Effect of Climate on the Distribution of *Fusarium* spp. Causing Crown Rot of Wheat in the Pacific Northwest of the United States

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ABSTRACT

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Fusarium crown rot (FCR) is one of the most widespread root and crown diseases of wheat in the Pacific Northwest (PNW) of the United States. Our objectives were to characterize crown rot severity and distribution throughout the PNW by conducting a survey of 210 fields covering the diverse dryland wheat-producing areas of Washington and Oregon and to utilize a factor analysis statistical approach to determine the effects of climate and geography on species distribution and disease severity. Climatic variables were based on 30-year averages and 2008 and 2009 separately (the 2 years of the survey). Mean annual temperature, mean temperature in the coldest month, mean temperature in the warmest month, mean annual precipitation, snowfall, elevation, soil type, and cropping intensity were highly intercorrelated. The factor analysis of the climate variables resulted in the development of two latent factors that could be used as predictor variables in logistic regression models for the

presence or absence of *Fusarium* spp. and of FCR disease scores. Isolates of *Fusarium* spp. were recovered from 99% of 105 fields sampled in 2008 and 97% of fields in 2009. There were differences between years for responses of FCR and nodes scores, and isolations of *Fusarium pseudograminearum* with more significant results in 2008, due to warmer drier weather. Results of the factor analysis showed that the distribution of *F. pseudograminearum* occurred in a greater frequency in areas of the PNW at lower elevations with lower moisture and higher temperatures in 2008, whereas *F. culmorum* occurred in greater frequency in areas at higher elevations with moderate to high moisture and cooler temperatures consistently across both years. Disease scores increased with increasing levels of factors 1 (primarily temperature) and 2 (primarily precipitation). Both the frequency of pathogen species and disease scores were influenced by the year, indicating that soilborne pathogens are responsive to short-term changes in environment. This factor analysis approach can be utilized in studies to determine the effects of climate and other environmental (soil, cropping system, and so on) factors on the distribution and severity of root diseases.

Additional keywords: *Fusarium culmorum*.

Fusarium crown rot (FCR) is a major yield-limiting disease of dryland wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.). Crop yields are reduced due to rotting seed, seedlings, roots, crowns, and basal stems resulting in seedling mortality, premature lodging, and impaired grain filling (30,36,43). In the Pacific Northwest (PNW) region of the United States, the disease causes average annual yield losses of 9.5% at a value of as much as US\$69 million, based on 2007 production figures (41). The presence of FCR decreased yield in 13 commercial fields in the PNW by as much as 35%; yields were decreased by up to 61% under inoculated experimental conditions (41).

The disease is caused by a complex of species of which *Fusarium pseudograminearum* (O'Donnell & T. Aoki) (= *F. graminearum* group I, = *Gibberella coronicola*) and *F. culmorum* (W. G. Sm.) Sacc. are the most significant (8,27,42). Infection results in chocolate to reddish-brown symptoms on roots or shoot

internodes (4,13). Lesions extending to the fourth or fifth node can be accompanied by salmon-colored sporodochia, which are masses of macroconidia. The infection of the crown (lower stem) region constricts the vascular system and limits water transport capacity (8,40). Subsequent drought stress experienced in the later stages of wheat crop growth results in formation of whiteheads containing little to no seed (8,10). Whiteheads are often used as an indicator of FCR injury to quantify the amount of disease present but this method can be misleading because above-ground symptoms are not always obvious (8,41). Whiteheads can be also caused by other root-rotting pathogens (20,43).

The earliest documentation of FCR in the PNW was reported by Cook (12). Using the nomenclature of the time, more than 90% of the isolates from diseased fields were *F. roseum* f. sp. *cerealis* 'Culmorum' and *F. roseum* f. sp. *cerealis* 'Graminearum', with Culmorum being predominantly present. *F. roseum* f. sp. *cerealis* 'Avenaceum' was isolated occasionally from those samples. A more recent survey of the wheat-growing areas of eastern Oregon and southern Washington documented the occurrence of *F. pseudograminearum* more often than *F. culmorum* in crops with crown rot in nine counties, while the opposite was true in three counties (12,43). *F. culmorum* was the primary causal agent of FCR in southeastern Idaho, dominated by higher eleva-

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tions (46). Root-rot-causing organisms in Montana were identified as *Bipolaris sorokiniana* (15%), *F. culmorum* (13%), and *F. pseudograminearum* (8%) (25).

Surveys of root-rot-causing organisms in dryland wheat have been conducted throughout the world (2,5,7,10,12,17,25,35, 43,45,46). Although the causal agents of FCR are most frequently a complex of *F. pseudograminearum* and *F. culmorum*, other pathogens capable of causing crown infection include *F. avenaceum* (Fr.) Sacc. (= *G. avenacea*) and *Microdochium nivale* (Fr.) Samuels & I. C. Hallett (= *Monographella nivalis*) (41). It is widely accepted that *F. pseudograminearum* is the dominant species responsible for causing crown rot in arid zones of the PNW and Australia (3,10,11,42,43).

Several other genera also cause root rots of cereal grains, including the causal agent of common root rot, *Bipolaris sorokiniana* (Sacc.) Shoemaker (= *Cochliobolus sativus*) (12,14,25, 27,32); the causal agent of take-all, *Gaeumannomyces graminis* (Sacc.) Arx & D. L. Olivier and *G. graminis* var. *tritici* J. Walker; *Rhizoctonia* spp. (*Rhizoctonia solani* Kühn and *R. oryzae* Ryker & Gooch); and *Pythium* Pringsh. spp. (38,43,45). In the PNW, the last three tend to be more prevalent in spring wheat cropping systems (38). Eyespot (caused by *Oculimacula acufornis* (Boerma, R. Pieters & Hamers) Crous & W. Gams and *O. yallundae* (Wallwork & Spooner) Crous & W. Gams) is also a major yield-limiting factor in winter wheat where precipitation is high (22).

