	0.9	0.9	0.5	2.6	0.6	0.4	0.4	2.9	0.6	0.2	0.5	<0.001	0.042	<0.001
Root axis no./plant (5-cm depth)	22	23	21	NS	18	23	22	4	16	22	21	4	0.001	0.074	0.072
Plant height (cm)	32.9	32.3	28.9	2.9	26.7	30.5	29.4	1.9	22.7	27.8	26.5	3.0	0.002	<0.001	0.001
Plant growth stage	5.0	4.3	4.1	NS	3.9	4.4	4.2	0.2	3.8	4.0	3.9	NS	0.622	0.021	0.074
Plant weight (mg)	560	602	467	90	448	540	493	62	380	448	422	51	<0.001	<0.001	0.092
Pasteurized soil mix															
Root rot indices															
Seminal roots (0–5)[c]	4.6	4.2	0.1	0.4	4.5	4.0	0.2	0.4	4.4	3.1	0.0	0.6	<0.001	0.028	0.178
Coronal roots (0–4)[d]	3.0	2.7	0.0	0.3	2.9	1.6	0.1	0.4	3.3	0.9	0.0	0.6	<0.001	0.223	0.013
Root axis no./plant (5-cm depth)	13	21	27	3	14	24	29	3	6	26	32	2	<0.001	0.118	<0.001
Plant height (cm)	25.8	30.7	28.8	3.1	20.9	28.9	28.4	2.3	11.6	27.0	28.2	2.2	<0.001	<0.001	<0.001
Plant growth stage	3.8	4.1	4.0	NS	3.6	3.9	4.0	0.1	2.7	3.8	3.8	0.4	<0.001	<0.001	<0.001
Plant weight (mg)	410	474	468	51	302	442	435	29	249	382	403	16	<0.001	<0.001	0.001

[a] Diurnal temperatures of soil columns; foliage was at ambient temperatures.

[b] The probability of obtaining a larger value of F for the effect of inoculum in an analysis of variance.

[c] Root-rot severity index for seminal roots: 0 = no lesions; 1 = lesions on <25% of first-order and <50% of second-order lateral branches; 2 = lesions on 25–50% of first-order and >50% second-order lateral branches; 3 = lesions on >50% of first-order lateral branches; 4 = lesions on 1–2 main axes; and 5 = lesions on three or more main axes.

[d] Root-rot severity index for crown roots, based on percentages of main root axes with lesions: 0 = none, 1 = <25%, 2 = 26–50%, 3 = 51–75%, and 4 = >76%.

TABLE 4. Influence of *Rhizoctonia solani* AG-8 and *R. oryzae* on root rot and growth of winter wheat seedlings in the field and on grain yield during 1987–1988

	Inoculum				
	R. solani	*R. oryzae*	Control	LSD $P = 0.05$	$P > F$[a]
300 growing-degree days					
Root-rot index (0–5)[b]	4.0	2.8	1.9	0.8	0.005
Root axis no./plant (5-cm depth)	7.1	25.4	30.3	10.7	0.006
Plant height (cm)	28.4	56.1	58.1	7.1	<0.001
Tillers/plant	1.0	3.1	3.1	0.7	0.001
Plant weight (mg)	43	269	361	162	0.014
Plant maturity					
Grain yield (g/m row)	24	337	364	36	<0.001
Grain yield (kg/ha)	624	8,724	9,444	870	<0.001

[a] The probability of obtaining a larger value of F for the effect of inoculum in an analysis of variance.
[b] Root-rot severity index for seminal roots: 0 = no lesions; 1 = lesions on <25% of first-order and <50% of second-order lateral branches; 2 = lesions on 25–50% of first-order and >50% second-order lateral branches; 3 = lesions on >50% of first-order lateral branches; 4 = lesions on 1–2 main axes; and 5 = lesions on three or more main axes.

