Agroecological Factors Correlated to Soil DNA Concentrations of *Rhizoctonia* in Dryland Wheat Production Zones of Washington State, USA

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ABSTRACT

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The necrotrophic soilborne fungal pathogens *Rhizoctonia solani* AG8 and *R. oryzae* are principal causal agents of Rhizoctonia root rot and bare patch of wheat in dryland cropping systems of the Pacific Northwest. A 3-year survey of 33 parcels at 11 growers' sites and 60 trial plots at 12 Washington State University cereal variety test locations was undertaken to understand the distribution of these pathogens. Pathogen DNA concentrations in soils, quantified using real-time polymerase chain reaction, were correlated with precipitation, temperature maxima and minima, and soil texture factors in a pathogen-specific manner. Specifically, *R. solani* AG8 DNA concentration was negatively correlated with precipitation and not correlated with temperature minima, whereas *R. oryzae* concentration

was correlated with temperature minima but not with precipitation. However, both pathogens were more abundant in soils with higher sand and lower clay content. Principal component analysis also indicated that unique groups of meteorological and soil factors were associated with each pathogen. Furthermore, tillage did not affect *R. oryzae* but affected *R. solani* AG8 at $P = 0.06$. Lower soil concentrations of *R. solani* AG8 but not *R. oryzae* occurred when the previously planted crop was a broad-leaf ($P < 0.05$). Our findings showed that *R. solani* AG8 concentrations were consistent with the general distribution of bare patch symptoms, based on field observations and surveys of other pathogens, but was present at many sites in which bare patch symptoms were not evident. Management of Rhizoctonia root rot and bare patch should account for the likelihood that each pathogen is affected by a unique group of agroecological variables.

Additional keywords: agroclimate zone, direct seed.

Rhizoctonia root rot, bare patch, and damping-off have long been recognized as chronic, yield-reducing diseases in small-grain cereal production systems in the Pacific Northwest (PNW), United States, and Australia (3,12,37). Principal causal agents in the PNW are *Rhizoctonia solani* Kühn AG8 (teleomorph *Thanatephorus cucumeris* (A. B. Frank) Donk) and *R. oryzae* Ryker & Gooch (teleomorph *Waitea circinata* Warcup & P. H. B. Talbot) (17,23,27). *R. solani* AG8 is associated with root rot and bare patches in small-grain cereals planted to direct-seeded (no-till) fields (4,24,26). Infections of *R. oryzae* cause uneven stand height and, in severe cases, seedling death of wheat and barley (27,34) and can cause symptoms in pea and other legumes (22). *R. oryzae* is often present in the same locations as *R. solani* AG8. Genotype III of *R. oryzae* was abundant and the most virulent of the three genotypes found in the PNW (14,17); hence, it was selected for this survey. Based on internal transcribed sequence (ITS) sequence identities, *R. oryzae* genotype III was most closely related to *W. circinata* var. *circinata* (17). Current management of *R. solani* AG8 and *R. oryzae* includes a combination of tillage, fungicide seed treatment, and control of volunteers and weeds

between plantings (green bridge control), and is based on the assumption that the pathogens occur as a complex.

The dryland wheat cropping zone of eastern Washington (east of the Cascade Range) encompasses a contiguous area of >150,000 km², has been cropped for >100 years, and covers a wide range of soil and climatic variations (31) (<http://www.wsdot.wa.gov/publications/fulltext/hydraulics/wameanannprecip.pdf>). In central Washington, in the rain shadow of the Cascades, annual precipitation is <200 mm but increases to >600 mm in the eastern part, along the Idaho border (known as the Palouse area). Likewise, there is a west–east gradient of soil texture, with lighter, sandy silt loams in the western arid zone and silt-loams with higher clay content in the eastern section. In addition, the topography in the eastern section is steep, with hills of deep wind-deposited silt loams up to 100 m in height. Finally, there is a general north–south gradient of temperature and a longitudinal west–east decrease in temperature associated with the elevation increase in the Palouse. Because of the precipitation limitations, three general cropping zones can be recognized. The first is the winter wheat–summer fallow zone in the driest areas (150 to 300 mm of annual precipitation), where a crop is only planted every other year. The fallow year is used to store moisture in the soil profile. Winter wheat is planted in August to September into a moisture zone under a dust mulch, and harvested the following July to August. In the second zone (300 to 400 mm), a cereal crop (spring or winter wheat or spring barley) is planted 2 out of 3 years, with a fallow the third year. In the wettest zone (400 to 600 mm) a crop is planted every year in a 3-year rotation (winter wheat/spring wheat or spring barley/broadleaf crop. The broadleaf

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crop is usually canola or a grain legume such as pea, lentil or chickpea).

Over the last decade, efforts have been made to identify the major pathogenic *Rhizoctonia* spp. and understand how species distribution of *Rhizoctonia* is related to climate and cropping practices in different growing regions. The ultimate goal is to optimize management of *Rhizoctonia* root rot and bare patch for each growing region. Much of the work was based on culturing fungi from soil and plants using a toothpick baiting assay (25). In the mid 2000s, a real-time quantitative polymerase chain reaction (PCR) method was developed to quantify *Rhizoctonia* spp. from the soil (17,32). We used this technique in a 3-year survey to quantify soil DNA concentrations of *R. solani* AG8 and *R. oryzae* at variety test locations and grower fields across PNW cropping zones. In addition, we correlated pathogen distributions with the meteorological factors (precipitation and temperature) and soil texture factors to better understand how these abiotic factors shape the geographic distribution of pathogens across this large, diverse cropping region.