Winter wheat is the predominant crop in much of the dryland region of the PNW (also referred to as the Inland Northwest or the Columbia Basin) but the environment is quite diverse within these ≈160,000 km². Mean annual temperature (MAT) ranges from 6 to 12.5°C, annual precipitation in the region ranges from <125 to >600 mm, and elevation rises from sea level to >1,500 m. Most annual precipitation occurs from October through March, with only 5 to 10% occurring from July through September (37). These climate differences and geological history combined to create great diversity in soil types (several thousand soil series are identified and mapped in Washington state alone) (18). Soil depths range from <1 to >7 m (18). In the Columbia Basin, sandy silt loams predominate in the southwest, with clay slit loams in the northeastern part of the region. Due to soil and climate variability, dryland cropping systems in the region range from a 3-year rotation of winter wheat, spring cereal, and spring legume to a 2-year rotation of winter wheat and fallow and are planted under conventional or conservation tillage systems (37). These differentiating factors of growing degree days, annual precipitation, and soil depth were used to delineate six agronomic zones of the PNW, which could be used as a geographical base for extrapolating research results for the PNW (15,16).

Complex interactions among climate, cropping systems, and tillage also influence the distribution of *Fusarium* spp. as well as disease severity (3,25,39,40,43). *F. pseudograminearum* has been found more frequently in low precipitation zones (250 to 500 mm) while *F. culmorum* occurred in zones with higher precipitation (>500 mm) (2). In the PNW, the incidence of FCR was the greatest in seasons with low precipitation (41). A moderate but significant negative correlation was reported for the occurrence of *F. pseudograminearum* with precipitation and elevation; however, the six PNW agronomic zones did not explain the occurrence or frequency of FCR pathogens (43). Strausbaugh et al. (46) reported that *F. culmorum* dominated in the cooler, higher elevations surveyed in Idaho. Soil type and winter- versus spring-habit wheat also influenced species distribution (25). Tillage has also been shown to influence *Fusarium* spp. presence and quantity as well as distribution within a field (6,29,47). Backhouse and Burgess (3) reported significant associations between climate and *Fusarium* spp. distribution in Australia. FCR is well known for a high degree of variation between host cultivars and years due to the nature of the infection mechanism and influence of climate on

species distribution and disease severity (41,43,44). Smiley et al. (44) described the highly variable nature of FCR across experimental locations and years from data with experiments conducted utilizing >16 cultivars over 8 years at several locations.

Although previous surveys of the presence of *Fusarium* spp. associated with the crown rot disease have been conducted in eastern Oregon and southern Washington (41), an extensive area of Washington comprising the Columbia Basin and areas north was not surveyed. Crown rot disease is prevalent in this region, where most of the dryland winter wheat of the PNW is produced. The objectives of this work were to (i) determine the occurrence of FCR and *Fusarium* spp. distributions covering the broad geographic region comprising the major wheat-producing areas of Washington and Oregon and (ii) determine which climate, cropping system, and geographical factors most influence species distribution and FCR disease in this region.

MATERIALS AND METHODS

Sampling of field sites. Field locations were selected randomly and sampled systematically over a broad geographic area covering the dryland wheat region from 14 Washington counties, four Oregon counties, and one location in northern Idaho. Survey sites included 210 randomly selected commercial wheat fields, including 21 Washington State University Cooperative Extension Cereal Variety Testing sites for winter wheat. The survey was conducted during summer 2008 and 2009.

Samples were taken from winter wheat stubble shortly after harvest. Sampling began near Pendleton, OR on 7 July 2008 and 10 July 2009. Sampling followed the harvest pattern throughout the region until 15 September 2008 and 25 September 2009, finishing near Pullman and near Spokane in eastern Washington, respectively. The sampling distance between fields was 17 to 80 km. Sampling density was greater where FCR had previously been reported in Oregon and north-central Washington and in areas that had not been sampled previously. All fields sampled were geo-referenced using a Magellan global positioning system (GPS) meter (Triton model; Magellan Mfg., San Dimas, CA) at each 1-m row subsample in 2008 (see below) but only at each field in 2009. Fields sampled in 2009 were from winter wheat stubble in the closest proximity of those sampled in 2008, within 3.2 km.

Five subsamples were taken from each field. A subsample was defined as a 1-m row of wheat stubble and roots dug to a depth of 10 cm below the crown. A single subsample was obtained after walking 100 m into a field from the edge, and four additional subsamples were taken from that point by walking 25 m between each sample in a zigzag pattern. Each subsample was placed in a labeled paper bag and dried at ambient temperatures prior to scoring.

FCR disease scores. At the time of scoring, 10 stems were randomly chosen from plants within the subsample excised from the dug-up crowns at the base of the stem. Each stem was scored for FCR disease severity based on a 0 to 10 scale, where 0 = no disease; 1 to 2 = minor symptoms on crown within the first internode region; 3 to 4 = obvious symptoms on crown within the first internode region; 5 to 6 = pronounced symptoms on the crown, with obvious darkened plant tissue due to infection penetrating to the third leaf; 8 to 9 = advanced darkened symptoms; and 10 = severe darkened symptoms throughout tissues (as modified from Nicol et al. [27]). The number of internodes (node score) with disease symptoms was also recorded for each stem. In total, 5,100 stems were selected and scored each year (2008 and 2009), with 10,200 stems rated in all.

Species isolation, culture, and identification. A stem was randomly selected from each subsample, with five stem samples per field (500 isolates total per year). The stems that were selected tended to be symptomatic. A 2-cm section was cut from each

stem, surface disinfested in 0.05% NaOCl for 30 s followed by a 6-min rinse in double-distilled water, and placed on Synthetischer Nährstoffärmer agar (SNA) (28) (1 g of KH_2PO_4 , 1 g of KNO_3 , 0.5 g of $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.5 g of KCl, 0.2 g of glucose, 0.2 g of saccharose, and 20 g of agar per 1 liter of media). Cultures were placed at room temperature in natural light for 3 days.

After 3 days, 1-cm² pieces were cut from the SNA and fungal growth surrounding each cut stem piece was transferred to a fresh SNA plate. Plates were incubated for 3 weeks in the dark. Fungal species present were identified for each subsample from each field on the basis of morphological characters of macroconidia observed through a light microscope at $\times 40$ and $\times 100$ (9,21,26).

