Development of Weather- and Airborne Inoculum-Based Models to Describe Disease Severity of Wheat Powdery Mildew

Xueren Cao, State Key Laboratory for Biology of Plant Disease and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, and Key Laboratory of Integrated Pest Management on Tropical Crops, Ministry of Agriculture, Environment and Plant Protection Institute, Chinese Academy of Tropical Agricultural Sciences, Haikou 571001, China; **Dongming Yao**, State Key Laboratory for Biology of Plant Disease and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, and College of Plant Protection, Anhui Agricultural University, Hefei 230036, China; **Xiangming Xu**, East Malling Research, New Road, East Malling, Kent ME19 6BJ, UK; **Yilin Zhou**, State Key Laboratory for Biology of Plant Disease and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193; **Kejian Ding**, College of Plant Protection, Anhui Agricultural University, Hefei 230036, China; **Xiayu Duan** and **Jieru Fan**, State Key Laboratory for Biology of Plant Disease and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China; and **Yong Luo**, Department of Plant Pathology, China Agricultural University, Beijing 100193, China

Abstract

Cao, X., Yao, D., Xu, X., Zhou, Y., Ding, K., Duan, X., Fan, J., and Luo, Y. 2015. Development of weather- and airborne inoculum-based models to describe disease severity of wheat powdery mildew. *Plant Dis.* 99:395-400.

Disease severity of wheat powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, was recorded weekly in fungicide-free field plots for three successive seasons from 2009 to 2012 in Langfang City, Hebei Province, China. Airborne conidia of *B. graminis* f. sp. *tritici* were trapped using a volumetric spore sampler, and meteorological data were collected using an automatic weather station. Cumulative logit models were used to relate the development of wheat powdery mildew

to weather variables and airborne conidia density. Density of airborne conidia was the most important variate; further addition of weather variables, although statistically significant, increased model performance only slightly. A model based on variables derived from temperature and humidity had a generalized R^2 of 72.4%. Although there were significant differences in model parameters among seasons, fine adjustment did not increase model performance significantly.

Powdery mildew of wheat, caused by the obligate fungal parasite *Blumeria graminis* f. sp. *tritici*, occurs in wheat-growing regions worldwide. The disease is most damaging in cool and moist regions such as China, Europe, South America, the southeastern United States, and some West Asian and North African countries (23). Yield losses as high as 12, 27, and 34% were reported in the midwestern, eastern, and southeastern United States, respectively (27). In China, this disease has become severe since the late 1970s, mainly due to the high input of nitrogenous fertilizer, use of semidwarf wheat cultivars, and expansion of irrigated production areas. Wheat production in China affected by powdery mildew was over 12.0 million ha in 1990 and 1991, causing an estimated grain yield loss of 1.44 and 0.77 million metric tons, respectively (20).

Use of resistant cultivars and application of fungicides are the primary disease management strategies (40). However, intensive production of wheat cultivars with one or few resistance genes exerted strong selective pressure on the pathogen population, resulting in a rapid increase of fungal population(s) possessing matching virulence genes. Subsequently, cultivars lose their resistance in a relatively short period of time. Application of fungicides is still effective and essential for disease management whenever yield potential is high (31). Therefore, it remains important to time fungicide applications based on disease prediction.

The relationship between disease development and environmental factors is key and often the only component of disease forecasting systems (37). Models have been developed for predicting plant diseases based on weather variables, including lettuce downy mildew (32), sorghum ergot (24), rose downy mildew (1), Asian soy-

bean rust (10), Sclerotinia blight of peanut (35), and Phoma stem canker of canola (13). The use of weather variables in disease prediction has been extensively reviewed (4,9,17,39). It is important to recognize that sole reliance on weather factors for disease forecasting assumes that inoculum is always present.

Inoculum is important for developing forecasting systems, and the source/type of inoculum may greatly influence the formulation of forecasting schemes. Jeger (16) developed models to describe the relationship between apple powdery mildew and the cumulative numbers of trapped spores. Xu et al. (41) derived models for infection of strawberry flowers by *Botrytis cinerea* based on inoculum only, weather variables only, and both inoculum and weather variables, and demonstrated that the models using both weather variables and inoculum gave the best predictions. Carisse et al. (6) reported that the relationship between incidence of powdery mildew on the vine leaves and the cumulative concentration of airborne conidia was significant. A significant relationship between disease and inoculum was reported for strawberry powdery mildew (3) and *Cercospora* leaf spot caused by *Cercospora beticola* (18).

