Modeling Winter and Early Spring Survival of *Puccinia recondita* in Wheat Nurseries During 1980 to 1993

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ABSTRACT

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Survival of Puccinia recondita inoculum between wheat crops is critical to the occurrence of severe leaf rust epidemics, which result in economic yield reductions in the Great Plains wheatproducing region of the U.S. Meteorological variables occurring prior to spring green-up of the wheat crop during 1980 to 1993 at Manhattan, KS, were used to model survival of inoculum throughout the winter and early spring in wheat nurseries. Stepwise multiple regression techniques were used to determine those weather variables that explained the most variation in levels of inoculum surviving on 15 March. Inoculum levels were recorded on a 0 to 9 scale with 0 indicating no inoculum survival and 9 indicating inoculum on all plants. Daily maximum and minimum temperatures, fungal temperature equivalence function, precipitation and snow cover, cumulative precipitation and fungal temperature function, and daily deviations from the 10-year average of those variables were averaged for 10-day periods prior to a date of prediction and used as independent variables. Models that explained 99% of the variation in overwintering with five or six variables were developed for the fifteenth of each month from December through March. Models for December, January, and February used five of the same variables, but the minimum temperature deviation used in the December model was replaced by the January rainfall deviation in the January and February models. The model for March used a different set of temperature variables and included daily deviations in snow cover for December and February to explain a significant portion of the overwintering of P. recondita inoculum.

Additional keywords: modeling, Triticum aestivum

Development and survival of primary inoculum of *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* between wheat (*Triticum aestivum* L.) crops is critical for the development of severe leaf rust epidemics. Inoculum for the initiation of wheat leaf rust epidemics in the central Great Plains originates either as airborne urediniospores deposited from air masses that have traversed areas of infected wheat, or urediniospores from *P. recondita* infections that have survived the winter and early spring in the local field. *Puccinia recondita* survives the winter throughout the winter wheat production region in the

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Great Plains either as sporulating or dormant mycelium (1,4,5), or as viable urediniospores in uredinia on dead host material (1,2,5,6,8,12–14). Our previous work on winter and early spring survival of urediniospores of *P. recondita* indicates that temperatures near or below 0°C severely reduce germination within 24 h (10). We also found that yield reductions resulting from wheat leaf rust epidemics were not less than 2% when *P. recondita* survived the winter and early spring on host tissue within the local field (11,16).

The primary objective was to determine meteorological variables occurring during the epidemic year that could be used to model survival of P. recondita inoculum assessed on 15 March. In studies reported here, we have used regression techniques to identify and quantify meteorological variables useful in constructing a series of models to forecast overwintering of P. recondita inoculum in nurseries. A separate model was constructed to forecast P. recondita overwintering prior to the time crop production decisions would be made: on cultivar selection and planting in September; after stand establishment in October; during winter dormancy in November, December, January, February; and as a result of the crop conditions at spring green-up in March.

MATERIALS AND METHODS

Survival of P. recondita during the winter and early spring phases of an epidemic was assessed in wheat nurseries at Manhattan, KS, during the crop years 1980 to 1993. Trison, TAM 107, and/or Newton wheat cultivars, each susceptible to a different percentage of the prevailing P. recondita population, were planted in $1.2- \times 50$ -m plots replicated eight times. Trison was replaced with Karl in 1987 to 1993. Weather permitting, replicated plots of each cultivar were planted within 3 days of 10 August, 1 September, 20 September, 5 October, and 25 October for the 1980 to 1985 crop years and 5 October for the 1986 to 1993 crop years. The recommended wheat planting date for the Manhattan area is 5 October. Occurrence and development of leaf rust were recorded at 10- to 14-day intervals throughout the crop year as either percentage of the leaf area infected by P. recondita (17) or level of inoculum survival. Level of survival of P. recondita during the winter and early spring development of the rust epidemic was recorded on a 0 to 9 scale (Table 1). During periods in the winter or early spring when no signs of leaf rust were visible in the field, wheat plants were transplanted into 10-cm² diameter pots and transferred to a 20°C greenhouse to allow development of latent infections. Plants were examined after 10 to 14 days, and uredinia development recorded either on the 0 to 9 scale or the percent leaf area infected. Winter and early spring observations were not made on plants in plots

Table 1. Codes used in determining levels of survival of *Puccinia recondita* during winter and early spring development of an epidemic

Code	Explanation ^a						
0	No uredinia found in the field or on transplanted plants.						
1	One or two uredinia found in the field or on transplants.						
2	Uredinia can be found in the field by close examination.						