Single-spore cultures were made for each field. Each SNA plate was viewed under the dissecting scope and a 1-cm piece of agar containing sporodochia was cut out and placed in 1 ml of water in a 5-ml tube. The tube was vortexed for 5 s and 90 μl was pipetted onto a half-strength potato dextrose agar plate containing chloramphenicol. Plates were incubated for 24 h at 22°C. Species presence was scored as 1 (present) or 0 (absent) for each species identified from each subsample. For the archived collection, monospore isolations were made by viewing these plates under the dissecting microscope, then excising and transferring single germinated spores to new SNA plates.

Climate, crop, and geographic data. Elevation was obtained for each sample location from the Digital Elevation Model included in the climate databases. Climate data were downloaded from the database developed by the United States Department of Agriculture (USDA) Forest Service Moscow Forestry Sciences Laboratory (<http://forest.moscowfs.wsu.edu/climate/>). These data include 21 variables for 30-year norms for the period 1961 to 1990. Data were obtained as in Rehfeldt (34) for each of the GPS coordinates from which samples were taken. The variables were derived from monthly climate surfaces using Hutchinson's thin-plate splines and were selected based on their predictive importance in biology (34). A correlation analysis of these 21 variables indicated that most were highly correlated. As a result, a subset including MAT, mean annual precipitation (MAP), mean temperature in the coldest month (MTCM), mean temperature in the warmest month (MTWM), and snowfall (SNOW) were the only variables kept for the analyses described below. Data obtained were based on 30-year averages as well as within-season variables for each GPS location in 2008 and 2009. We modeled daily snowfall liquid equivalents using concomitant daily mean temperature and accumulated precipitation obtained by extracting data from co-located 4-km raster data from the daily surface meteorological data set of Abatzoglou (1). The percent precipitation that fell as snow on any day was estimated using an empirical transformation based on temperature derived from worldwide temperature-precipitation phase relationships from land-based stations. Soil data for each of the sample locations based on GPS coordinates were obtained from the USDA Natural Resources Conservation Service Web Soil Survey (<http://websoilsurvey.sc.egov.usda.gov/App/Hopepage.htm>). Soil textures were coded as one of three classification categories: sandy-loam, loam, or silty-loam. The categories cover a range of values for percent sand, silt, or clay. We chose the center point of each category to define percent sand, silt, or clay for each field that was sampled. For the centers of these three categories, the amounts of sand and silt were almost perfectly negatively correlated. Therefore, we chose the percent sand content as a replacement variable for the original categorical soil texture variable. Cropping intensities in survey locations were recorded by examining the pixel intensity of data layers on ArcGIS models. This raster set was produced by R. Rupp by using the National Agricultural Statistic Service Crop Layer product, derived from satellite imagery in 2007. These data were used as an indicator for cropping system because a 3-year rotation with annual cropping would have a higher cropping intensity than the 2-year wheat-fallow rotation.

For example, annual cropping systems would have a value of 100%, whereas areas cropped every other year, such as the wheat-summer fallow areas, would have a value of 50%. The final data set for the climate and geographic variables included elevation, MAT, MAP, MTCM, MTWM, SNOW, cropping intensity, and percent sand.

Statistical methods. Factor analysis. Pearson correlations were calculated to estimate relatedness among the 30-year averaged continuous climate and geographic variables. Correlations were calculated between elevation, MAT, MAP, MTCM, MTWM, SNOW, cropping intensity, and percent sand content. The highly correlated climate variables complicated our efforts to perform regression analysis of the effects of climate, soil type, and cropping system on disease scores and species presence. Therefore, factor analysis was used to reduce the 30-year interrelated variables into compact latent factors based on the climate, crop, and geographic variables for ease of interpretation and to increase the strength and resolution of the analysis. Only variables which had correlation coefficients of >0.5 with at least one other variable were included in the factor analysis; therefore, sand content and cropping system were not included. Prior to conducting factor analysis, locations with supplemental irrigation were excluded. All data analyses were conducted using SAS software (version 9.3; SAS Institute Inc., Cary, NC). Graphs were generated in SAS and using code written in R (33).

Factor analysis was conducted using the FACTOR and SCORE procedures with the common factor method in SAS to estimate latent factor values for each field sampled for two rotated factors. Analysis was limited to two factors because only the first two eigenvalues of the correlation matrix were >1 (the Kaiser-Guttman rule) (23) and the scree plot of eigenvalue by the number of factors with a near linear trend starting at 3 (23). The initial factor solution was rotated to improve interpretation using a varimax rotation. This rotation was chosen because it yields orthogonal latent factors, and the primary goal of our factor analysis was to avoid multicollinearity in the linear modeling that followed.

Logistic regression analysis of *Fusarium* spp. presence. The binary trait presence or absence of *F. culmorum* and *F. pseudograminearum* from five subsamples from each field was related to climate and geographic variables and year effects using logistic regression with a logit link in the LOGISTIC procedure in SAS. The model included the two estimated latent factors plus sand content and cropping system, which were not included in the factor analysis, and their interactions as fixed effects. Separate analyses were conducted for each species and each year, due to significant interactions of treatment effects with year. In order to further explore the differences between 2008 and 2009, individual climate variables for each of those years (within growing season) were used in logistic regression models for the species presence or absence for that year. Thus, for 2008, the 2008 MAT, MAP, MTWM, MTCM, and SNOW were used as predictor variables for the presence of *F. culmorum* or *F. pseudograminearum* obtained from fields sampled in 2008. The same analysis was repeated for 2009.

Logistic analysis of disease scores. The disease scores, crown score, and node score were scored as ordinal variables (1 to 10 for crown score and 1 to 5 for node score); therefore, logistic regression was used to determine significant effects on those two response traits. Initially, an analysis was performed over the 2 years of the trial with year, the 30-year averaged climate variables, and their interactions with year as the predictor variables and the disease scores as response variables. Because of significant interactions with year, regression models were run within years using the latent factors, plus sand content, as predictor variables in logistic regression models for the response variables crown score or node score. Additional logistic model analyses were conducted using in-season climate variables as predictors and the 2008

or 2009 crown score or node score as response variables, as described above.