MATERIALS AND METHODS

Sampling sites and sample collection. Soil samples were collected at 33 parcels from 11 grower locations and 60 plots at 22 locations of the Washington State University (WSU) Cereal Variety Testing Program. Growers' parcels ranged in area from 5,600 to 30,000 m², and variety test plots were ≈2,000 to 3,000 m². Soils were collected from the end of April through mid-June, depending upon the soil moisture at each site. Global Positioning System (GPS) coordinates for growers' parcels were determined in the first year of sampling using an AGGPS 332 GPS receiver (Trimble Navigation Ltd., Sunnyvale, CA); these coordinates were used in the two subsequent years. GPS coordinates of the variety test plots, which moved from year to year, were obtained using Google Earth (9). Soil cores (2.5 cm in diameter by 15 cm deep) were obtained from the root zone in the seeded row. Samples from grower parcels consisted of five cores taken along each of three parallel transects per parcel (Fig. 1A). Samples from cereal variety test plots consisted of five cores from each of five diagonal transects per plot (Fig. 1B). The five cores from each transect were pooled, constituting one subsample. The less intensive sampling (fewer samples per unit area) at growers' parcels was mainly due to the economics of sample processing. In total, 582 samples were obtained from soil collections carried out in 2006, 2007, and 2008. Soil samples were stored at 4°C prior to

DNA extraction. The subsamples served as replicates for the parcel or plot in statistical analyses.

Soil extractions and real-time PCR. Total DNA was extracted from 0.5 g fresh weight of soil for each sample, as described by Okubara et al. (16). Briefly, soil was suspended in 300 µl of bead solution, 60 µl of buffer S1, and 120 µl of Inhibitor Removal Solution (UltraClean Soil DNA Kit; MO BIO Laboratories, Solana Beach, CA) and subjected to 15 cycles of 35,000 psi (235 MPa) for 20 s alternated with 5 s of ambient pressure. Following the pressure cycling extraction, samples were processed according to the UltraClean soil DNA kit protocol (16). Primers for real-time PCR are described by Okubara et al. (17). Standard curve equations for pathogen DNA quantification were cycle threshold (Ct) = -3.805(log pg DNA) + 28.388 for *R. solani* AG8 and Ct = -3.857(log pg DNA) + 29.814 for *R. oryzae* genotype III. Pathogen concentration was calculated from the standard curves as picograms of DNA per gram of soil.

Meteorological and agroclimate data. The meteorological data consisted of precipitation (in millimeters), and maximum and minimum temperatures (in °C) from 1979 to 2010, scaled to 4 km (1). We extracted data from pixels co-located with site GPS coordinates. For correlations between pathogen concentrations and meteorological data, we used the following subsets of precipitation data: (i) cumulative precipitation (Pre; in millimeters) for October of the year prior to sampling through June of the sampling year (Oct-Jun), representing the wettest 9-month interval of the winter wheat growing season; (ii) cumulative precipitation for the 3 months prior to the sampling date (March to May [Mar-May]); and (iii) cumulative precipitation for the three driest months in the year prior to sampling (July to September [Jul-Sep]). For the Bickleton sites, data for April to June (Apr-Jun) was used instead of that for Mar-May, because these sites were sampled in mid-June. Average maximum (Max) and minimum (Min) temperatures were determined for the same Oct-Jun and Mar-May intervals. Additionally, we considered Jul-Sep, as used for precipitation, for the "warmest" maximum temperature interval, and November of the year prior to sampling through March of each sampling year (Nov-Mar) for the "coldest" minimum temperature interval.

Each sampling location was assigned a precipitation zone (PZ1 to 3) based on previous annual rainfall averages listed at the WSU Cereal and Grain Legume Variety Testing website (<http://variety.wsu.edu/>), where PZ1 = <305 mm (12 in.), PZ2 = 305 to 508 mm (12 to 20 in.), and PZ3 = >508 mm of annual precipitation. Agroclimate zones (ACZs) were determined from the GPS coordinates for each location using ArcMap 9.3 (ArcGIS Server 9.3; ESRI, Redlands, CA). The ACZs were defined by Douglas et al. (5) as 1 = annual crop-wet-cold, 2 = annual crop-wet-cool, 3 = annual crop-fallow-transition, 4 = annual crop-dry, 5 = grain-fallow, and 6 = irrigated, and were adjusted to current cropping practices, in cases where they had shifted in the transition zones over the last 20 years.

Soil texture properties. The percentages of silt, clay, and sand were determined for all GPS coordinates using ArcMap 9.3 (ESRI) (21). The rating options were "weighted average" for Aggregation Method, "higher" for Tie-Break Rule, and top depth of 1 cm and bottom depth of 10 cm for Layer Options. These specifications generated soil texture values from data for the upper 10 cm of soil where available.

Tillage and rotation. Tillage practice and crop field history (rotation) data were collected from the grower cooperators in this study (Table 1). Tillage and cropping history were assigned numbers for subsequent analysis of their effects on pathogen DNA concentration using JMP (SAS Institute, Inc., Cary, NC), as described in the "Analysis of variance and pairwise correlation analyses" section. Parcels were categorized as 1 if they were direct-seeded at the time of sampling and 2 if they were tilled. Crop types were cereal (wheat or barley) = 1, broadleaf (pea,

Fig. 1. Diagrams of soil cores taken from **A**, growers' parcels and **B**, variety test plots. Five pooled soil cores from each of three subsamples were collected from each of the growers' parcels across the width of the parcel. Five pooled cores from each of five subsamples were collected diagonally across the length of each plot. Black shapes in A and in B indicate where global positioning system coordinates were acquired relative to the cores.

chickpea, lentil, or canola) = 2, and fallow = 3. Information about the crop planted immediately prior to the sampled wheat in variety test plots was available through the WSU Cereal and Grain Legume Variety Testing website.