A dynamic simulation model of wheat powdery mildew was developed based on the relationship between the disease cycles, weather conditions, and host characteristics (28). Te Beest et al. (36) assessed weather factors that can be used quantitatively for forecasting powdery mildew on wheat. In another study, mean hourly *B. graminis* f. sp. *tritici* conidia per cubic meter of air over a 7-day period was significantly correlated with development of wheat powdery mildew (5). However, there are no studies predicting disease severity of wheat powdery mildew using weather variables and/or airborne inoculum. This paper describes development of predictive models for disease severity of wheat powdery mildew based on field data that relate disease severity to weather variables and airborne inoculum concentration.

Materials and Methods

Experimental field and inoculation. Experiments were conducted in three growing seasons, 2009–10, 2010–11, and 2011–12,

Corresponding author: Yilin Zhou, E-mail: yilinzhou6@aliyun.com

Accepted for publication 23 September 2014.

in the same field at Langfang Experimental Station of the Chinese Academy of Agricultural Sciences (39°30'42"N, 116°36'07"E) in Hebei Province, China. The field was cropped with a winter wheat/soybean rotation since 2002. Flood irrigation was performed six times and fertilizer was applied twice during each growing season. Hand weeding was used to control weeds and no fungicides were used. The experimental field was maintained with conventional agronomic practices for wheat production in China (44). Each year in the first week of October (Table 1), the cultivar Jingshuang 16, highly susceptible to wheat powdery mildew, was sown. Plants were grown in a 6 × 20 m plot with row spacing of 0.25 m.

To ensure the presence of initial inoculum in the spring, infected plants with sporulating lesions from artificial inoculations were introduced to the plot. Seedlings of the cultivar Jingshuang 16, growing in a greenhouse, were used. Fifty seeds of Jingshuang 16 were sown in a 10-cm pot. Ten days after sowing, plants were inoculated by spreading conidia of a Chinese field isolate of *B. graminis* f. sp. *tritici* onto leaves; this isolate was maintained on the cultivar Chancellor by monthly transfer to fresh plants, on the leaves. The inoculated plants were incubated at 18°C for 7 days. In the spring of each year (Table 1), pots containing infected seedlings were placed in the experimental plot. One pot of the infected seedlings was used in every five rows.

Data collection. *Airborne inoculum concentration data.* A 7-day volumetric spore sampler (Burkard Manufacturing Co. Ltd., Rickmanworth, Hertfordshire, UK) was installed in the experimental field to sample conidia of *B. graminis* f. sp. *tritici* in the air. The sampler was placed in the center of the field 2 weeks after introduction of infected seedlings and operated at a constant flow rate of 10 liters of air per minute. The sampling orifice was 0.6 m above the ground in all three seasons. Four longitudinal traverses of the 48-mm tape surface were examined with a compound microscope (×400) to count the number of conidia. Counts were corrected to compensate for the area sampled and recorded as the number of conidia per cubic meter of air sampled per day (25). *B. graminis* f. sp. *tritici* conidia were identified by their morphological characteristics: size (25 to 30 × 8 to 10 μm), colorless, nearly ovoid to cylindrical shape (15).

Weather data. Meteorological data were collected using a Dynamet weather station (Dynamax, Inc., Houston, Texas, USA) placed about 50 m away from the experimental field. A data logger (CR1000, Campbell Scientific, Logan, UT) was used to record weather data at hourly intervals. Air temperature (*T*) and relative humidity (*RH*) were recorded with a HMP50 temperature and RH probe (Vaisala, Helsinki). Precipitation (*P*) was measured with a tipping bucket rain gauge (Texas Electronics, Dallas, TX). A silicon radiation sensor (LI-200SZ, Li-Cor, Lincoln, NE) was used to measure solar radiation (*SR*). Wind speed (*WS*) was recorded by 3 Cup Anemometer AC (RM Young Wind Sentry, Traverse, MI). The CS106 Barometer (Campbell Scientific, Logan, UT) was used to measure vapor pressure deficit (*VPD*). The average daily *T*, *RH*, *WS*, *SR*, *VPD*, and daily accumulative *P* were then calculated from the recorded data.

Disease data. Disease severity was assessed at 7-day intervals from about one month after introduction of infected seedlings at tillering stage (growth stage, GS 5) to milky ripe stage (GS 11.1) (19). Powdery mildew severity was rated visually on a scale of 0 to 9 as follows: 0, free from symptoms; 1, a few isolated lesions on only the lowest leaves; 2, moderate (25 to 50% of leaf surface covered with lesions) to severe (>50% of leaf surface covered with lesions) disease on the lowest leaves; 3, light disease (<25% of leaf

surface covered with lesions) on the lower third of the plant with the lower most leaves diseased at moderate to severe levels; 4, moderate to severe on the lower third of the plant with a few isolated lesions on the middle leaves; 5, severe disease on lower leaves with light to moderate disease on the middle leaves; 6, severe disease on lower leaves with moderate to severe disease on the middle leaves; 7, severe disease on both lower and middle leaves with some disease on the flag leaf as well; 8, severe disease on both lower and middle leaves with moderate to severe disease on the flag leaf as well; and 9, severe disease on all leaves with spikes diseased as well (29,33). For each disease assessment, plants at 15 positions, each with 20 stems, were selected arbitrarily within the plot and evaluated.