RESULTS

Comparison of 30-year averages to within-season values for 2008 and 2009. Monthly precipitation for 2008 and 2009, compared with the 30-year averages, is shown in Figure 1. These monthly comparisons were made at three locations to cover the major precipitation zones of the survey. In the dry zone (Ritzville), the fall and spring of 2009 were much wetter than 2008. Both Pendleton and Pullman also had a wetter spring in 2009 than 2008, although the relative increase was greater in the dry areas. Mean monthly temperatures were also higher in the early spring in 2008 compared with 2009 in Ritzville and Pendleton but not in Pullman (Fig. 2).

Correlations among climate variables. Several highly significant correlations were detected among the climate variables (Table 1). Elevation was negatively correlated with the temperature variables. The three temperature variables were highly intercorrelated. Precipitation was strongly positively correlated with cropping intensity, reflecting the tendency to plant annual

crops rather than wheat–fallow rotations with higher precipitation. The soil texture variables were not correlated with other climate variables but percent sand and percent silt were completely negatively correlated, as noted above. Cropping intensity was weakly correlated with everything except MTCM.

Subjecting the variables of the correlation matrix to factor analysis identified two latent variables, factor 1 and factor 2 (Fig. 3). Higher positive values of factor 1 were associated with lower elevation, lower SNOW, and higher annual temperatures, as well as higher temperatures in both the coldest and warmest months (Fig. 3). Higher positive values of factor 2 were associated with greater annual precipitation, and to a lesser extent, higher SNOW and lower MTWMs.

Species distribution. The mean frequency of isolation of *F. culmorum* and *F. pseudograminearum* was similar over both survey years (Fig. 4; Table 2). Within years, the frequency of isolation for *F. pseudograminearum* was slightly lower in 2009 than in 2008. Other species were also isolated from infected stems, including *F. torulosum*, *F. acuminatum*, *F. equisiti*, and *B. sorokiniana* (Table 2). We discovered *F. pseudograminearum* in 33%, *F. culmorum* in 36%, and both species in 26% of all fields sampled (data not shown).

F. culmorum was more frequently isolated from wetter and cooler locations (zones 1 and 4), whereas *F. pseudograminearum* occurred in significantly greater frequency in warmer zones

Fig. 1. Monthly average precipitation for three locations. **A**, Pullman (high rainfall) (factor 1 = -0.27; factor 2 = 1.65); **B**, Pendleton (moderate rainfall) (factor 1 = 1.05; factor 2 = 0.57); and **C**, Ritzville (low rainfall) (factor 1 = 0.21; factor 2 = -1.03). These locations represent three different agroclimatic regions in the Pacific Northwest.

Fig. 2. Monthly average temperature for three locations. **A**, Pullman (high rainfall) (factor 1 = -0.27; factor 2 = 1.65); **B**, Pendleton (moderate rainfall) (factor 1 = 1.05; factor 2 = 0.57); and **C**, Ritzville (low rainfall) (factor 1 = 0.21; factor 2 = -1.03). These locations represent three different agroclimatic regions in the Pacific Northwest.

(zones 3 and 5) (Fig. 4). Both species were often present within a particular field in areas of high precipitation. It is interesting to note that the isolation of *F. pseudograminearum* was negatively correlated overall with that of *F. culmorum*, showing that their distribution may not overlap in certain areas (Table 1). Also, *F. pseudograminearum* was positively correlated with temperature and negatively correlated with precipitation, showing that its distribution dominated in warmer and drier conditions, while *F. culmorum* was negatively correlated with temperature parameters, showing that its distribution dominated under cooler MAT conditions. *F. culmorum* was positively correlated with elevation, showing a greater abundance at higher elevations. *F. culmorum* was also negatively correlated with node symptoms, showing a lack of aboveground symptoms on the plants with *F. culmorum* infection.

In terms of environmental effects on species distribution, factor 2 was significant for the isolation of *F. culmorum* in both years (2008 and 2009) (Table 3). As factor 2 (precipitation and snowfall) increased, the probability of *F. culmorum* isolation increased from 60 to 80% in both years (Table 3; Fig. 5A and B). In 2008, there was a significant effect of factor 1 (temperature) on the isolation of *F. pseudograminearum*; infection increased as temperature increased (Table 4; Fig. 5C). Factor 2 was also significant in 2008 but not in 2009 for *F. pseudograminearum* isolation.

In both 2008 and 2009, there was a significant factor 2-cropping intensity interaction on the probability of *F. culmorum* isolation (Table 3). There was a decreasing probability of *F. culmorum* isolation as cropping intensity increased under environments with higher precipitation (Fig. 6A and C), but an increase in *F. culmorum* with increasing cropping intensity under low moisture conditions (Fig. 6B and D). The opposite trend was seen with *F. pseudograminearum*. *F. pseudograminearum* isolation in both 2008 and 2009 showed decreasing probability of infection as cropping intensity increased (Table 4), especially under low precipitation conditions (Fig. 7).

Fusarium crown disease scores. The mean FCR severity rating (rated 0 to 10) over all samples was 2.2 in 2008 and 2.9 in 2009. Ratings for FCR severity were 0.2 to 5.1 in 2008 and 0.5 to

5.4 in 2009. The mean node score (1 to 4 nodes) over all samples was 1.3 in 2008 and 1.5 in 2009. Node score ratings were 0.7 to 1.6 in 2008 and 1.4 to 1.8 in 2009.

Fusarium crown score. Low but significant positive correlations with crown score were observed for MAT ($r = 0.19$; $P = 0.01$), MTCM ($r = 0.30$; $P < 0.0001$), and cropping intensity ($r = 0.15$; $P = 0.04$) and negative correlations were observed with SNOW ($r = -0.15$; $P = 0.04$), showing increased disease severity in locations with higher temperature and lower snowfall (Table 1). In the logistic model, factor 1 was significant for crown score in 2008 ($P = 0.002$) and factor 2 was close to significant in 2009 ($P = 0.11$) (Table 5). For the within-season variables, MAT and

Fig. 3. Biplot of rotated factor pattern. Factor 1 explained 67.7% and factor 2 explained 32.2% of the variation among climate and geographical variables.

