Effects of Climate Change on Epidemics of Powdery Mildew in Winter Wheat in China

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Abstract

Powdery mildew is a highly destructive winter wheat pathogen in China. Since the causative agent is sensitive to changing weather conditions, we analyzed climatic records from regions with previous wheat powdery mildew epidemics (1970 to 2012) and investigated the long-term effects of climate change on the percent acreage (PA) of the disease. Then, using PA and the pathogen's temperature requirements, we constructed a multi-regression model to predict changes in epidemics during the 2020s, 2050s, and 2080s under representative concentration pathways RCP2.6, RCP4.5, and RCP8.5. Mean monthly air temperature increased from 1970 to 2012, whereas hours of sunshine and relative humidity decreased ($P < 0.001$).

Year-to-year temperature changes were negatively associated with those of PA during oversummering and late spring periods of disease epidemics, whereas positive relationships were noted for other periods, and year-to-year changes in relative humidity were correlated with PA changes in the early spring period of disease epidemics ($P < 0.001$). Our models also predicted that PA would increase less under RCP2.6 (14.43%) than under RCP4.5 (14.51%) by the 2020s but would be higher by the 2050s and 2080s and would increase least under RCP8.5 (14.37% by the 2020s). Powdery mildew will, thus, pose an even greater threat to China's winter wheat production in the future.

The Earth's climate has undergone dramatic changes since the Industrial Revolution and is projected to undergo further changes in the near future (Pachauri et al. 2014). For example, the global mean surface air temperature has increased by $0.74 \pm 0.18^\circ\text{C}$ over a 100-year period (1906–2005) and is predicted to rise by an additional 1.0 to 3.7°C by the end of the 21st century, owing to the accumulation of greenhouse gasses (Anderson et al. 2016; Deryng et al. 2014; Huang et al. 2017; Jiang and Fu 2012; Pachauri et al. 2014; Solomon et al. 2007). Climate change has also had a significant impact on the occurrence and epidemics of crop pests and diseases (Coakley et al. 1999; Fischer et al. 1995; Goudriaan and Zadoks 1995; Rosenzweig and Parry 1994; Rosenzweig et al. 2001).

As an example, wheat powdery mildew (caused by *Blumeria graminis* f. sp. *tritici*) has become one of the most important wheat diseases in China, owing to weather conditions, the susceptibility of cultivated varieties, extensive irrigation, and the use of nitrogen fertilizer (Cao et al. 2010, 2013; Shen et al. 2015). In fact, during 1990 and 1991 alone, over 12.0 million ha were affected by the disease, which resulted in estimated grain yield losses of 1.44 and 0.77 million tons, respectively (Liu and Shao 1994; Xue et al. 2009). Alarmingly, the areas of occurrence of wheat powdery mildew have gradually extended from southwest China toward the east and north, which has resulted in increased disease frequency and severity since the 1970s (Cao et al. 2013; Li et al. 2013). The frequency distribution of *B. graminis* f. sp. *tritici* isolates with different temperature sensitivities indicates that the pathogen populations have been influenced by selection pressure from changing temperature (Wan et al. 2010). Thus, given the severity of wheat powdery mildew epidemics in China, the association of pathogens and climate change, and our current understanding of the conditions under which wheat powdery

mildew thrives, it is important to elucidate the effects of climate change on epidemics of wheat powdery mildew.

Although the influence of climate on plant diseases has been widely investigated, most findings were based on seasonal- or annual-scale data (Coakley 1988; Coakley et al. 1988; Johnson et al. 1996). The paucity of more long-term investigations can be attributed to the lack of long-term disease monitoring data as well as to the challenges of eliminating the influence of slowly changing factors, including crop varieties and management practices. As a result, some studies have used an approach based on first-difference time series, i.e., the difference in values from one year to the next (Coakley et al. 1999; Lobell and Field 2007; Nicholls 1997), and model-based methods have also been used to predict the influence of climate on plant pests and disease at various spatio-temporal scales (Jurossek and von Tiedemann 2013). For example, Salinari et al. (2006) used the GISS and HadCM3 general circulation models (GCMs) to predict that epidemics of grapevine downy mildew (caused by *Plasmopara viticola*) will increase in the wine-producing regions of Italy near Turin in the 2030s, 2050s, and 2080s.

When predicting the response of agricultural systems to climate change, these studies have shown that GCMs and climate scenarios are significant sources of uncertainty (Madgwick et al. 2011), and the role of scenario has been discussed extensively (Siebold and von Tiedemann 2012). However, variation between different GCMs can also influence biological consequences (Madgwick et al. 2011) and predicting biological impacts based on projections from only one single GCM can yield misleading results (Skelsey and Newton 2015). As a result, the use of multiple GCMs has recently become a common practice in impact studies (Buisson et al. 2010; Jiang and Fu 2012; Rosenzweig et al. 2013; van Bruggen et al. 2015b). For example, Hu et al. (2015) analyzed the overwintering boundaries of planthoppers (*Nilaparvata lugens*) in China by using temperature data generated by 15 different GCMs. Therefore, we were interested in using the strategy to investigate the influence of climate change on wheat powdery mildew epidemics in China.

Accordingly, the objectives of the present study were i) to analyze trends in climatic variables during periods of wheat powdery mildew epidemics from 1970 to 2012 in winter wheat-producing regions of

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China; ii) to construct a model of the association between climate change and wheat powdery mildew epidemics, based on meteorological data and distribution; and iii) to predict the influence of future climate change on wheat powdery mildew epidemics, using multiple climate models.