⁵ Uredinia can be found in the field easily.

⁸ Uredinia can be found on most plants in the field.

⁹ Uredinia on all plants.

^a Plants transplanted from the field into pots in a 20°C greenhouse and inspected 10 to 14 days later for presence of latent infections.

while snow cover existed. Yield reductions from wheat leaf rust were obtained by harvesting four treated and four nontreated $1.2 - \times 50$ -m plots of each cultivar for each date of planting in each year. Leaf rust in treated plots was controlled by application of triadimefon at 153 g a.i./ha at boot stage and mancozeb at 2.25 kg a.i./ha applied in a spray volume of 225 liters per ha at 10day intervals after boot stage.

We used stepwise multiple regression techniques to determine those weather variables that explained most variation in the level of wheat leaf rust inoculum observed on 15 March in replicated plots. The epidemic year was defined as the period from physiological maturity (23 June at Manhattan) of one wheat crop to physiological maturity of the next crop. Daily maximum and minimum temperatures, precipitation and snow cover for Manhattan, KS, were obtained from 1970 to 1993 records of the National Weather Service. Moving 10-year averages were determined for each daily weather variable or variable calculated from daily observations. For example, the 10-year average maximum temperature for 1981 was determined using data for 1971 to 1980 and the 1982 10-year average maximum temperature used data for 1972 to 1981.

In our models, the dependent variable was the level (0 to 9) of wheat leaf rust inoculum observed on 15 March in each replication. Independent variables were the following: the daily observations of average maximum temperature (MX) during the prior 2 to 30 days; average minimum temperature (MN) during the prior 2 to 30 days; average precipitation (P) during the prior 2 to 30 days; average snow cover (SC) during the prior 2 to 30 days; cumulative precipitation (TP) since the start of the epidemic year; average fungal temperature equivalence function (SIN), developed by Schrödter (15) and modified by others (3,7), during the prior 2 to 30 days; cumulative fungal temperature equivalence function (CSIN) since the start of the epidemic year; and, average daily deviations (MXD, MND, PD, SCD, TPD, SIND, CSIND) from the 10-year average for each of the preceding variables (MX, MN, P, SC, TP, SIN, CSIN) during the prior 2 to 30 days. Preliminary models were constructed for every day from 23 June, the beginning of the epidemic year, to 15 March using the independent weather variables averaged during the previous 2, 3, 4, . . . , 29, or 30 days. A total of 29 models, one for each period during which the weather was averaged, could be constructed for each day between 23 June and 15 March. Models to forecast P. recondita overwintering constructed for seven dates of prediction (Table 2) throughout the fall and winter included all daily variables recorded from 23 June to date of prediction.

Hourly temperatures used in the fungal growth function (SIN) were calculated on the basis of a 10-h linear rise from a minimum temperature at 6 a.m. to a maximum temperature at 4 p.m. and a linear 14-h drop to the next day's minimum temperature. For each year used in developing or verifying the models, the preceding 10 years' data were used to obtain an updated 10-year average for each variable.

Stepwise regression identified combinations of variables that explained a significant amount of variation in inoculum survival on 15 March. Constant values and partial regression coefficients for those variable combinations with highest R^2 values that significantly reduced variation in the survival of inoculum were used to predict P. recondita inoculum survival on 15 March of years not included in the formulation of the model. We tested the precision of the models by calculating average variation between observed and predicted survival (9). Models with the highest R^2 , lowest average variation, and fewest independent variables were selected as working models.

Preliminary analysis of data indicated that data summed or averaged over 10 days gave the best fit to a model, but summing or averaging data over 3 to 15 days did not significantly affect the precision of the model. However, data for periods shorter than 3 days or longer than 15 days tended to lower R^2 values and reduce precision of the model. Models were developed from data for the 1980 to 1985 crop years and verified using data from the 1986 to 1993 crop years. Survival data from wheat nurseries not included in the generation of models in 1980 to 1985 were used for verification during those years.