Data analysis. A cumulative logit model was used to model the mildew score (Y_i), which was recorded in 10 categories ($J = 10$). Y_i follows a multinomial distribution with a parameter π . π_{ij} denotes the probability that i th plant falls in the mildew score j . A cumulative logit is defined as:

$$\logit[P(Y_i \leq j)] = \logit(\pi_{i1} + \dots + \pi_{ij}) = \ln \left\{ \frac{P(Y_i \leq j)}{1 - P(Y_i \leq j)} \right\} = \ln \left\{ \frac{P(Y_i \leq j)}{P(Y_i > j)} \right\} \quad (1)$$

A cumulative logit does not exist for the last category of the response variable (i.e., $j = 10$ in the present case). A cumulative logit model is a regression model for a cumulative logit (30) for $j = 1, \dots, J - 1$:

$$\ln \left\{ \frac{P(Y_i \leq j)}{P(Y_i > j)} \right\} = \alpha_j - \sum \beta_k x_{ik} \quad (2)$$

where x_{ik} represents the k th explanatory variate, β_k the effect of x_{ik} , and α_j the intercept for each cumulative logit. The regression part $\sum \beta_k x_{ik}$ is independent of j . The larger the value of $\sum \beta_k x_{ik}$, the higher the probability of Y_i falling in a category at the upper end of the category scale. The α_j values determine the horizontal displacements of the cumulative probability; the larger the α_j value, the further it moves to the right. The α_j values may also be interpreted as cut-off points on a latent variable that underlines the categorical scale.

Equation 2 describes a linear relationship of the logit of the odds ratio of the response being below/above a particular category with explanatory variates. It is the extension of the common logistic model with only two possible outcomes (i.e., diseased or healthy). Thus, cumulative logit models are a class of generalized linear models, assuming that the errors follow a binomial distribution. This model satisfies

$$\ln \left\{ \frac{\Pr(Y_i \leq j | x_1) / \Pr(Y_i > j | x_1)}{\Pr(Y_i \leq j | x_2) / \Pr(Y_i > j | x_2)} \right\} = \beta(x_2 - x_1) \quad (3)$$

for all j (i.e., proportional odds property, hence it is also called proportional odds model). Thus, β estimates the change in the explanatory odds ratio (on the ln scale) for one unit increase in the explanatory variate x .

Weather variables and inoculum concentration were explanatory variates. Inoculum concentration was logarithmically transformed on the natural base to reduce heterogeneity in variance (11). In addition, several other variables were derived from weekly average temperature (TP), including TP² and TP³ included as explanatory variates. In addition, annual differences were included as a random effect variable. To reduce small estimates of coefficients, TP² and TP³ were divided by 100 and 1,000, respectively. A generalized R^2 was estimated based on likelihood (30). Nest models were used to

Table 1. Growing season, planting date, inoculation date, date of first rating, and date of last rating used for development of disease prediction models

Season	Planting date	Inoculation date	Date of first rating	Date of last rating
2009–10	6 Oct 2009	2 Apr 2010	27 Apr 2010	1 Jun 2010
2010–11	6 Oct 2010	25 Mar 2011	27 Apr 2011	1 Jun 2011
2011–12	6 Oct 2011	23 Mar 2012	27 Apr 2012	30 May 2012

determine whether the dependence of logit ($P[Y_i \leq j]$) on each explanatory variate (i.e., β_k) varied with year. Comparing nested models was based on the likelihood test. In addition to the likelihood test, an explanatory variate was only included in a model if the increase in the generalized R^2 was $>0.3\%$.

Results

Disease epidemics in the field. The 2009–10 season was the wettest of the three seasons, with approximately twice the amount of rainfall of the other two seasons (Table 2). Differences in temperature and humidity among the seasons were not apparent. At the last assessment, all plants had mildew severity scores greater than five (Fig. 1). In all 3 years, wheat powdery mildew developed slowly from the first disease assessment (GS 7) to the second (GS 10); nearly all plants were either mildew-free or had mildew scores in the first category (Fig. 1). The disease developed rapidly from GS 10 to GS 10.5.3. Thereafter, the rate of disease development slowed down from GS 10.5.4 to GS 11.1.