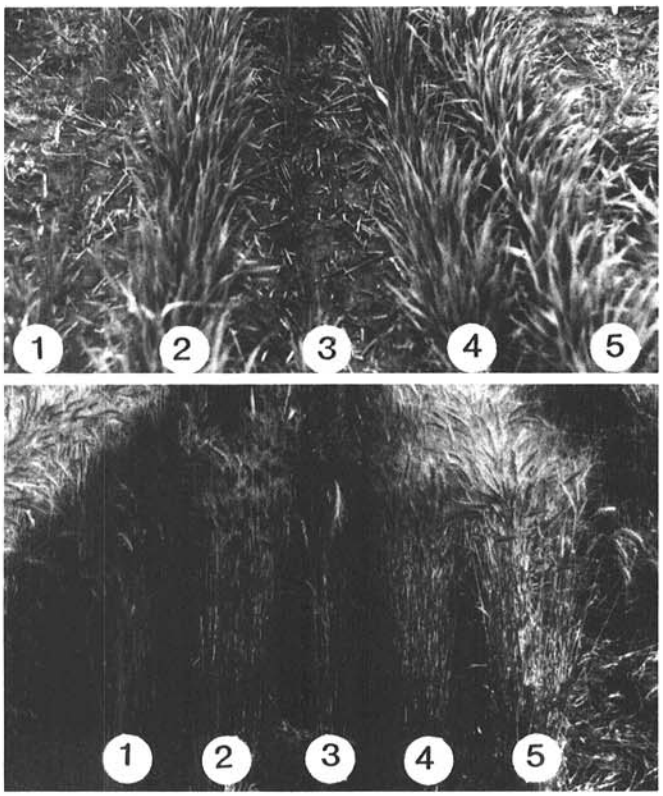

Fig. 1. Growth of seedling (top) and mature (bottom) winter wheat inoculated with *Rhizoctonia solani* AG-8 (rows 1 and 3, from left), *R. oryzae* (rows 2 and 5), or neither pathogen (row 4) during 1987–1988.

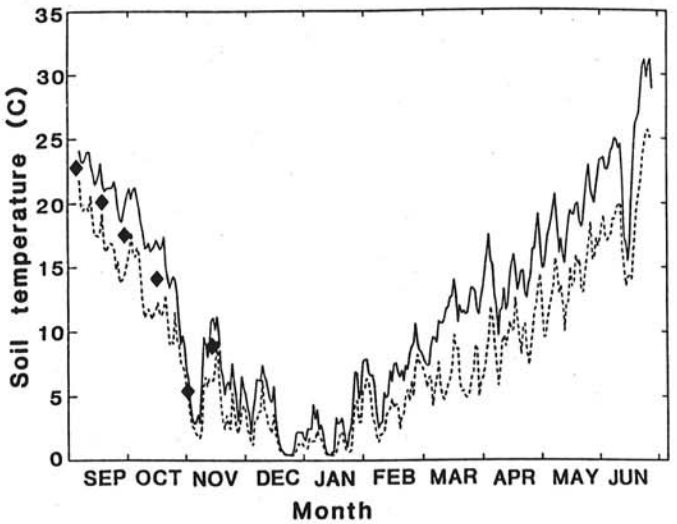

Fig. 2. Maximum and minimum soil temperatures at 10-cm depth from September 1991 to June 1992, and mean daily temperature for six planting dates (diamond) for winter wheat.

Seedlings infected with *R. solani* were always shorter than seedlings in control and *R. oryzae* treatments (Table 5). In contrast, *R. oryzae* never suppressed seedling height.

Plant development was always retarded by *R. solani* (Table 5). *R. oryzae* suppressed development of seedlings in the 15 September planting (measurement taken on 29 October), but the persistence of this effect into the spring could not be determined. Natural senescence of lower leaves during winter could have complicated or prevented springtime measurements of plant development for the September and early October plantings. These plantings, therefore, were sampled when plants in control treatments reached Haun scale readings of 4 to 6. Measurements of plant development and tillering reported in Table 5 for the 1 and 15 September plantings were made on 17 and 29 October, respectively. Senescence of lower leaves did occur for September plantings. The progression of developmental stages for each planting date are therefore comparable only for the October and November plantings, as measured on 11 March.

Development of tillers was also strongly affected by *R. solani* (Table 5). Measurements of tillers for September plantings were made during October and measurements for October and November plantings were made during March. Coleoptilar tillers (T_0) were formed in low numbers and were not affected by treatments. *R. solani* reduced the formation of tillers subtended by the first true leaf (T_1) for all except the earliest planting. This pathogen failed to reduce percentages of T_2 tillers only for the 1 October planting. Plants did not form high percentages of T_3 or T_4 tillers even in the controls, and *R. solani* had an additional suppressive effect only in the 1 September planting. *R. oryzae* reduced tillering only for plantings made on 1 (T_4 only) and 15 (T_2 only) September.

Mature plant weight, height, heads/m row, and grain yield varied significantly ($P < 0.001$) with pathogen treatments and planting dates; their interaction was significant ($P < 0.01$) for shoot weight and height, but not heads/m of row or grain yield. Additionally, 1,000-kernel weight was significantly affected by planting dates but not by pathogens or pathogen × planting date interaction. Kernel weights (g per 1,000) for the succession of six planting dates were 50, 50, 48, 49, 45, and 42 ($LSD_{0.05} = 2$).