Pathogen data transformations. Values for pathogen DNA were converted from picograms per gram of soil to femtograms per gram + 1, to assign a positive value of 1.0 to samples in which no pathogen was detected. Transformed values, converted to log₁₀ femtogram DNA, were used for all statistical analyses. Year-by-year comparisons were done on samples from 28 growers' parcels at nine locations and 20 variety test plots at 11 locations that were obtained in all three sampling years (2006 to 2008). Samples in which pathogen was not detected or quantified were excluded from correlation analyses and principal component analyses (PCAs), after frequency analysis showed that these zero samples were evenly distributed across all climate zones and comprised 40 to 60% of the samples in all locations. Data from growers' parcels and variety test plots were combined for *R. solani* AG8 and *R. oryzae*.

Analysis of variance and pairwise correlation analyses. One grower location in each of three cropping zones was selected for year-to-year comparisons of precipitation and temperature maxima and minima. Parcels CH1 to CH3, HJ1 to HJ4, and DH1 to DH3 represented PZ1, PZ2, and PZ3, respectively. Means and standard deviations were obtained for each sampling year, and means were separated into classes using Fisher's protected least significant difference at $P < 0.05$ (Statistix version 8.1; Analytical Software, Tallahassee, FL).

Effects of tillage and previously planted or current crop type (cereal, broadleaf, or fallow) were tested for effects on log-transformed concentrations of *R. solani* AG8 or *R. oryzae* using the Fit Model algorithm of JMP 10.0.0 (SAS Institute, Inc.). The number of samples from direct-seeded and tilled parcels was balanced ($n = 58$ of each for 2006 to 2008). Significance of effects was examined using Student's *t* test or Tukey's honestly significant difference models in JMP. Data from all three sampling years were combined for this analysis. Effect tests were also performed to determine whether pathogen DNA concentration varied by PZ or by year.

Pearson's algorithm of the PROC CORR Procedure (SAS version 9.2; SAS Institute, Inc.) was used to carry out pairwise correlation analyses between pathogen DNA concentrations and meteorological or soil texture data from the combined 2006 to 2008 data set, with grower fields and variety testing sites combined.

PCA. For PRINCOMP analysis, growers' parcels BS and PM (collected in 2007 and 2008), SM3-SM5 (collected in 2006, 2007, and 2008, respectively), and variety test plot samples from Bickleton (collected only in 2008) were omitted because they were not represented in all 3 years of the survey. Each set of pathogen DNA data was analyzed simultaneously with precipitation, temperature, and soil texture variables that were found to be significantly correlated in the PROC CORR analysis; variables with no significant correlation to the specific pathogen were omitted. Variables (factors) were co-analyzed using PRINCOMP (SAS Institute, Inc.). The number of principal components (Prins)

TABLE 1. Grower parcels sampled for this survey, and corresponding soil texture properties

Parcel ^a	Location ^b	Tillage	Rotation ^c	PZ ^d	ACZ	Soil texture properties (%) ^e		
						Silt	Clay	Sand
DH1	Pullman, Whitman	Tilled	Chickpea-WW-SW	3	2	67.7	21.0	11.3
DH2			SW-SW-chickpea	3	2	67.7	21.0	11.3
DH3			WW-SW-chickpea	3	2	67.7	21.0	11.3
BN1	Farmington, Whitman	Direct seeded	SW-pea-WW	3	2	71.0	15.0	14.0
BN2			Pea-WW-SW	3	2	71.0	15.0	14.0
BN3			WW-SW-lentil	3	2	67.7	21.0	11.3
RP1	Garfield, Whitman	Direct seeded	WW-WW-WW	3	2	67.7	21.0	11.3
RP2			WW-WW-WW	3	2	68.0	22.5	9.5
RP3			SW-SW-WW	3	2	52.0	21.0	24.5
RP4			WW-WW-SW	3	2	68.0	10.3	9.5
BS1	Spangle, Spokane	Direct seeded	ns-SW-lentil	2	4	69.5	19.9	10.6
BS2			ns-lentil-WW	2	4	69.5	19.9	10.6
HJ1	Davenport, Lincoln	Tilled	WW-SW-fallow	2	4	73.2	12.5	14.3
HJ2			Barley-WW-SW	2	4	73.2	12.5	14.3
HJ3			SW-SW-SW	2	4	73.2	12.5	14.3
HJ4			Canola-SW-WW	2	4	73.2	14.0	14.3
JA1	Almota, Whitman	Direct seeded	SW-SW-WW	2	3	67.7	21.0	11.3
JA2			WW-SW-WW	2	3	67.7	21.0	13.6
PM1	Spangle, Spokane	Direct seeded	(SW)-lentil-WW	2	4	65.4	14.5	20.1
PM2			(SW)-lentil-WW	2	4	65.4	14.5	20.1
RS1	Steptoe, Whitman	Tilled	WW-SW-pea	2	2	67.7	21.0	11.3
RS2			SW-pea-WW	2	2	67.7	21.0	11.3
RS3			Pea-WW-SW	2	2	67.7	21.0	11.3
CH1	Ralston, Adams	Tilled	WW-tilled fallow-WW	1	5	70.8	7.5	21.7
CH2			SW-tilled fallow-WW	1	5	70.8	7.5	21.7
CH3			Canola-SW-WW	1	4	70.8	7.5	21.7
RJ1	Ritzville, Adams	Direct seeded	SW-SW-SW	1	5	70.8	7.5	21.7
RJ2			Fallow-WW-fallow	1	5	70.8	7.5	21.7
RJ3			WW-fallow-WW	1	5	70.8	7.5	21.7
SM1	Bickleton, Klickitat	Direct seeded	SW-SW-SW	1	4	71.8	14.0	14.2
SM2			WW-SW-SW	1	4	71.8	14.0	14.2