Modeling with weather variables only. When season was not included, a weather-only model contained six weather variables (TP, RH, TP², TP³, WS, and SR), with the generalized R^2 of 84.1% (Table 3). Rainfall and vapor pressure deficit were also statistically significantly related to the disease score, but their inclusion only increased the generalized R^2 by $<0.2\%$. A best model with temperature and humidity-related variates (TP, RH, TP², and TP³) produced a generalized R^2 of 72.4% (Table 4). When season was included as a random factor in the intercept, there was an increase of 0.8% in the generalized R^2 (Table 3). A few slope parameters did vary with years, but accounted for very little variability in the data.

Modeling with the inoculum only. The cumulative logit model based on airborne inoculum density produced a generalized R^2 of 82.6% (Tables 3 and 4). Figure 2 shows this fitted model for three disease severity scores. Season affected both the intercept and the slope parameters, leading to an increase of 3.4% in the generalized R^2 . The response to inoculum was greatest and least in 2009–10 and 2011–12 seasons, respectively.

Table 2. Weekly accumulated number of *Blumeria graminis* f. sp. *tritici* conidia per cubic meter of air and weather conditions at different growth stages in Langfang City, Hebei Province, during the 2009–10, 2010–11 and 2011–12 seasons

Season	Days after inoculation	GS ^a	C	T/°C	RH/%	SR/W m ⁻²	WS/m s ⁻¹	VPD/mbar	P/mm
2009–10	25	7	3.1	11.4	46.4	4.5	2.4	1013.8	6.6
	33	10	8.9	18.03	41.9	5.2	2.3	1005.4	15.2
	39	10.5	19.1	18.5	38.1	5.6	2.0	1006.6	0.3
	46	10.5.3	65.8	18.3	59.2	4.5	1.5	1010.7	5.1
	54	10.5.4	151.7	24.1	41.5	6.0	1.7	1004.8	0.0
	61	11.1	208.3	20.8	70.2	4.3	1.1	1010.5	21.6
2010–11	33	7	4.8	12.6	58.4	3.8	1.7	1008.6	9.1
	40	10	5.6	17.2	40.8	5.0	2.0	1006.3	0.5
	47	10.5	9.6	17.0	57.9	4.1	1.5	1004.8	12.2
	54	10.5.3	41.9	20.8	32.2	6.2	2.5	1006.1	0.0
	61	10.5.4	99.1	20.2	37.5	5.6	2.5	1010.1	0.0
	68	11.1	156.3	22.7	54.8	5.4	1.8	1006.3	3.6
2011–12	36	7	1.3	15.7	61.2	3.8	1.9	1003.2	14.5
	43	10	6.5	18.9	46.7	4.6	1.2	1008.1	1.5
	49	10.5	42.5	22.1	38.2	5.0	1.5	1006.5	0.0
	55	10.5.3	183.1	19.3	54.2	4.8	1.8	1005.9	0.5
	62	10.5.4	153.8	22.4	53.4	5.0	1.5	1008.3	6.6
	69	11.1	244.4	22.2	48.1	5.7	1.6	1008.4	0.3

^a Growth stages (GS) were recorded according to Feekes scale illustrated by Large (19); weekly accumulated number of *B. graminis* f. sp. *tritici* conidia per cubic meter of air (C); mean temperature per week (T), mean relative humidity per week (RH), mean solar radiation per week (SR), mean wind speed per week (WS), mean vapor pressure deficit per week (VPD), total rainfall per week (P). Disease severity was assessed by using a scale from 0 to 9.

Fig. 1. Observed (A to C) and fitted (D to F) number of wheat plants in each mildew score on each assessment date in Langfang City, Hebei Province, during the 2009–10, 2010–11, and 2011–12 seasons. The fitted values were from a cumulative logit model fitted to both inoculum and weather variables over the three seasons (model details are presented in Table 5). Powdery mildew on each plant was assessed on a scale from 0 to 9 (29,33; see text for more details). On each date, 300 plants were assessed. Growth stages (GS) were recorded according to Feekes scale illustrated by Large (19).

Modeling with both inoculum and weather variables. Inclusion of weather variables RH, TP², WS, and SR and inoculum produced a cumulative logit model with a generalized R² of 86.2% (Table 3). There also was a significant difference among seasons in terms of the model intercept: inclusion of this seasonal difference led to an increase of 1.2% in the generalized R² (Table 3).