TABLE 1. Pearson pairwise correlations among climate and geographic field descriptors based on 2-year averages, $n = 188^a$

	ELEV	MAT	MAP	MTCM	MTWM	SNOW	SAND	CROP	CS	NODE	FP	FC
ELEV	1	...	...	...	...	...	...	...	...	...	...	...
P value	...	...	...	...	...	...	...	...	...	...	...	...
MAT	-0.57	1	...	...	...	...	...	...	...	...	...	...
P value	<0.0001	...	...	...	...	...	...	...	...	...	...	...
MAP	0.22	-0.29	1	...	...	...	...	...	...	...	...	...
P value	0.0023	<0.0001	...	...	...	...	...	...	...	...	...	...
MTCM	-0.49	0.80	0.14	1	...	...	...	...	...	...	...	...
P value	<0.0001	<0.0001	0.0654	...	...	...	...	...	...	...	...	...
MTWM	-0.56	0.81	-0.44	0.58	1	...	...	...	...	...	...	...
P value	<0.0001	<0.0001	<0.0001	<0.0001	...	...	...	...	...	...	...	...
SNOW	0.44	-0.80	0.55	-0.56	-0.63	1	...	...	...	...	...	...
P value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	...	...	...	...	...	...	...
SAND	0.09	-0.18	-0.09	-0.31	0.03	0.22	1	...	...	...	...	...
P value	0.2329	0.0164	0.2044	<0.0001	0.6514	0.003	...	...	...	...	...	...
CROP	0.24	-0.21	0.48	-0.02	-0.34	0.30	-0.28	1	...	...	...	...
P value	0.0009	0.0032	<0.0001	0.8088	<0.0001	<0.0001	0.0001	...	...	...	...	...
CS	-0.14	0.19	0.23	0.30	0.10	-0.15	-0.22	0.15	1	...	...	...
P value	0.0581	0.0086	0.0018	<0.0001	0.1646	0.0434	0.0024	0.0408	...	...	...	...
NODE	-0.23	0.28	0.28	0.41	0.13	-0.17	-0.25	0.24	0.85	1	...	...
P value	0.0016	0.0001	0.0001	<0.0001	0.0813	0.0221	0.0006	0.0009	<0.0001	...	...	...
FP	-0.27	0.34	-0.13	0.34	0.26	-0.27	-0.11	-0.18	0.08	0.04	1	...
P value	0.0002	<0.0001	0.0837	<0.0001	0.0004	0.0002	0.1474	0.0166	0.2505	0.6115	...	...
FC	0.36	-0.38	0.05	-0.44	-0.31	0.26	0.16	0.00	-0.28	-0.30	-0.57	1
P value	<0.0001	<0.0001	0.4651	<0.0001	<0.0001	0.0003	0.0275	0.9699	0.0001	<0.0001	<0.0001	...

^a ELEV = elevation, MAT = Mean annual temperature, MAP = mean annual precipitation, MTCM = mean temperature in the coldest month, MTWM = mean temperature in the warmest month, CROP = cropping intensity (100% = high intensity with annual cropping), SNOW = annual snowfall, SAND = percent sand, CS = crown score, NODE = node rating, FP = *Fusarium pseudograminearum* incidence per field per five samples, and FC = *Fusarium culmorum* incidence per field per five samples.

MTWM were almost significant in 2008 ($P = 0.09$), while MAP was significant in 2009 ($P = 0.002$), results which closely resembled the 30-year historical data variables that went into the factors. The increase in crown score with factor 1 in 2008 is shown in Figure 8A and the increase in crown score with precipitation in 2009 is shown in Figure 9A.

Node symptom rating. Significant positive correlations with node score were observed with MAT and MAP ($r = 0.28$, $P = 0.001$), MTCM ($r = 0.41$, $P < 0.0001$), and cropping intensity ($r = 0.24$, $P = 0.009$), with negative correlations for elevation ($r = -0.23$, $P = 0.0016$) and SNOW ($r = -0.17$, $P = 0.02$) (Table 1). This indicates that higher node scores are present in areas with higher temperature and total precipitation but less in cool areas with higher elevations and more snow. In the logistic model, factor 1 was significant for node score in 2008 and MAP in season was significant in 2009 (Table 6). The increase in node score with factor 1 in 2008 is shown in Figure 8B and the increase in node score with precipitation in 2009 is shown in Figure 9B.

DISCUSSION

Climate studies tend to be conducted with foliar pathogens of wheat, such as *Fusarium* head blight, due to the requirement for suitable temperature and moisture on the leaf surface needed for germination of spores and infection (49). Few studies have examined the distribution of soilborne or residue-borne pathogens

across a large geographical region and attempted to relate populations and disease to climatic and geographic variables (2,3). Cook (12) reported that the distribution of *F. pseudograminearum* and *F. culmorum* was linked to geographical county locations. Others have reported that monthly temperature, elevation, and other climate parameters significantly affect the distribution of *Fusarium* spp. (2,27,39,43).

Douglas et al. (15,16) classified the PNW dryland wheat production region into six agronomic ecological zones (agroecozones), primarily on the basis of temperature, precipitation, and soil depth. When we related disease and the distribution of *F. pseudograminearum* and *F. culmorum* to these agroecozones, we found the highest FCR scores in zone 3 (fallow-transition) but other areas showed moderate levels of disease which varied between the 2 years, making it difficult to establish a trend. The incidence of fields with both species ranged from 9 to 50% among climate zones, making it difficult to say which species was more predominant. *F. culmorum* occurred alone in 73% of the fields in zone 1 (cool and wet) and in 50% of zone 4 (cool and dry), characterized by cooler winter temperatures and a higher elevation, whereas *F. pseudograminearum* occurred alone in 63% of the fields in zone 3 (fallow-transition) and 42% of the fields in zone 5 (grain-fallow) (Fig. 4) (31).