^a Parcels BS1-BS2 and PM1-PM2, sampled in 2007 and 2008, and SM3, SM4, and SM5, sampled in 2006, 2007, and 2008, respectively, were omitted from ANOVA because they occurred at different Global Positioning System locations.

^b Nearest town, county.

^c Crops in the parcel in 2006, 2007, and 2008. SW = spring wheat; WW = winter wheat; parentheses = rotation known but sample not taken that year; ns = rotation unknown, sample not taken.

^d Precipitation zone, where 1 = <305 mm (12 in.), 2 = 305 to 508 mm (12 to 20 in.), and 3 = >508 mm (20 in.) of annual precipitation.

^e Agroclimate zone (ACZ) and soil texture properties determined using ArcMap 9.3 (ArcGIS Server 9.3; ERSI, Redlands, CA), where ACZs are 1 = annual crop-wet-cold; 2 = annual crop-wet-cool; 3 = annual crop-fallow-transition; 4 = annual crop-dry; and 5 = grain-fallow (5).

used in the analyses was determined by the number of eigenvalues of the correlation matrix >1.0. Component Pattern plots were generated to observe the relative variation within each variable and to plot clustering of variables. Component Score plots were used to visualize the sampling sites relative to the two major components of variation, Prin1 and Prin2, to determine which groups of factors explained the separation of sampling sites.

A second analysis was done using JMP 10.0 Principal Component (SAS Institute, Inc.); pathogen DNA concentration data; and all precipitation, temperature, and soil texture variables, regardless of whether they were significantly correlated in the PROC CORR analysis. Data from growers' parcels and variety test plots for 2006 to 2008 were combined but Bickleton samples were omitted. Biplots showing the vector length and directions of the variables were constructed using the Multivariate Methods program, and significant ($P < 0.05$) correlations among factors were determined using the Multivariate and Pairwise Correlations algorithms of JMP 10.0.

RESULTS

Our parcel/plot sampling scheme, shown in Figure 1, was intended to account for the patch-like occurrence of *Rhizoctonia* spp. in the field (28). In total, 582 soil samples were collected in 2006 to 2008. These included growers' parcels (Table 1) and variety test plots (Table 2). However, a subset of 495 samples that

carried *R. solani* AG8 or *R. oryzae* and were from locations common to all 3 years were used for analyses. Analysis of variance (ANOVA) showed no significant differences in pathogen DNA concentration among the sample reps or subsamples (transects) within each parcel. However, 40 to 60% of the samples were zero values (no DNA detected). The frequency of zero values for *R. solani* AG8 at all sites, plotted relative to total precipitation for the Mar-May interval, is shown in Supplemental Figure 1. Rainfall varied from year to year; therefore, the data in each bar did not always represent a single PZ; however, the expected trend is that bars at the left portion of the graph mainly comprised samples from PZ1. Despite the expectation that *R. solani* AG8 should occur more often in low-PZs, the zero samples were evenly distributed across all zones. This was attributed to the equal occurrence and distribution of spots or patches of the pathogens in all zones (28). Analysis of correlations and PCAs were carried out using only the data where the pathogen was detected or quantified. Growers' parcels were monotonic with respect to cultivar and GPS location and were sampled less intensively than variety test plots. However, spatial variability in pathogen DNA concentration was similar for the sampling scales at both types of sites, and parcels or plots did not give significant effects in ANOVA.

Yearly variation in meteorological and pathogen data. The growers' parcels and variety test plots used in this study were representative of dryland wheat production systems in the state of Washington. The sites generally sustained more precipitation and

TABLE 2. Washington State University cereal variety testing sites and corresponding soil properties used in this survey