However, because WS and SR are usually not recorded, we derived another model that contained only inoculum, temperature and relative humidity (Table 4). This model increased 1% in the generalized R² over the model based on inoculum only without the seasonal effect (Table 4). This model described the observed data well (Fig. 1); differences between the fitted and observed values were mainly restricted to neighboring disease categories. At a given disease score, this model indicated that an increase of 1% in relative humidity, 1 in T², and 1 in inoculum (on the ln scale) will lead to a corresponding increase of the odds ratio of being above the disease score by ca. 1.5, 2.1, and 11.7 times, respectively.

Discussion

In this study, we developed cumulative logit models relating development of wheat powdery mildew to weather variables and airborne conidial density. Of all the variables, the most important variate was airborne conidial density; further addition of weather variables, although statistically significant, increased model performance only slightly. Although there were significant differences in model structure among the three seasons, such fine adjustment only resulted in ca. 1 to 3% increase in the generalized R².

It is generally agreed that environmental conditions are the driving force for disease epidemics (14). A model with only weather variables resulted in a generalized R² of 84%, close to the best performing model identified in this study. However, interpretation

Fig. 2. Fitted cumulative logit models for three categories of wheat powdery mildew severity scores in relation to weekly accumulated number of *Blumeria graminis* f. sp. *tritici* conidia per cubic meter of air. The three curves represent the cumulative probability of $P(Y_i \leq j = 1, 3, \text{ and } 5)$, i.e., mildew score of 0, 2, and 4, and the probability of mildew score >4 (i.e., category of $j > 5$) equals to $1 - P(Y_i \leq j = 5)$.

Table 3. Summary of cumulative logit regression analyses relating the probability of wheat plants in a particular mildew category to weather variables only, inoculum only, or both weather and inoculum variables^a

Model	Season	Explanatory variates		
		Weather ^b	Inoculum	Weather + Inoculum
Without season	Generalized R ²	82.7%	82.6%	86.2%
	Variables	TP (–), WS (+), SR (+), RH (+), Rain (–), TP ² (+), TP ³ (–)		WS (+), RH (+), SR (+), T ² (+), C (+)
With season	Generalized R ²	85.4%	86.0%	87.4%
	Intercept/slope	Intercept only	Intercept & slope	Intercept only

^a Data were collected over three seasons; the seasonal effect was included as a random effect (in intercept) and/or as interactions with other variates (i.e., slope).

^b TP, RH, WS, SR, Rain, TP², TP³, and C were average weekly temperature, relative humidity, wind speed, solar radiation, square and cubic of temperature (divided by 100 and 1,000, respectively), and inoculum density, respectively; actual values of these variates are presented in Table 2. The ‘+’ and ‘–’ after each variable indicated the sign of slope estimates.

Table 4. Parameter estimates of two cumulative logit models relating the probability of wheat plants in a particular mildew category to weather variables only, inoculum only, or both weather and inoculum variables^a

Parameters ^b		Model		
		Weather ^c	Inoculum	Inoculum + Weather
Intercept (α_j)	α_1	–105.29 ± 3.747	2.06 ± 0.092	5.32 ± 0.219
	α_2	–102.36 ± 3.746	6.45 ± 0.113	9.83 ± 0.236
	α_3	–101.92 ± 3.744	7.29 ± 0.125	10.68 ± 0.242
	α_4	–101.04 ± 3.738	8.84 ± 0.149	12.25 ± 0.257
	α_5	–100.06 ± 3.729	10.54 ± 0.175	14.00 ± 0.277
	α_6	–99.07 ± 3.723	12.06 ± 0.194	15.55 ± 0.293
	α_7	–97.69 ± 3.717	13.61 ± 0.212	17.30 ± 0.317
	α_8	–95.73 ± 3.708	15.31 ± 0.222	19.17 ± 0.335
	α_9	–92.85 ± 3.704	18.05 ± 0.254	21.97 ± 0.358
Slope (β_k)	C		2.81 ± 0.043	2.46 ± 0.047
	TP	–20.29 ± 0.677		
	TP ²	117.74 ± 3.896		0.75 ± 0.045
	TP ³	–21.18 ± 0.722		
	RH	11.13 ± 0.296		3.98 ± 0.304
Generalized R ²		72.4%	82.6%	83.6%

^a Data were collected over three seasons from 2009 to 2012 in Langfang City, Hebei Province.

^b See equation 2 for parameter description and Table 2 for explanation in explanatory variates.