RESULTS

Fall leaf rust infections from natural inoculum were observed in the overwintering nurseries in every year from 1980 to 1993. Trace amounts of leaf rust survived in at least one replication of the nursery until mid-January in every year except 1981. Puccinia recondita survived the winter and early spring in the overwintering nurseries in 11 of the 14 years at Manhattan. Puccinia recondita survived in 1984 until snow cover was melted by 12 to 15°C afternoon temperatures, and -10°C temperatures at night caused infected wheat leaves to senesce in areas of the nurseries where snow cover was not present. Snow cover was also a factor in inoculum survival in 1985 to 1991, because leaf rust was observed in areas of the nurseries where snow cover was present during periods of extremely low temperatures. However, as soon as the snow cover disappeared, infected leaves quickly senesced when temperatures were 10 to 20 degrees below freezing.

Models for prediction of inoculum survival observed on 15 March developed from data for the epidemic year date of prediction are presented in Table 2. Models derived from data for up to 7 days either side of those reported for the fifteenth day of a month resulted in similar precision in modeling overwintering (data not shown). Models constructed to forecast survival on 15 March from dates prior to 15 September used only deviations from

Table 2. Weather variables, their partial regression coefficients and coefficient of determination (R2), for estimating levels of Puccinia recondita overwintering on 15 March at Manhattan, KS

Date of prediction ^a	Variables ^b												
	PDJUL	TPSEP	TPOCT	SINDO	SINDD	MNDEC	PDJAN	MNDAUG	SCDDEC	SINFEB	SCDFEB	MNDMAR	R ²
15 September	16.37	-2.6											0.593
15 October	12.14	-2.1	1.51	-0.35									0.654
15 November	12.14	-2.1	1.51	-0.35									0.654
15 December	10.23	-1.5	1.38	-0.23	13.27	-0.004							0.999
15 January	10.67	-1.6	1.39	-0.24	13.7		-2.4						0.999
15 February	10.67	-1.6	1.39	-0.24	13.7		-2.4						0.999
15 March								-0.18	7.52	8.46	0.16	0.98	0.999

^a A model for each date of prediction was constructed to forecast inoculum survival on 15 March using data observed before 15 September, 15 October, 15 November, 15 December, 15 January, 15 February, or 15 March.

b Variables used in the models are 10-day averages prior to the fifteenth of the month: PDJUL and PDJAN = deviations from 10-year average precipitation of July and January, respectively; TPSEP and TPOCT = cumulative precipitation from 20 June to 15 September and 15 October, respectively; SINDO and SINDD = deviations of daily temperature equivalence function for 15 October and 15 December, respectively; SINFEB = daily temperature equivalence functions for 15 February; MNDEC = minimum temperatures for December; MNDAUG and MNDMAR = averages of deviations from the daily minimum temperature for August and March, respectively; and SCDDEC and SCDFEB = deviations from 10-year average snow cover for December and February, respectively.

the 10-year average rainfall in July and cumulative rainfall for 15 September as none of the other variables were significant in reducing variation in the level of leaf rust observed on 15 March. Variables for cumulative rainfall and the deviation of the fungal temperature function for 15 October were added to derive the October and November models. Five of the six variables that were used to derive the December model also were used in the January and February models. In the latter two models, the January precipitation variable was substituted for the December minimum temperature variable. The model for March used a completely different set of variables. Deviations in average snow cover for 15 December and 15 February were very important in explaining variation in the March model.

Forecasts of expected levels of overwintering of leaf rust in the nurseries at Manhattan were rounded to the next higher positive number (9 or lower) (Table 3). Forecasts for the 1988 crop year indicated no survival of leaf rust; however, several uredinia were observed to have overwintered in the nurseries. December through February forecasts for the 1990 crop year indicated that no P. recondita would survive, but the March forecast for severe overwintering was correct. Overwintering was forecast to be moderate in 1989, a year with severe drought at Manhattan, but only scattered uredinia were observed to have survived the winter.

DISCUSSION

Attempts to correlate fall leaf rust severities and the final leaf rust severities observed the next spring have not indicated any significant relationships between fall and spring wheat leaf rust epidemics. In previous studies, we found that overwintering of *P. recondita* in Kansas always resulted in at least a 2% statewide reduc-

tion in wheat production (11). However, in this study, we could not determine a significant relationship between the level of overwintering and percent yield reduction. The observed level of overwintering was 8 in five of the years between 1980 to 1993. Yield reductions were measured between 13.6 and 53.4% for those same 5 years (Table 3).