Test plot ^a	County	Years sampled	PZ ^b	ACZ	Soil texture properties (%) ^c		
					Silt	Clay	Sand
Bickleton SW	Klickitat	2008	1	4	71.8	14.0	14.2
Bickleton WW		2008	1	4	68.8	10.0	21.1
Connell SW	Franklin	2006, 2007, 2008	1	5	70.8	7.5	21.7
Connell WW		2006, 2007, 2008	1	5	70.8	7.5	21.7
Harrington WW1	Lincoln	2006, 2008	1	5	70.8	7.6	21.7
Harrington WW2		2007	1	5	69.9	8.5	14.6
Lind SW	Adams	2006, 2007, 2008	1	5	70.8	7.5	21.7
Lind WW1		2006, 2008	1	5	70.8	7.5	21.7
Lind WW2		2007	1	5	70.8	7.5	21.7
Ritzville SW	Adams	2006, 2007	1	5	70.8	7.5	21.7
Ritzville WW		2006, 2007, 2008	1	5	70.8	7.5	21.7
Dayton SW1	Columbia	2006	2	2	68.9	17.5	13.6
Dayton SW2		2007	2	2	67.7	21.0	11.3
Dayton SW3		2008	2	2	68.9	17.5	13.6
Dayton WW		2006, 2007, 2008	2	2	68.9	17.5	13.6
Dusty SW1	Whitman	2006	2	3	73.2	12.5	14.3
Dusty SW2		2008	2	3	68.9	17.5	13.6
Dusty WW1		2006	2	3	73.2	12.5	14.3
Dusty WW2		2007, 2008	2	3	57.4	9.5	33.1
St. John SW	Whitman	2006, 2007, 2008	2	3	68.9	17.5	13.6
St. John WW		2006, 2007, 2008	2	3	68.9	17.5	13.6
Walla Walla SW1	Walla Walla	2006, 2008	2	3	73.2	12.5	14.3
Walla Walla SW2		2007	2	3	71.8	14.0	14.2
Walla Walla WW1		2006, 2007	2	3	73.2	12.5	14.3
Walla Walla WW2		2008	2	2	71.8	14.0	14.2
Colton WW1	Whitman	2006	3	2	71.0	15.0	14.0
Colton WW2		2007	3	2	68.6	23.5	11.4
Colton WW3		2008	3	2	52.0	23.5	24.5
Farmington SW	Whitman	2006, 2007, 2008	3	2	71.0	15.0	14.0
Farmington WW1		2006	3	2	71.0	15.0	14.0
Farmington WW2		2007	3	2	54.0	23.5	19.0
Farmington WW3		2008	3	2	54.0	27.0	19.0
Pullman SW	Whitman	2006, 2007, 2008	3	2	67.7	21.0	11.3
Pullman WW1		2006	3	2	54.0	27.0	19.0
Pullman WW2		2007	3	2	54.0	27.0	19.0
Pullman WW3		2008	3	2	69.3	18.2	12.6

^a In all, 36 winter wheat (WW) and spring wheat (SW) trials grouped by precipitation zone (PZ). Sites (plots) are labeled 1 to 3 among the sampling years if their Global Positioning System coordinates resulted in differences in one or more variables. In total, 60 samples were collected at the 36 sites from 2006 to 2008.

^b PZ1 = <305 mm (12 in.), PZ2 = 305 to 508 mm (12 to 20 in.), and PZ3 = >508 mm (20 in.) of annual precipitation.

^c Soil texture properties and agroclimate zones (ACZs) obtained using ArcMap 9.3 (ArcGIS Server 9.3; ERSI, Redlands, CA), where ACZs are as follows: 1 = annual crop-wet-cold; 2 = annual crop-wet-cool; 3 = annual crop-fallow-transition; 4 = annual crop-dry; and 5 = grain-fallow (5).

slightly higher minimum temperatures in 2006 compared with 2007 and 2008, as represented by selected grower sites (Supplemental Table 1). Maximum temperatures were slightly higher in PZ1 and PZ2 in 2007. *R. solani* AG8 and *R. oryzae* genotype III were present in growers' parcels in all three sampling years (Table 3). JMP-based effect tests indicated that both pathogen DNA concentrations significantly ($P < 0.05$) differed by year but only that of *R. solani* AG8 was affected by PZ (data not shown). It is important to note that DNA values for each pathogen result from a pathogen-specific standard curve and are not directly comparable across pathogen species.

Pathogen DNA concentrations are correlated to meteorological and soil texture properties in a pathogen-specific manner. Correlation coefficients and P values (<0.05 only) for pathogen DNA concentrations in growers' parcels and variety test plots, plus meteorological or soil texture variables, are shown in Table 4. *R. solani* AG8 DNA concentration was negatively correlated ($P < 0.05$) with cumulative rainfall for the 3 months prior to sample collection (Mar-May), to the "wettest" interval (Oct-Jun) prior to and during pathogen sampling, and to the "driest" 3-month interval prior to sample collection (Jul-Sep) (Table 4; Fig. 2). Significant correlations also were observed between *R. solani* AG8 and percent clay (negative) or percent sand (positive). Average monthly maximum temperatures for the Mar-May and Jul-Sep intervals and percent sand were significantly ($P < 0.05$) and positively correlated with *R. solani* AG8 (Table 4). These findings indicate that *R. solani* AG8 is more abundant in areas with lower precipitation, higher sand or lower clay content, and

higher average air temperatures. Concentrations of *R. oryzae* DNA were similarly associated with average maximum temperature for the Mar-May interval and clay and sand content. However, *R. oryzae* was also positively correlated to average monthly temperature maxima for the Oct-Jun interval but not the Jul-Sep interval, and to average monthly temperature minima for all three intervals. This pathogen was not correlated to precipitation (Table 4). The data suggest that *R. oryzae* occurs across all PZs, in areas having sandy rather than clay soil and cooler average air temperatures in the summer months relative to *R. solani* AG8.

Effects of tillage and rotation on *Rhizoctonia* DNA concentrations. To test the hypotheses that *Rhizoctonia* spp. accumulated more in direct-seeded than in tilled fields, we analyzed the effect of tillage practice on pathogen concentrations in growers' parcels across three Washington PZs and four ACZs for the combined three sampling years. *R. solani* AG8 was higher in direct-seeded plots at $P = 0.06$, with a significant interaction with year ($P = 0.002$). The values (direct-seed/tilled) were 2.79/2.44, 3.16/2.76, and 3.22/3.11 log fg DNA in 2006, 2007, and 2008, respectively. However, there was no effect of tillage on *R. oryzae* ($P = 0.22$).