One of the difficulties with these agroecozone classifications is that they combine both precipitation and temperature into categories with definitive geographic boundaries but without the ability to account for gradients or variation within a zone. With the development of geographic information systems and satellite imagery, we can now examine these continuous climate and geographical variables with a much higher degree of resolution across a continuous gradient rather than using categorical geographical-based zones. The strength of the factor analysis approach using 30-year average data is the ability to classify each field with a factor score associated with a range of climatic conditions, thus increasing the resolution for making climatic comparisons.

The climate data sets used in this study are available at spatial resolutions of 4 km (1) and 1 km (34), allowing an approximation for each sampling location. The development of the crop layer

Fig. 4. Six agronomic zones for the dryland Pacific Northwest developed by Douglas et al. (16) on the basis of precipitation, growing degree days, and soil type. Agronomic regional zones are depicted by color polygons: region 1 (tan), region 2 (pink), region 3 (green), region 4 (purple), region 5 (red), and region 6 (blue).

TABLE 2. Frequency of isolation of each respective species from the total ($n = 525$) sampled wheat stems

Fungal species ^a	Frequency of isolation ^b		
	2008	2009	Mean ^c
<i>Fusarium pseudograminearum</i>	34	26	30
<i>F. culmorum</i>	38	23	31
<i>F. torulosum</i>	12	14	13
<i>F. acuminatum</i>	2	1	1
<i>F. equiseti</i>	1	0	0
<i>Bipolaris sorokiniana</i>	1	2	2

^a Fungal species were identified according to Burgess et al. (9). Stem isolates were cultured from Synthetischer Nährstoffärmer agar media and placed on slides for morphological identification.

^b Frequency of isolations represent the proportion of samples (per 525) isolated from the entire survey for 2008 and 2009 survey years, respectively.

^c Mean represents the average for each species isolated across the 2008 and 2009 survey years.

TABLE 3. Tests of effects from logistic regression analysis of *Fusarium culmorum* from collected stems in the Pacific Northwest during 2008 and 2009

Parameter	2008		2009	
	Wald χ^2	P value	Wald χ^2	P value
Intercept ^a	0.23	0.63	4.10	0.04
Factor 1	1.89	0.17	0.03	0.87
Factor 2	11.51	0.0007	6.11	0.01
Factor 1 $\times$ factor 2	0.26	0.61	0.84	0.36
SAND	0.01	0.94	0.28	0.60
Factor 1 $\times$ SAND	0.85	0.36	0.07	0.79
Factor 2 $\times$ SAND	0.57	0.45	9.61	0.0019
CROP	1.25	0.26	0.00	0.97
Factor 1 $\times$ CROP	0.03	0.86	1.89	0.17
Factor 2 $\times$ CROP	10.43	0.0012	9.58	0.002
Intercept ^b	18.57	<0.0001	3.66	0.05
MAT in season	24.74	<0.0001	1.97	0.16
MAP in season	13.57	0.0002	2.13	0.14
MTWM in season	28.80	<0.0001	0.13	0.72
MTCM in season	0.01	0.91	0.16	0.69
SNOW in season	5.83	0.02	0.26	0.61

^a Factor 1 = first factor from analysis described by temperature, factor 2 = second factor from factor analysis described by precipitation, MAT = mean annual temperature, MAP = mean annual precipitation, MTCM = mean temperature in the coldest month MTWM = mean temperature in the warmest month, CROP = cropping intensity, SNOW = annual snowfall, and SAND = percent sand.

^b Within-season variables were included in a separate logistic regression model for within-season (2008 and 2009) MAT, MAP, MTCM, MTWM, and SNOW.

data set from the National Agricultural Statistics Service based on high-resolution satellite imagery provided us with a cropping intensity variable, based on a model of cropping intensity derived from all the surrounding fields in a 4- to 10-km area. Thus, data-intensive models were used to describe how these climatic and cropping factors influence pathogen distribution.

Climate is highly variable across the regions and locations we surveyed throughout the PNW, with several measured parameters available from weather stations. How does one sort out which are important and which may have biological relevance? A number of multivariate techniques have been used in the plant pathology literature to answer these questions. Correlation models have often been used to identify weather or climate variables that are associated with disease. For example, Smiley (44) used simple correlations and showed a negative correlation between precipitation and FCR severity in winter wheat in a wheat–summer fallow system in Oregon, and a stronger positive correlation with temperature. The strongest negative correlation was with the ordinal day of planting (i.e., more disease with early planting in the fall), which supported a well-known understanding among growers that later plantings have less disease. Another approach has been to use multiple regressions to develop predictive models. For example, the most important factor affecting eyespot infection in wheat was the number of days with rainfall >3 mm in October to April (24). Eyespot is also a crown disease, caused by the fungus *O. yallundae* and *O. acufiformis* (22).

We theorized that latent factors related to climate were underlying our observed variables and decided to use a factor analysis

TABLE 4. Tests of effects from logistic regression analysis of *Fusarium pseudograminearum* from collected stems in the Pacific Northwest during 2008 and 2009

Parameter	2008		2009	
	Wald χ^2	P value	Wald χ^2	P value
Intercept ^a	0.59	0.43	0.19	0.67
Factor 1	5.63	0.02	0.08	0.78
Factor 2	11.32	0.0008	1.78	0.18
Factor 1 $\times$ factor 2	0.02	0.90	0.00	0.98
Sand	0.10	0.75	1.49	0.22
Factor 1 $\times$ SAND	2.12	0.15	3.87	0.05
Factor 2 $\times$ SAND	1.93	0.16	3.28	0.07
CROP	5.66	0.02	4.21	0.04
Factor 1 $\times$ CROP	2.10	0.15	0.32	0.57
Factor 2 $\times$ CROP	9.27	0.002	2.56	0.11
Intercept ^b	7.74	0.005	0.09	0.76
MAT in season	5.39	0.02	2.02	0.16
MAP in season	12.37	0.0004	0.84	0.36
MTWM in season	7.34	0.006	0.67	0.41
MTCM in season	0.49	0.49	0.08	0.78
SNOW in season	0.13	0.72	0.00	0.99

^a Factor 1 = first factor from analysis described by temperature, factor 2 = second factor from factor analysis described by precipitation, MAT = Mean annual temperature, MAP = mean annual precipitation, MTCM = mean temperature in the coldest month MTWM = mean temperature in the warmest month, CROP = cropping intensity, SNOW = annual snowfall, and SAND = percent sand.