Mature plants in *R. solani*-infested soil were stunted and had lower shoot weights than plants in noninfested soil at each of the six planting dates (Table 6). Plants infected by *R. solani* also had fewer heads/m of row than controls and *R. oryzae*- infected plants, but this was not significant in most instances. Likewise, the suppression in grain yield by *R. solani* was significant ($P < 0.05$) only for plantings on 1 September and 1 October. Differences in yields between the control and *R. solani* treatments declined

for plantings made from 1 September (2,387 kg/ha) to 15 October (199 kg/ha), and then remained similar until 15 November (384 kg/ha) (Table 6). These differences among treatments were significant for the intervals between 1 and 15 September, 15 September and 1 October, and 1 and 15 October. Yields in control treatments declined ($P < 0.05$) with delay of planting date from 1 to 15 October and 15 October to 1 November.

Several root and lower culm diseases other than Rhizoctonia root rot were present on wheat during this experiment (data not presented). Take-all occurred in several subplots but always affected fewer than 2% of the roots and was not consistent among replicates. Pythium root rot was also present on fewer than 2% of the roots, except for ratings up to 6% in control and *R. oryzae*-infested subplots during the first three planting dates. Eyespot (lesions on the lower culm, caused by *Pseudocercosporella herpotrichoides*) reached a relatively high incidence: 54, 57, 10, 22, 21, and 0% affected seedlings occurred in control subplots for the six respective planting dates ($LSD_{0.05} = 9$, $P = 0.05$). Subplots infested with *R. solani* always had a lower incidence of eyespot than the *R. oryzae* and control subplots. Significant main-effects of pathogens, planting dates, and their interaction (all $P < 0.01$) occurred for eyespot incidence. For individual planting dates, however, this relationship was significant ($P < 0.05$) only in the 1 September planting, for which percentages of plants with eyespot lesions on the culm were 54, 50, and 20 for the control and *R. oryzae*- and *R. solani*-infested subplots, respectively.

Eyespot caused up to 3% of heads to ripen prematurely (whiteheads). Significant main effects ($P < 0.001$) of planting dates but not pathogens ($P = 0.08$) occurred, and the planting date × pathogen interaction was not significant. Whiteheads in control subplots were 2, 2, 1% for the first three planting dates, and only a trace occurred in the last three plantings. Percentages of whiteheads were correlated ($P < 0.0001$) with percentages of eyespot lesions on seedlings but not with incidence or severity of Rhizoctonia root rot, Pythium root rot, take-all, or common root rot.

DISCUSSION

Rhizoctonia root rot of winter wheat was much more damaging when caused by *R. solani* AG-8 than by *R. oryzae*. Both pathogens are present in many cereal production fields (15), but soil temperatures and/or interactions with other soil microbiota appear to minimize damage to winter wheat by *R. oryzae*. Although we examined only one isolate of each pathogen, previous research (15) demonstrated a high level of stability in virulence among isolates at various temperatures.

Root damage from these pathogens in greenhouse experiments

TABLE 5. Influence of planting date on Rhizoctonia root rot caused by *R. solani* AG-8 or *R. oryzae* and on growth and development of winter wheat in the field[a] during 1991–1992