Data from the growers' parcels and variety test plots were combined for analysis of the effect of the previously planted crop on *R. solani* AG8 and *R. oryzae*. The effect of previous crop on *R. solani* AG8 was found to be significant ($P = 0.0234$) and was attributed to a reduction in pathogen concentration when the previously planted crop was a broadleaf, usually a legume such as pea. There was no interaction between previous crop and year

TABLE 3. Pathogen concentrations found at growers' parcels and variety test plots averaged over the 3-year survey period^a

Species	Growers' parcels			Variety test plots		
	PZ	fg DNA ^b	Prevalence	PZ	fg DNA ^c	Prevalence
<i>Rhizoctonia solani</i> AG8	1	5,000 ± 1,865	0.917	1	1,096 ± 372	1.000
	2	1,520 ± 980	0.733	2	820 ± 212	0.909
	3	261 ± 78	0.633	3	164 ± 42	0.867
<i>R. oryzae</i>	1	1,990 ± 688	0.583	1	1,117 ± 731	0.600
	2	1,470 ± 875	0.667	2	561 ± 218	0.500
	3	597 ± 301	0.433	3	594 ± 322	0.600

^a PZ = precipitation zone: 1 = <305 mm (12 in.), PZ2 = 305 to 508 mm (12 to 20 in.), and 3 = >508 mm (20 in.) of annual precipitation; and Prevalence = fraction of parcels or plots in which the pathogen was detected or quantified.

^b Means ± standard error (SE) for pathogen concentrations expressed as fg g⁻¹ of soil +1. PZ1 = three locations, 8 parcels per year, $n = 24$; PZ2 and PZ3 = three locations, 10 parcels per year, $n = 30$.

^c Means ± SE for soil DNA concentrations in fg g⁻¹ of soil +1. PZ1 = four locations, six to seven plots per year, $n = 20$; PZ2 = four locations, seven to eight plots per year, $n = 22$; and PZ3 = three locations, five plots per year, $n = 15$.

TABLE 4. Correlation coefficients and probabilities (in parentheses) between pathogen concentrations in log fg DNA and global positioning system-based precipitation, temperature, or soil texture properties in growers' parcels and variety test plots^a

Properties	<i>Rhizoctonia solani</i> AG8	<i>R. oryzae</i>
Cumulative precipitation ^b		
March–May	–0.29951 (<0.0001)	ns
October–June	–0.32585 (<0.0001)	ns
July–September	–0.35941 (<0.0001)	ns
Maximum temperature ^c		
Average March–May	0.19185 (0.0011)	0.24408 (0.0016)
Average October–June	ns	0.22204 (0.0042)
Average July–September	0.25238 (<0.0001)	ns
Minimum temperature ^c		
Average March–May	ns	0.20001 (0.0100)
Average October–June	ns	0.25156 (0.0011)
Average November–March	ns	0.23971 (0.0019)
Soil properties ^d		
Percent clay	–0.23769 (<0.0001)	–0.31077 (<0.0001)
Percent sand	0.25224 (<0.0001)	0.19873 (0.0105)
Percent silt	ns	ns

^a Probabilities (in parentheses) if $P \leq 0.05$; ns = not significant ($P > 0.05$).

^b Cumulative precipitation (mm) for the specified intervals relevant to each sampling year.

^c Monthly average maximum or minimum temperatures for the specified intervals relevant to each sampling year.

^d Obtained using ArcMap 9.3 (ArcGIS Server 9.3; ESRI, Redlands, CA).

($P = 0.7587$); thus, the average value for *R. solani* was 2.9 log fg DNA when the previous crop was a cereal, 2.5 when the previous crop was a broadleaf, and 2.8 when in fallow the previous year. No effect of previously planted crop on *R. oryzae* soil concentrations was observed.

***Rhizoctonia* pathogens are associated with different groups of meteorological and soil variables in PCA.** The *Rhizoctonia* spp. were analyzed individually, because pairwise correlation analyses indicated that each was affected by different variables. A separate PCA was done for *R. solani* AG8 data from each year to reduce the complexity of the PCA output. For all but one of the analyses, 75 to 80% of the variance in the data was explained by two Prins; three components explained the variance for the *R. solani* AG8 year 3 (2008) data set.

Component scores plots were generated to visualize each sample relative to the major PCA components. Except for the

example described below, the factors within each component had nearly equal loadings (weights). An example of a plot of each sample relative to components 1 and 2 for year 1 of the *R. solani* AG8 data set is shown in Figure 3. In this case, component 1 comprised the factors PreOct-Jun, MaxMar-May, soil pH, percent clay, and percent sand, and component 2 comprised PreMar-May, PreJul-Sep, and MaxJul-Sep. The PreJul-Sep factor was the dominant factor in component 2. The low-precipitation, high-sand samples, such as Connell and Lind variety test plot samples, fell at the right of the plot along component 1, whereas the high-precipitation, high-clay samples were at the left. Component 2 distinguished high PreMar-May/low PreJul-Sep samples (at the top of the plot) from those having low PreMar-May/high PreJul-Sep (bottom of plot). Samples harboring quantifiable levels (≥ 2.5 log fg DNA) of *R. solani* AG8 are shown in large- and medium-sized dots in Figure 3 and color-coded in Supplemental Table 2.