^b Within-season variables were included in a separate logistic regression model for within-season (2008 and 2009) MAT, MAP, MTCM, MTWM, and SNOW.

Fig. 5. Estimated influence of factor 2 on the probability of infection by *Fusarium culmorum* in A, 2008 and B, 2009. Estimated influence of C, factor 1 (temperature) in 2008 and D, precipitation on the probability of infection by *F. pseudograminearum*. Gray background around regression line indicates 95% confidence limits.

approach to reduce these variables to latent factors that could be regressed against disease parameters (48). Using factor analysis, we constructed two latent factors: factor 1, based primarily on temperature and elevation, and factor 2, based on precipitation, snowfall, and elevation. Both temperature and precipitation explained much of the variability in the climate of our field sites (4). Several important and significant trends were identified from this research.

There was a significant difference between years 2008 and 2009 for crown score, node, and the isolation of *F. pseudograminearum*, whereas there were similarities between years in the levels of *F. culmorum* isolations and their interactions with environmental and cropping intensity patterns. The first weather difference between years to note is that 2008 was characterized by warmer temperatures in February, March, and May (greater than the 30-year average) than that of 2009, especially in the drier areas. An increase in FCR scores and *F. pseudograminearum* isolations was associated with increasing values of factor 1 (largely defined by increasing temperature). May in the PNW is a critical time period in plant development, where plants are typically under water stress during grain development that has been known to be a time period associated with FCR infection (14). Crown score, node symptoms, and the levels of *F. pseudograminearum* increased in locations with higher mean temperature, a trend that was significant only in 2008. Plants are predisposed to more intense development of FCR when under drought stress (29,40, 44). Increased temperature increases transpiration and plants more quickly deplete the stored moisture (29). The authors be-

lieved that this difference between years for these parameters was due to higher spring temperatures in 2008 leading to greater crown rot disease severity (in crowns and nodes). Our research and others have noted that there are significant correlations between *F. pseudograminearum* levels and crown rot severity ratings. The linkage between FCR disease ratings and *F. pseudogrami-*

Fig. 7. Relationship between cropping intensity and the probability of infection by *Fusarium pseudograminearum* under low levels of factor 2 in 2008.

Fig. 6. Relationship between cropping intensity and factor 2 under A, high and B, low levels of factor 2 in 2008 and C, high and D, low levels in 2009 on the probability of infection by *Fusarium culmorum*. Gray background around regression line indicates 95% confidence limits.

TABLE 5. Tests of effects from logistic regression analysis of Fusarium crown rot crown score from collected stems in the Pacific Northwest during 2008 and 2009

Parameter	2008		2009	
	Wald χ^2	P value	Wald χ^2	P value
Intercept ^a	228.97	<0.0001	137.63	<0.0001
Factor 1	9.39	0.002	1.64	0.20
Factor 2	0.64	0.42	2.55	0.11
Factor 1 $\times$ factor 2	0.52	0.47	3.10	0.08
Sand	0.02	0.88	0.46	0.50
Factor 1 $\times$ SAND	0.02	0.88	0.00	0.98
Factor 2 $\times$ SAND	1.67	0.20	0.57	0.45
Intercept ^b	0.29	0.59	3.46	0.06
MAT in season	2.82	0.09	0.06	0.80
MAP in season	1.94	0.16	9.39	0.002
MTWM in season	2.85	0.09	0.22	0.64
MTCM in season	0.74	0.39	0.55	0.46
SNOW in season	2.01	0.16	0.80	0.37

^a Factor 1 = first factor from analysis described by temperature, factor 2 = second factor from factor analysis described by precipitation, MAT = Mean annual temperature, MAP = mean annual precipitation, MTCM = mean temperature in the coldest month, MTWM = mean temperature in the warmest month, CROP = cropping intensity, SAND = percent sand, and SNOW = annual snowfall.

^b Within-season variables were included in a separate logistic regression model for within-season (2008 and 2009) MAT, MAP, MTCM, MTWM, and SNOW.

nearum at higher temperatures levels agrees with that of others (2,3,8,10,14,27,40,41,43).

The second weather difference to note between the years is that spring precipitation (February to May) was considerably greater in 2009 than 2008, especially in the drier areas. The lack of significant crown score, node symptoms, and *F. pseudograminearum* isolations in 2009 agrees with the fact that these symptoms are associated with warmer and drier spring conditions that were more typical of 2008 (8,12–14). However, it appears that the significant association of *F. culmorum* isolations between factor 2 and MAP was significant in both 2008 and 2009, showing more consistency in this species occurrence across years. This trend seemed to be stronger in 2008 than 2009, again probably due to drier spring conditions in 2008. Likewise, the increase in significant effects of *F. culmorum* isolations under these conditions also agrees with that of others, that *F. culmorum* is found under cooler and wetter conditions. However, this difference may be more defined by regions rather than years because *F. culmorum* isolations increased significantly in locations with increasing levels of factor 2 (defined by increasing precipitation) (2–4,8).

Although mean annual precipitation varied across our field sample sites, winter precipitation followed by terminal drought and heat stress during wheat ripening was common throughout. It is likely that larger plants were produced in areas with higher annual precipitation, resulting in plants with more tillers that

Fig. 8. Factor 1 effect (characterized by increasing temperature and decreasing elevation) on A, Fusarium crown rot crown score and B, node symptoms during 2008. Gray background around regression line indicates 95% confidence limits.

Fig. 9. Effect of mean annual precipitation (MAP) on the levels of A, Fusarium crown rot crown score and B, node symptoms during 2009. Gray background around regression line indicates 95% confidence limits.

depleted terminal moisture, causing stress and more evidence of FCR disease development. Likewise, plant density per unit of area is greater in higher-precipitation regions because seed is planted at lower densities in rows spaced at ≈ 41 -cm intervals in low-precipitation areas and at higher densities in rows spaced at ≈ 25 -cm intervals in higher-precipitation areas.