Planting date and pathogen	Root-rot index		Roots/plant		Seedling height (cm)	Plant development stage	Tiller type (% plants)				
	Seminal[b]	Coronal[c]	3-cm depth	5-cm depth			T_0	T_1	T_2	T_3	T_4
September 1											
Control	0.7	0.3	24	20	40	5.9	7	97	92	68	33
R. oryzae	2.6	0.3	22	17	41	5.6	7	90	72	46	7
R. solani	4.8	3.7	10	4	26	4.7	4	83	49	27	2
LSD (0.05)	0.4	0.3	5	2	4	0.4	NS	NS	32	31	16
September 15											
Control	0.5	0.4	37	32	43	4.4	8	97	86	5	0
R. oryzae	2.5	0.5	41	36	44	3.9	7	90	53	2	0
R. solani	4.9	3.5	24	16	35	3.2	4	22	5	1	0
LSD (0.05)	0.2	0.4	9	7	4	0.3	NS	8	21	NS	...
October 1											
Control	0.3	0.3	25	22	31	6.7	12	90	94	35	0
R. oryzae	1.1	0.3	21	17	30	6.8	7	82	89	29	0
R. solani	4.7	2.9	15	10	20	5.8	2	65	78	22	0
LSD (0.05)	0.4	0.4	4	4	5	0.9	NS	11	NS	NS	...
October 15											
Control	0.3	0.2	13	11	22	5.4	6	97	81	8	0
R. oryzae	0.5	0.3	13	11	22	5.5	8	100	93	21	0
R. solani	4.8	3.1	9	5	17	4.9	0	57	40	4	0
LSD (0.05)	0.2	0.4	2	3	3	0.4	NS	20	32	NS	...
November 1											
Control	0.3	0.3	12	10	17	4.8	4	97	74	3	0
R. oryzae	0.2	0.3	11	10	16	4.7	1	90	74	3	0
R. solani	4.6	2.5	9	5	12	4.4	4	49	35	0	0
LSD (0.05)	0.1	0.2	1	2	1	0.3	NS	11	19	NS	...
November 15											
Control	0.2	0.1	9	7	14	3.9	5	61	42	0	0
R. oryzae	0.3	0.2	9	7	14	4.0	4	58	39	0	0
R. solani	4.3	2.0	5	2	11	3.4	1	17	7	0	0
LSD (0.05)	0.5	1.0	1	2	2	0.3	NS	32	31	...	...
Table of least significant differences ($P = 0.05$)[d] between											
Planting dates	0.2	0.3	3	2	2	...	...	...	...	...	...
Pathogen	0.1	0.2	2	1	1	...	...	...	...	...	...

[a] Most samples collected on 11 March for root-rot index, root numbers, seedling height and growth stage, and tillering. (Exception: Plants in both September plantings became highly developed during the autumn and sustained natural senescence of lower leaves during winter; therefore, plant development stages and tillering reported for the 1 and 15 September plantings were measured on 17 and 29 October, respectively.)

[b] Root-rot severity index for seminal roots: 0 = no lesions, 1 = lesions on <25% of first-order and <50% of second-order lateral branches, 2 = lesions on 25–50% of first-order and >50% second-order lateral branches, 3 = lesions on >50% of first-order lateral branches, 4 = lesions on 1–2 main axes, and 5 = lesions on three or more main axes.

[c] Root-rot severity index for crown roots, based on percentages of main root axes with lesions: 0 = none, 1 = <25%, 2 = 26–50%, 3 = 51–75%, and 4 = >76%.

[d] The probability of obtaining a larger value of F in an analysis of variance was less than 0.001 for all parameters with respect to planting dates, pathogen treatments, and planting date × pathogen interactions.

differed in pasteurized and nonpasteurized soils. *R. oryzae* and *R. solani* were both damaging to roots at all temperatures in pasteurized soil. This has been reported previously (2,15). In pasteurized soil, *R. oryzae* was as virulent as *R. solani* on barley, pea, and wheat, as has also been reported (15). Although *R. solani* caused equivalent levels of root rot at all temperatures in pasteurized soil, this pathogen had a greater effect on plant growth at low than at high temperature. This response in pasteurized soil was similar to that in nonpasteurized soil. In contrast, root damage by *R. oryzae* was strongly moderated in soil that had not been pasteurized. The parasitic fitness of *R. oryzae* is apparently much lower than of *R. solani* in the presence of competitive and/or antagonistic microbiota in natural soils. A similar conclusion was reported earlier (12).

In field experiments, *R. solani* severely damaged seminal roots during each of the six planting dates. Coronal root rot became less severe as the date was delayed and soil became colder. *R. oryzae* never caused significant rotting of coronal roots, and the effect of this pathogen on seminal root rot was greatly reduced as the planting date was delayed. *R. solani* was clearly the more important of these pathogens. Disintegration of cortical tissue by *R. solani* typically led to a severe rotting of the stele, which culminated in the root being severed. In contrast, *R. oryzae* caused cortical rotting that usually did not advance into the stele and did not sever the root. The lower level of root damage by *R. oryzae* than *R. solani* was characterized by a minor, statistically insignificant depression in yield of early-seeded winter wheat by *R. oryzae* and a more pronounced depression of yield by *R. solani* for all planting dates.