Fig. 2. Relationship between **A**, *Rhizoctonia solani* AG8 concentration (log fg DNA/g of soil) and cumulative precipitation (mm) for the October to June interval or **B**, average monthly temperature maxima ($^{\circ}\text{C}$) for the July to October interval. Data from growers' parcels and variety test plots for 3 years were pooled; r = Pearson's correlation coefficient. Zero values were excluded from the analysis.

Fig. 3. Component scores plots (PRINCOMP, SAS Institute, Inc.) for the *Rhizoctonia solani* AG8 data set from growers' parcels and variety test plots for 2006 (year 1), showing the distribution of sampling sites by cumulative precipitation (Pre) in the October to June (Oct-Jun) interval, average monthly temperature maxima in the March to May (Mar-May) interval, percent clay, and percent sand (component 1), plotted against cumulative precipitation in the Mar-May and July–September (Jul-Sep) intervals, and average monthly temperature maxima in the Jul-Sep interval (component 2). Gray dots indicate samples harboring quantifiable levels (≥ 2.5 log fg DNA) of the pathogen, where the size of the dot is proportional to pathogen DNA concentration; open dots indicate samples in which pathogen was detectable but not quantifiable (< 2.5 log fg DNA). A key to the sample numbers is given in Supplemental Table 2.

The trends in component factors seen for *R. solani* AG8 in year 1 also were observed in year 2. In year 3, however, component 2 separated the samples according to PreJul-Sep only, the PreMar-May factor was associated with component 1, and MaxMar-May and MaxJul-Sep factors were captured in a third component.

The distribution of the *R. oryzae* samples in years 1 and 2 was explained by high MaxOct-Jun, high MinMar-May, high MinOct-Jun, and high MinNov-Mar (component 1) and high MaxMar-May, low clay, and high sand (component 2). Because the distributions were very similar, data from both years were combined. Year 3 data for *R. oryzae* were omitted because they comprised a relatively small number of samples ($n = 21$), all having detectable but not quantifiable (<2.5 log fg DNA) pathogen levels. In summary, *R. solani* AG8 accumulated in low to intermediate PZs, in areas having higher temperature maxima and sandy soils, whereas *R. oryzae* persisted in areas having low temperature minima.

JMP Principal Component analysis, conducted using all variables for 2006 to 2008, resulted in a biplot of the vectors of the independent and dependent variables for *R. solani* and *R. oryzae* (Fig. 4). Longer vectors indicated factors that had major contributions to variation in the dataset, whereas shorter vectors indicated factors that were relatively minor. Vectors having the same directionality are positively correlated to each other, whereas those in opposing directions are negatively correlated. The JMP Principal Component analysis generally identified the same sets of variables associated with *R. solani* AG8 or *R. oryzae* DNA concentration as did PRINCOMP (Fig. 4A). The vector for *R. solani* AG8 (logAG8) was directionally the same as that for sand but opposite the precipitation and clay vectors, indicating that DNA concentrations of this pathogen are higher in sandy soils and lower in soils from high-clay and high-precipitation regions. The concentration of AG8 DNA was more closely aligned with maximum than minimum temperature. Overall, the first two components explained 61% of the variation. The short *R. oryzae* (log Ro) vector indicated that it is not a major factor in explaining the variation within the dataset, and was neither positively nor negatively correlated to precipitation and soil

properties (Fig. 4B). However, the log Ro vector was weakly correlated, if at all, to temperature maxima and minima in JMP Principal Component analysis compared with PRINCOMP. Components 1 and 2 explained $\approx 69\%$ of the variation.

DISCUSSION

Our survey has identified meteorological, soil texture, and cropping factors correlated to the abundance of *R. solani* AG8 and *R. oryzae* in soils of Washington state. This is the first report, to our knowledge, of the quantitative distribution of *Rhizoctonia* spp. across a large geographical area on a common host, and the relationship of distribution to climatic and soil factors. This biogeographical study only could have been possible in the last decade, because of two technological developments: (i) sensitive molecular techniques to quantify specific microorganisms from soil and (ii) the development geographic information systems, low-cost GPSs, and higher-resolution climate data at the 4-m² area scale. The former development is especially important for *Rhizoctonia* spp. because it occurs at low soil population densities that cannot be accurately quantified with traditional dilution plating techniques.

The relationship of climate and weather factors to disease distribution of foliar pathogens, such as rusts, is well understood. Models have been developed to relate weather factors to the distribution of stripe rust of wheat (35), soybean rust (20), and *Septoria tritici* on wheat (29) using the defined influences of temperature, precipitation, and relative humidity on the infection process and disease progression. Fewer studies have been conducted on the distribution of soilborne pathogens as affected by climate. Poole et al. (30) demonstrated that the two causal agents of Fusarium crown rot of wheat are differentially distributed in the PNW; *Fusarium pseudograminearum* O'Donnell & T. Aoki was more dominant in areas with higher temperature, lower elevation, and lower precipitation whereas *F. culmorum* (W. G. Sm.) Sacc. was associated with higher precipitation areas and higher elevations. In a similar study, population densities of root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) were

Fig. 4. Biplots of principal component analysis vectors (JMP; SAS Institute, Inc.) showing the relationships of *Rhizoctonia* concentrations (log fg DNA/g of soil) of **A**, *Rhizoctonia solani* AG8 or **B**, *R. oryzae* to cumulative precipitation (Pre), average temperature maxima (Max), average temperature minima (Min), and soil texture factors (clay, sand, or silt). Data from 3 years of growers' parcels and variety test plots were pooled; r = Pearson's correlation coefficient. Zero values were excluded from the analysis. Factors with significant ($P < 0.05$) correlations to pathogen DNA concentrations are shown in italicized bold font.

more abundant in areas of high precipitation and continuous cropping, as opposed to drier areas where wheat was only grown every 2 years (10).