^c Weather variables including average weekly temperature and relative humidity.

of individual variables contained in the model in terms of their effect on epidemic components is difficult because of the inter-correlation among the seven weather variables, multi-faceted effects of these variables on mildew epidemics (spore production, dispersal, infection, and subsequent colonization), and the variables being averaged over a 7-day period. Overall, the signs of parameter estimates agree with our current understanding of *B. graminis* f. sp. *tritici* epidemiology. The greater the average wind speed, the more severe the mildew epidemic. Thus, the positive effect of wind in spore dispersal (38) outweighs its negative effect on reducing humidity, which may inhibit mildew development (38). Increasing relative humidity led to increasing mildew development as reported previously (38). Rain has a negative effect on sporulation and spore survival as observed in previous studies (26,34). The effects of temperature are complicated by the fact that three temperature-related variates were included (temperature and its quadratic and cubic terms). This may be related to the fact that high temperature (>25°C) may inhibit mildew (22,36). Although in the present study, average temperatures over a period of 7 days were all less than 25°C, average values were >20°C on many occasions, indicating there must be many episodes with temperature greater than 25°C.

Encouragingly, the effects of weather variables on mildew development did not vary significantly with years. The overall differences between seasons are mainly manifested in the overall mildew severity (i.e., in affecting the intercept in the cumulative logit model). Unfortunately, of the several variables included in the model, wind speed and solar radiation (and to a lesser extent, rainfall) are usually not recorded. Temperature and humidity are two weather variables commonly recorded under field conditions. Hence, a cumulative logit model was developed based on temperature and humidity only without incorporating seasonal effects. This model fitted the data with a generalized R^2 of 72.4%, which is respectable for field data (42,43). It would be interesting to compare this simple weather-based model with other models in future studies.

Inoculum density has often been featured in disease forecasting models, such as for *Botrytis* leaf blight of onion (7) and grape powdery mildew (6). In the present study, the model with only airborne inoculum density had a similar predictive power to that containing seven weather variables. Adding further weather variables to the inoculum-only model improved the model performance slightly. The nature of the sampling scheme used in the present study may explain why the inoculum variable was so highly related to mildew symptoms. Disease development was assessed weekly together with weather and inoculum data. The *B. graminis* f. sp. *tritici* incubation period (from infection to visible lesion) is expected to be longer than 7 days under field fluctuating conditions (12). Thus, any infection from conidia released early during the 7-day sampling period would not likely result in visual symptoms on the assessment day. On the other hand, a single lesion is likely to sporulate for several days (2). Given that conditions for spore production and dispersal were not sufficiently limiting, the number of airborne conidia effectively represents the amount of sporulating lesions (i.e., visual lesions) during the preceding 7 days. Following the same logic, if all visible lesions were assumed to produce conidia and their dispersal was not limited, the density of airborne conidia can then be used to represent the amount of visual symptoms. Given the limited effects of adding further variables into the inoculum-only model, we may conclude that weather conditions were indeed not limiting factors for conidia dispersal and production.

Cumulative logit models were used in the present study to reflect the nature of the ordinal score system used. Although there were temporal correlations among observation within each year, inherent in nearly all field epidemiological studies, it was not possible to incorporate such temporal correlation in the framework of cumulative logit regression models. Nevertheless, we would expect that such temporal correlation would not affect outcomes of this study too much for two reasons. First, the same 300 plants were

not assessed over time. Second, we used data from 3 years to develop models.

Use of any disease predictive scheme needs to consider the relevance of model predictions to practical disease management. For example, disease predictions need to be closely aligned with an action threshold for a given disease. Cumulative logit models developed in the present study predict the probability of mildew severity in each of the 10 categories. This information may guide users to apply fungicides to suppress fungal sporulation and/or protect new leaves from infection if the predicted mildew severity is over an action threshold. Although for research purposes we assessed mildew severity using the 0 to 9 scale, fewer categories may be needed for practical disease prediction. For instance, severity scores over five in commercial production can be treated as the same (severe disease). Similarly, we could adjust the predicted risks for cultivar susceptibility. For example, we may reduce the predicted category by one or more categories as appropriate for less susceptible cultivars. Cumulative logit models (with proportional odds) have an advantage that there is no need to develop new models when merging (collapsing) categories. For instance, we can merge categories 1 and 2 as light disease, 3 and 4 as moderate, and >4 as severe. We can generate the corresponding forecasts for the four new groups (healthy, light, moderate, and severe) using the current logit models with appropriate intercept (α_1 , α_3 , and α_5 in Table 4) without the need for further model development.

Further evaluation of models presented in Table 4 is necessary to validate these models under natural epidemic conditions without artificial inoculation and to establish an action threshold on cultivars with differing susceptibility to powdery mildew. For inoculum quantification, molecular methods (instead of laborious spore trapping) can be used. Real-time PCR methods for quantification of airborne inoculum have been reported in other diseases such as brown rot of stone fruit (21) and leaf blight of onion (8). Similar methods may be developed for wheat powdery mildew.