Perhaps the most important factor determining overwintering of P. recondita in the winter wheat-growing region of the central Great Plains is the presence of mycelium in the living tissues of the host (4). Survival of the host tissue harboring the mycelium is critical. In addition, P. recondita urediniospores are capable of surviving winter and early spring within uredinia on wheat tissue and debris. When leaf rust does not overwinter in a field or nursery within the area, then long-distance transport may become the mechanism of introduction of primary leaf rust inoculum, and the first uredium is observed on or about 25 April at Manhattan, KS.

When overwintering has occurred, the fungus usually is capable of 13 to 15 reproductive generations during the spring phase of the epidemic in the Manhattan area. However, if primary infection must result from long-distance transport, only 9 to 11 reproductive generations may occur (M. G. Eversmeyer, unpublished data). Models constructed for September and October, which could be used to forecast inoculum overwintering prior to wheat planting, forecast overwintering in all but three of the years that inoculum survival was observed on 15 March. These models for September and October did not forecast the level of overwintering with a high degree of accuracy.

Models were developed using weather data for the epidemic year prior to 15 December, January, February, and March that could accurately estimate overwintering levels of leaf rust at Manhattan on 15 March. A temperature variable, either the minimum temperature or the hourly temperature equivalence function, was the most important factor in explaining variation in overwintering of leaf rust (Table 2). Deviations from the optimal temperature for leaf rust development in December accounted for a large portion of the variation in overwintering each year. The inclusion of a precipitation variable for July (PDJUL), September (TPSEP), and October (TPOCT) indicates the importance of moisture in the establishment of volunteer wheat in the area and infection of those volunteer plants by P. recondita early in the summer and prior to fall planting. One of the recommendations for control of wheat leaf rust in the central Great Plains has been elimination of volunteer wheat during the summer and fall months prior to fall wheat planting.

Reinfection periods during the winter and early spring are extremely important in winter survival of P. recondita when snow cover is not present. Positive average deviations of the fungal temperature equivalence function for leaf rust and of cumulative rainfall indicate periods when reinfections can occur during the overwintering phase of the epidemic. Snow cover, which protects the infected wheat tissue from drastic temperature fluctuations during the winter and early spring, is apparently more important than the actual minimum temperature in survival of wheat leaf rust from fall infection to spring initiation of the epidemic. The deviation from the 10-year average snow cover on 15 December and 15 February combined with deviation in minimum temperature explained most of the variation in overwintering in the March model.

Expansion of these models or development of new models specific for crop reporting districts within the central Great

Table 3. Observed levels of *Puccinia recondita* overwintering on 15 March and predicted levels of overwintering obtained from models developed using weather averaged 10-days prior to the fifteenth of September, October, November, December, January, February, and March and the percent reduction in grain yield at Manhattan, KS, for the years 1980 to 1993

Yeara	Actual ^b	September	October	November	December	January	February	March	Yield loss(%)d
1980	0	0	1	1	0	0	0	0	1.0
1981	0	0	0	0	0	0	0	0	1.5
1982	2	8	3	3	2	2	2	2	12.8
1983	2	0	1	1	2	2	2	2	12.17
1984	0	2	1	1	0	0	0	0	1.5
1985	8	3	4	4	8	8	8	8	53.4
1986	8	9	6	6	8	8	8	8	49.6
1987	5	2	2	2	5	5	5	9	24.9
1988	1	0	2	2	0	0	0	0	3.4
1989	2	0	4	4	5	5	5	3	7.9
1990	8	2	0	0	0	0	0	9	13.6
1991	8	5	5	6	7	7	7	9	26.7
1992	8	4	4	9	9	9	9	9	31.1
1993	5	4	4	9	9	9	9	9	29.8

^a Data for 1980 to 1986 used to construct models, data for 1987 to 1993 used to verify models.

^b See Table 1 for explanation of codes.

^c See Table 2 for explanation of models.

d Increase in grain yield obtained by controlling leaf rust development by application of a fungicide on replicated plots.

Plains, using National Weather Service data and estimates of inoculum survival from field surveys and nursery data for locations within those areas, should increase our ability to construct regional models for long-range forecasts of severe leaf rust epidemics.

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