The third major finding in this study was the association of *Fusarium* spp. isolation with environmental and cropping intensity parameters. Again, *F. culmorum* isolation interactions with factor 2 and cropping intensity levels were consistent across 2008 and 2009. Under low levels of factor 2 (i.e., low precipitation), isolations of *F. culmorum* increased with increasing cropping intensity (i.e., more crop rotation) while those of *F. pseudograminearum* decreased. *F. pseudograminearum* is known to survive mainly as hyphae in residue, whereas *F. culmorum* originates more from chlamydospores with a greater chance of survival under crop rotation (8,19,39). These trends could also be correlated with greater crop residue amounts in higher-precipitation areas, or higher levels of N applied to increase grain protein of hard red wheat varieties, which have been planted on increasing acreage since 2000. Backhouse and Burgess (3) found similar trends with increases in distribution of *F. pseudograminearum* in warmer drier areas.

Year-to-year variation between species occurrence has been documented previously (3,4,8,13,27,39,41,43,44). A factor that could affect species distribution across the PNW is the inoculum source and overwintering structures. *F. pseudograminearum* and *F. culmorum* survive as chlamydospores in the soil and host residue. However, the survival of *F. culmorum* chlamydospores (8.5 years) has been reported to be much longer than that of *F. pseudograminearum* (5.5 years) (39). A greater decrease in *F. culmorum* chlamydospores occurred over time at Lind, WA in the dry, wheat-fallow region (survived 215 days) compared with Pullman, WA in the higher-precipitation annual-cropping region (survived 330 days) but field surveys indicated greater disease severity at Lind than Pullman (19). Environmental conditions had a greater influence than chlamydospore survival on the ability of the fungus to develop and persist as a pathogen.

Our most interesting finding, evident in both years, was that *F. culmorum* was more frequently isolated from cooler locations and at higher elevations, areas that experience significant amounts of snowfall, whereas *F. pseudograminearum* occurred in signifi-

cantly greater frequency in warmer, lower elevations. The analysis showed that temperature and cropping intensity played a more important role in *F. pseudograminearum* distribution and infection. With an increase in factor 1 components, defined by higher temperature and lower elevation, the probability of *F. pseudograminearum* increased. The dominance of *Fusarium* spp. also has changed over time in the crown rot complex. Cook (12) reported that 90% of the species isolated from the PNW were *F. culmorum* but *F. pseudograminearum* (*F. roseum* f. sp. *cerealis* Graminearum) dominated in Franklin, Walla Walla, and Benton counties in southern Washington. Both our survey and that of Smiley and Patterson (43) isolated a higher frequency of *F. pseudograminearum* throughout the PNW region.

Results of the current study agree with others that *F. pseudograminearum* and *F. culmorum* are associated with crown rot and can be found throughout the rain-fed dryland wheat production region of the PNW (12–14,41,43). The differences in the occurrence of *F. pseudograminearum* and effect of climate (greater in 2008) also agree with the previous research, suggesting that the distribution and infection of *Fusarium* spp. involved in crown rot is highly variable and related to climate and cropping system (2–4,8,10,13,14,20,27,43,46,47). The general trends found in this study apply to other wheat-producing areas of the world.

Although FCR disease symptom development has been thought previously to be associated with warmer temperatures and lower annual precipitation, conditions also associated with drought stress, our results show that symptom development and species distribution is variable and related to climate. Prior to this study, species distribution throughout the wheat-growing regions was less evident. The distribution of *F. culmorum* in areas with higher precipitation and cooler temperatures and the widespread distribution of *F. pseudograminearum* agree with that of others around the world, especially in Australia (2,3,6,8,10). The association of *F. pseudograminearum* with node score and greater FCR disease severity also agrees with research and general observations by others that it is a more aggressive species (3,8,12,41,43).

This study resulted in the collection of nearly 1,000 isolates, of which 280 have been catalogued and stored for use in future studies. Knowledge gained from this study in terms of FCR occurrence, disease severity, and species distribution has implications for breeding and management that can be utilized by researchers, agronomists, and growers. Future research should focus on current levels of resistance in local PNW cultivars and on identification of novel germplasm resistant to *Fusarium* isolates identified in this study. From a pathological perspective, it would be beneficial to screen the isolates collected in this study on current cultivars to determine their pathogenicity and potential crop damage. We expect that the factor analysis data and factor scores from our sites will be useful in the future to determine the effects of climate on other root- and crown-rotting diseases of wheat and other crops that in the region.

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TABLE 6. Tests of effects from logistic regression analysis of node symptoms from collected stems in the Pacific Northwest during 2008 and 2009

Parameter	2008		2009	
	Wald χ^2	P value	Wald χ^2	P value
Intercept ^a	48.08	<0.0001	23.20	<0.0001
Factor 1	7.07	0.007	2.02	0.16
Factor 2	0.30	0.58	3.61	0.06
Factor 1 $\times$ factor 2	0.94	0.33	0.51	0.48
SAND	0.00	0.98	0.07	0.79
Factor 1 $\times$ SAND	0.01	0.94	0.22	0.64
Factor 2 $\times$ SAND	0.62	0.43	1.07	0.30
Intercept ^b	0.63	0.43	1.18	0.28
MAT in season	1.96	0.16	0.02	0.90
MAP in season	0.40	0.53	6.31	0.01
MTWM in season	2.09	0.15	0.27	0.60
MTCM in season	0.16	0.69	0.00	0.95
SNOW in season	0.55	0.46	0.29	0.59

^a Factor 1 = first factor from analysis described by temperature, factor 2 = second factor from factor analysis described by precipitation, MAT = Mean annual temperature, MAP = mean annual precipitation, MTCM = mean temperature in the coldest month, MTWM = mean temperature in the warmest month, CROP = cropping intensity, SAND = percent sand, and SNOW = annual snowfall.

^b Within-season variables were included in a separate logistic regression model for within-season (2008 and 2009) MAT, MAP, MTCM, MTWM, and SNOW.

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