Acknowledgments

This work was financially supported by National Key Basic Research Program of China (2013CB127704), National Natural Science Foundation of China (31171793), Special Fund for Agro-scientific Research in the Public Interest (201303016), and National Key Technology R&D Programs of China (2012BAD19B04).

Literature Cited

1. Aegerter, B. J., Nuñez, J. J., and Davis, R. M. 2003. Environmental factors affecting rose downy mildew and development of a forecasting model for a nursery production system. *Plant Dis.* 87:732-738.
2. Aust, H. J. 1981. Über den Verlauf von Mehltau-epidemien innerhalb des Agro-Ökosystems Gerstenfeld. *Acta Phytomed.* 7:1-76.
3. Blanco, C., Santos, B. D. L., Barrau, C., Arroyo, F. T., Porras, M., and Romero, F. 2004. Relationship among concentrations of *Sphaerotheca macularis* conidia in the air, environmental conditions, and the incidence of powdery mildew in strawberry. *Plant Dis.* 88:878-881.
4. Bourke, P. M. A. 1970. Use of weather information in the prediction of plant disease epiphytotics. *Annu. Rev. Phytopathol.* 8:345-370.
5. Cao, X. R., Duan, X. Y., Zhou, Y. L., and Luo, Y. 2012. Dynamics in concentrations of *Blumeria graminis* f. sp. *tritici* conidia and its relationship to local weather conditions and disease index in wheat. *Eur. J. Plant Pathol.* 132:525-535.
6. Carisse, O., Bacon, R., and Lefebvre, A. 2009. Grape powdery mildew (*Erysiphe necator*) risk assessment based on airborne conidium concentration. *Crop Prot.* 28:1036-1044.
7. Carisse, O., McCartney, H. A., Gagnon, J. A., and Brodeur, L. 2005. Quantification of airborne inoculum as an aid in the management of *Botrytis* leaf blight of onion caused by *Botrytis squamosa*. *Plant Dis.* 89:726-733.
8. Carisse, O., Tremblay, D. M., Lévesque, C. A., Gindro, K., Ward, P., and Houde, A. 2009. Development of a TaqMan real-time PCR assay for quantification of airborne conidia of *Botrytis squamosa* and management of *Botrytis* leaf blight of onion. *Phytopathology* 99:1273-1280.
9. Coakley, S. M. 1988. Variation in climate and prediction of disease in plants. *Annu. Rev. Phytopathol.* 26:163-181.
10. Del Ponte, E. M., Godoy, C. V., Li, X., and Yang, X. B. 2006. Predicting severity of Asian soybean rust epidemics with empirical rainfall models. *Phytopathology* 96:797-803.
11. Everts, K. L., and Lacy, M. L. 1990. Influence of environment on conidia of