R. solani severely restricted yields of winter wheat during the 1987–1988 field experiment but caused relatively mild yield constraint during 1991–1992. Relationships among pathogens and plant growth, development, and yield during these contrasting seasons were examined by performing regression analyses on data collected. The number of root intercepts was inversely correlated with severity of Rhizoctonia root rot. Variability in grain yield during both years was related mostly to numbers of root intercepts below the caryopsis during seedling growth. Yield components that were strongly influenced by numbers of root intercepts were tillers/plant, percentages of plants with tillers T_1, T_2, and T_3, head per meter row, 1,000-kernel weight, shoot weight, plant height, and plant development stage. Yield potential of each tiller is inversely proportional to the tiller order, i.e., the highest yield potential is from T_1 tillers, and the lowest contribution to yield is from T_3 and T_4. Reduction in root numbers by *R. solani* during 1991–1992 was correlated with poor development of T_2 and T_3 tillers more than with T_1. All tillers were strongly suppressed by *R. solani* during 1987–1988, the year in which yield was most affected by *R. solani*. Damage to commercial crops by Rhizoctonia root rot was also much more prevalent during 1988 than 1992 (unpublished observations). Further assessment of the data revealed a significant relationship between root numbers and tiller development and grain yield in the noninoculated control subplots during the 1991–1992 experiment.

We conclude that damage to winter wheat affected by Rhizoctonia root rot in eastern Oregon is consistent with *R. solani* AG-8 as the principal causal agent. Research on the biology and control of Rhizoctonia root rot of winter wheat in the Pacific Northwest should place emphasis on control of *R. solani*. Further, we also conclude that Rhizoctonia root rot affects yield primarily by suppressing tiller development. A similar conclusion was reached for the relationship between powdery mildew and wheat yield

TABLE 6. Influence of planting date and *Rhizoctonia solani* AG-8 or *R. oryzae* on grain yield, yield components, and shoot height and weight of mature winter wheat in the field[a] during 1991–1992

Planting date and pathogen	Yield (g/m row)	Yield (kg/ha)	Shoot weight (g/m row)	Heads /m row	Plant height (cm)	1,000-kernel weight (g)	Head weight (g/head)
September 1							
Control	477	6,850	868	161	99	49	1.7
R. oryzae	394	5,651	698	154	96	50	1.4
R. solani	311	4,463	524	114	80	50	1.5
LSD (0.05)	136	1,951	185	NS	5	NS	NS
September 15							
Control	445	6,391	702	192	97	49	1.3
R. oryzae	379	5,439	623	174	94	50	1.2
R. solani	341	4,889	529	139	80	50	1.3
LSD (0.05)	NS	NS	154	38	3	NS	NS
October 1							
Control	433	6,215	659	178	93	47	1.4
R. oryzae	425	6,105	649	168	93	47	1.4
R. solani	363	5,205	532	157	83	48	1.3
LSD (0.05)	59	840	68	NS	4	NS	NS
October 15							
Control	342	4,914	511	138	89	48	1.4
R. oryzae	349	5,013	507	145	89	49	1.3
R. solani	329	4,715	455	122	79	49	1.5
LSD (0.05)	NS	NS	NS	NS	3	NS	NS
November 1							
Control	283	4,057	424	111	84	46	1.5
R. oryzae	275	3,953	408	102	81	46	1.5
R. solani	265	3,800	372	90	72	45	1.6
LSD (0.05)	NS	NS	44	NS	6	NS	NS
November 15							
Control	244	3,500	321	80	73	41	1.7
R. oryzae	224	3,214	292	77	73	41	1.6
R. solani	217	3,116	279	79	66	42	1.5
LSD (0.05)	NS	NS	NS	NS	3	NS	NS
Table of least significant differences ($P = 0.05$)[b] between							
Planting dates	41	595	59	17	3	2	0.2
Pathogen treatments	30	431	41	13	2	NS	NS
pathogen × date	NS	NS	**	NS	**	NS	NS

[a] Sampling was performed on 1 July 1992.

[b] The probability of obtaining a larger value of F in an analysis of variance was less than 0.001 for all parameters with respect to planting dates and pathogen treatments, and less than 0.01 (**) or not significant (NS) at $P = 0.05$ for pathogen × planting date interactions.

(5). In spring cereals that have less tillering capacity than winter wheat, yield was not directly related to severity of Rhizoctonia root rot and a 2- to-3- wk delay in plant maturation was associated with root damage from *R. solani* AG-8 (22). This pathogen consistently retarded plant development for winter wheat in the present study, but the maturation date for plants subjected to various treatments was not recorded. The effect of Rhizoctonia root rot on yield therefore appears to depend on interactions of disease with ever-changing environmental influences that also affect tillering (10,11,16,17,19,20,28). These complex interactions are expected to vary seasonally, annually, and possibly with inherent differences in tillering characteristics among cultivars of winter wheat (10).

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