We found that *R. solani* AG8 was distributed across the entire dryland cropping region but higher soil DNA concentrations were associated with lower precipitation, higher average atmospheric temperatures, and higher soil sand content. Soil temperature data were not available for the sites but would be highly correlated to atmospheric temperatures. Rhizoctonia bare patch symptoms are mostly observed in areas having these meteorological and soil conditions, a crescent from Ritzville to Connell, at the edge of the dryland cropping zone. Further west of this crescent, the annual precipitation is too low for growing wheat without irrigation. Bare patches also are observed south of Dayton and Walla Walla, which harbored relatively high soil pathogen DNA concentrations. Although *R. solani* is associated with bare patches in warm, dry regions, it also is manifest as general root rot and uneven stands in the higher-rainfall areas. It is clear that environment might affect not only the accumulation of inoculum in the soil but also the expression of the disease.

One unresolved question is why bare patch symptoms associated with acute infections do not develop in the higher-rainfall areas. Work of Australian researchers showed that sand was associated with higher disease levels. Gill et al. (6) found more root loss from *R. solani* AG8 in sandy soils compared with sandy loams or sandy clay loams. The clay soils of the high-rainfall areas of the PNW, having less sand, might be less conducive to the movement of the hyphae through the soil. Otten and colleagues (18,19) showed that hyphae of *R. solani* AG4 prefer larger soil pores for faster spread and colonization. In the field, *R. solani* AG8 survives primarily as thick-walled hyphae in root matter; hence, host infection gives rise to more inoculum. Observations of higher soil pathogen DNA concentrations in sandy areas support the likelihood of a causal link between higher inoculum deposition, greater degree of root infection, and higher disease levels.

The relationship between Rhizoctonia root rot, temperature, and moisture was reported by Gill et al. (7), who demonstrated that, in moist soil, the disease was more severe at lower temperatures (10°C). This observation confirmed the findings of Ogoshi et al. (15), who reported higher levels of disease at 10 compared with 20°C. Because optimum temperature in culture was 25°C, factors governing pathogen growth and disease under field conditions are distinct from those of the laboratory and even in pasteurized soils (P. Okubara, unpublished data). One explanation is that, under wetter, cooler conditions, soil microbes that normally suppress *Rhizoctonia* spp. are less active (8). For instance, decline of Rhizoctonia bare patches due to disease-suppressive rhizobacteria has been observed at a site near Ritzville, WA (13,38), under drier, warmer conditions.

In contrast to *R. solani* AG8, *R. oryzae* (*W. circinata* var. *circinata*) was more uniformly distributed throughout the dryland cropping regions of the state. Fewer studies have been done with *R. oryzae*, which can cause preemergence damping off of wheat and barley at cool temperatures (12°C) (14,34). Our study indicated that *R. oryzae* DNA concentrations were not affected by precipitation but were significantly ($P < 0.05$) and consistently correlated with temperature minima. This pathogen also attacks broadleaf crops such as pea (22) and forms microsclerotia in plant tissue. Its persistence in cropping soils might be attributed to a broad host range as well as to longevity as microsclerotia, making it refractory to precipitation. Because *R. oryzae* is often found with *R. solani* AG8 in bare patches and direct-seeded fields (27), we hypothesized that these two pathogens would be governed by similar environmental factors, and might be co-managed as a complex. However, our data indicate that each pathogen was associated with a unique set of variables, such that they should not be managed as a complex.

Cropping history and tillage also were addressed to a limited degree in our survey. Rotations practiced by growers are optimized for soil and precipitation factors and the economics of inputs and production. The finding that *R. solani* AG8 soil concentration was reduced if a broadleaf crop was planted immediately before wheat supported observations that cropping history has a role in disease manifestation. It also suggests that rotation might reduce *R. solani* AG8, despite its pathogenicity to legumes and brassicas. However, whether these reductions in population are significant enough to result in major differences in disease severity remains to be seen. In contrast, tillage, which is considered to be a negative driver of *Rhizoctonia* spp. soil accumulation, was not found to be significant in our study. It is possible that tillage can be over-ridden by environmental factors in short-term studies such as ours. In a previous study, *R. solani* was substantially reduced by tillage, whereas *R. oryzae* was not (33). The meteorological and soil texture factors used in this study explained <50% of the total of the variation, indicating that unaccounted factors were contributing to residual variation. These might include biotic factors such as crop cultivar or rhizosphere community structure. Taken together, the survey findings suggest that planting risks for growers will vary depending upon their location and whether *R. solani* AG8 is present in the soil. For instance, direct seeding in high-risk areas such as Lind and Connell are predicted to be more conducive to diseases caused by *R. solani* AG8 compared with Pullman and Colton, and growers in the former areas should consider seed treatments, green bridge control, and seed opener disturbance during planting as means of minimizing risk.

Finally, plant diseases are expected to be affected by climate changes (11). The affect of climatic factors on the frequency and distribution of Rhizoctonia root rot pathogens is unknown. However, our survey and other studies will provide a baseline for future disease forecasts, and fill a knowledge gap in this type of data (36), which is especially lacking for the soilborne microbes (2).

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