- Alternaria porri* in air and purple blotch incidence on onion. Phytopathology 80:1387-1391.
12. Friedrich, S. 1995. Calculation of the incubation period of powdery mildew under field conditions. Z. Pflanzenkrankh. Pflanzenschutz 102:348-353.
 13. Ghanbarnia, K., Fernando, W. G. D., and Crow, G. 2009. Developing rainfall- and temperature-based models to describe infection of canola under field conditions caused by pycnidiospores of *Leptosphaeria maculans*. Phytopathology 99:879-886.
 14. Hardwick, N. V. 2002. Weather and plant disease. Weather 57:184-190.
 15. He, J. M., He, W. L., Song, Y. L., and Zhang, Z. S. 1992. Wheat powdery mildew and its control. II The pathogen of wheat powdery mildew. Henan Agric. Sci. 9:17-19.
 16. Jeger, M. J. 1984. Relating disease progress to cumulative numbers of trapped spores: Apple powdery mildew and scab epidemics in sprayed and unsprayed orchard plots. Plant Pathol. 33:517-523.
 17. Jones, R. A. C., Salam, M. U., Maling, T. J., Diggle, A. J., and Thackray, D. J. 2010. Principles of predicting plant virus disease epidemics. Annu. Rev. Phytopathol. 48:179-203.
 18. Khan, J., Qi, A., and Khan, M. F. R. 2009. Fluctuations in number of *Cercospora beticola* conidia in relationship to environment and disease severity in sugar beet. Phytopathology 99:796-801.
 19. Large, E. C. 1954. Growth stages in cereals. Illustration of the Feekes scale. Plant Pathol. 3:128-129.
 20. Liu, W. C., and Shao, Z. R. 1994. Epidemiology, occurrence and analysis of wheat powdery mildew in recent years. Plant Prot. Tech. Ext. 6:17-20.
 21. Luo, Y., Ma, Z., Reyes, H. C., Morgan, D. P., and Michailides, T. J. 2007. Quantification of airborne spores of *Monilinia fructicola* in stone fruit orchards of California using real-time PCR. Eur. J. Plant Pathol. 118:145-154.
 22. Mathre, D. E. 1982. Compendium of Barley Diseases. American Phytopathological Society, St. Paul, MN.
 23. McIntosh, R. A. 1998. Breeding wheat for resistance to biotic stresses. Euphytica 100:19-34.
 24. McLaren, N. W., and Flett, B. C. 1998. Use of weather variables to quantify sorghum ergot potential in South Africa. Plant Dis. 82:26-29.
 25. Mediavilla-Molina, A., Angulo-Romero, J., Infante-García-Pantaleón, F., and Domínguez-Vilches, E. 1997. Influence of meteorological factors on the incidence of *Cladosporium* Link ex Fr. conidia in the atmosphere of Cordoba (Spain). Pages 117-126 in: Phenology in Seasonal Climates. I. H. Lieth and M. D. Schwartz, eds. Backhuys Publishers, Leiden, The Netherlands.
 26. Paulus, A. O. 1990. Fungal diseases of strawberry. HortScience 25:885-889.
 27. Persaud, R. R., and Lipps, P. E. 1995. Virulence genes and virulence gene frequencies of *Blumeria graminis* f. sp. *tritici* in Ohio. Plant Dis. 79:494-499.
 28. Rossi, V., and Giosuè, S. 2003. A dynamic simulation model for powdery mildew epidemics on winter wheat. EPPO Bull. 33:389-396.
 29. Saari, E. E., and Prescott, J. M. 1975. A scale for appraising the foliar intensity of wheat diseases. Plant Dis. 59: 377-380.
 30. Schabenberger, O., and Pierce, F. J. 2002. Contemporary Statistical Models for the Plant and Soil Sciences. CRC Press, Boca Raton, FL.
 31. Schepers, H., Bouma, E., Frahm, J., Wolk, T., and Secher, B. J. M. 1996. Control of fungal diseases in winter wheat with appropriate dose rates and weather-based decision support systems. OEPP Bull. 26:623-630.
 32. Schemm, H., and van Bruggen, A. H. C. 1994. Weather variables associated with infection of lettuce by downy mildew (*Bremia lactucae*) in coastal California. Phytopathology 84:860-865.
 33. Sheng, B. Q., and Duan, X. Y. 1991. Improvement of scale 0-9 method for scoring adult plant resistance to powdery mildew of wheat. Beijing Agric. Sci. 9:38-39.
 34. Sivapalan, A. 1993. Effects of impacting rain drops on the growth and development of powdery mildew fungi. Plant Pathol. 42:256-263.
 35. Smith, D. L., Hollowell, J. E., Isleib, T. G., and Shew, B. B. 2007. A site-specific, weather-based disease regression model for Sclerotinia blight of peanut. Plant Dis. 91:1436-1444.
 36. Te Beest, D. E., Paveley, N. D., Shaw, M. W., and van den Bosch, F. 2008. Disease-weather relationships for powdery mildew and yellow rust on winter wheat. Phytopathology 98:609-617.
 37. van Maanen, A., and Xu, X. M. 2003. Modelling plant disease epidemics. Eur. J. Plant Pathol. 109:669-682.
 38. Wiese, M. V. 1987. Compendium of Wheat Diseases. 2nd ed. American Phytopathological Society, St. Paul, MN.
 39. Wolf, E. D. D., and Isard, S. A. 2007. Disease cycle approach to plant disease prediction. Annu. Rev. Phytopathol. 45:203-220.
 40. Wolfe, M. S. 1984. Trying to understand and control powdery mildew. Plant Pathol. 33:451-466.
 41. Xu, X. M., Harris, D. C., and Berrie, A. M. 2000. Modeling infection of strawberry flowers by *Botrytis cinerea* using field data. Phytopathology 90:1367-1374.
 42. Xu, X. M., Madden, L. V., and Edwards, S. G. 2014. Relating HT2 and T2 toxin accumulation in field oat grains to environmental conditions. Phytopathology 104:57-66.
 43. Xu, X. M., Madden, L. V., Edwards, S. G., Doohan, F. M., Moretti, A., Hornok, L., Nicholson, P., and Rietini, A. 2013. Developing logistic models to relate the accumulation of DON associated with Fusarium head blight to climatic conditions in Europe. Eur. J. Plant Pathol. 137:689-706.
 44. Zhao, G. C. 2006. Cultivation Technologies for High-yielding and Good Quality of Wheat. China Agricultural Science and Technology Press, Beijing.