Materials and Methods

Wheat and powdery mildew occurrence data. We obtained the acreage of winter wheat (million hectares) in China from 1970 to 2012 as well as annual survey data regarding powdery mildew epidemics from the China Agricultural Yearbook 2012 (Ministry of Agriculture of the People's Republic of China 2013), the Chinese Statistical Yearbook 2012 (National Bureau of Statistics of China 2013), and the National Agro-Tech Extension and Service Center (<http://www.natesc.agri.cn/>). For each year (1970 to 2012), we recorded the number of wheat fields ≥ 1 ha that had a mean powdery mildew incidence of $\geq 5\%$, and, as measure of disease intensity, we calculated the percentage of total winter wheat acreage that was infected with powdery mildew (PA), using the following formula: $PA = (\text{acreage of winter wheat with powdery mildew} / \text{acreage of winter wheat planted}) \times 100\%$.

Climate data. Meteorological data. Climate data for the regions of China where winter wheat was affected by powdery mildew were collected from 610 weather stations via the China Meteorological Data Sharing Service System (<http://data.cma.cn/en/>). From each station, we obtained monthly mean air temperatures (T), monthly mean precipitation values (P), monthly mean relative humidity (RH), and monthly mean hours of sunshine (SH) for the period of 1970 to 2012, and the data were carefully checked for changes in some weather stations or observational problems and were adjusted as necessary. For the stations that had partial missing data ($<25\%$), the data of the nearest station was used as replacement. However, for those having more than 25% missing data in any single calendar month from 1970 to 2012, these stations were omitted from the analysis (Mitchell and Jones 2005).

Estimation of future temperature. We designated three 30-year periods for characterizing mean climate changes, in relation to the baseline climate of 1980–2009, i.e., 2020s (2010–2039), 2050s (2040–2069), and 2080s (2070–2099). The monthly mean air temperature data for the 2020s, 2050s, and 2080s were estimated based on extractions from 15 GCM simulations in the World Climate Research Program's Coupled Model Intercomparison Project phase 5 dataset (http://www-pcmdi.llnl.gov/ipcc/about_ipcc.php) (Table 1). In addition, we also considered three different representative concentration pathways (RCPs) (RCP2.6, RCP4.5, and RCP8.5) for each GCM, which we obtained from the Intergovernmental Panel on

Climate Change Special Report (van Vuuren et al. 2011). RCP2.6 assumes that radiative forcing will peak at about 3 W/m^2 before the year 2100 and then decline to 2.6 W/m^2 by year 2100, whereas RCP4.5 assumes that radiative forcing will stabilize at 4.5 W/m^2 after the year 2100 without exceeding the value beforehand, and RCP8.5 assumes that radiative forcing will increase to 8.5 W/m^2 by year 2100 and likely continue increasing afterward (van Vuuren et al. 2011). The gridded monthly temperatures from each GCM were interpolated to 610 weather stations, using an inverse distance weighting interpolation method in ArcGIS 9.3 (Environmental System Research Institute, Redlands, CA, USA).

Data analysis. All statistical analyses were conducted using the software package SPSS 16.0 (IBM, Armonk, NY, USA).

Climate change in regions with powdery mildew epidemics from 1970 to 2012. Based on the dynamics of powdery mildew epidemics, we considered five epidemic periods during each year, including the pathogen's overwintering period (July–August), autumn (September–November), the pathogen's overwintering period (December–February), early spring (March–April), and late spring (May–June) periods. The entire epidemic season, from July to the following June, was also considered. For each period, we analyzed the climatic variables of regions with powdery mildew epidemics, using linear regression and Kendall-tau statistics (Lobell et al. 2006), with year (1970 to 2012) as the independent variable and climatic variables (T, P, RH, or SH) as the dependent variables. In addition, a two-tailed Student's *t* test was used to compare the linear relationships between climate and time. The climate data of 610 stations were used to calculate the arithmetic mean of the monthly climatic variables (T, P, RH, and SH), which were subsequently used to calculate the mean values of T, P, RH, and SH for each epidemic period as well as for the entire epidemic period, in regions of powdery mildew epidemics.

Relationship between climate change and wheat powdery mildew epidemics from 1970 to 2012. In order to examine the effect of climate change on powdery mildew epidemics from 1970 to 2012, we used correlation and regression analyses of the first-difference time series of PA and each of the meteorological variables (T, P, RH, or SH), i.e., the difference in values from one year to the next, in order to evaluate the relationship between PA and climatic factors for each period of the epidemics (Lobell and Field 2007; Nicholls 1997). Next, we regressed the first differences of PA (ΔPA), as the dependent variable, against those of T (ΔT), P (ΔP), RH (ΔRH), and SH (ΔSH), as the independent variables, and used a two-tailed Student's *t* test for comparison.

Model construction for the relationship between climatic variables and wheat powdery mildew epidemics. Based on the results of the aforementioned analyses, multiple linear regressions were used

Table 1. Summary of the 15 general climate models used in the present study^a

Model	Research center	Longitude × Latitude
BCC-CSM1.1	Beijing Climate Center, China Meteorological Administration	$2.8^\circ \times 2.8^\circ$
BCC-CSM1.1(m)	Beijing Climate Center, China Meteorological Administration	$1.1^\circ \times 1.1^\circ$
BNU-ESM	College of Global Change and Earth System Science, Beijing Normal University	$2.8^\circ \times 2.8^\circ$
CCSM4	National Center for Atmospheric Research, USA	$1.25^\circ \times 0.9^\circ$
CESM1-CAM5	National Science Foundation, Department of Energy, National Center for Atmospheric Research, USA	$1.25^\circ \times 0.9^\circ$
CSIRO-Mk3.6.0	Commonwealth Scientific and Industrial Research Organization in collaboration with the Queensland Climate Change Centre of Excellence	$1.9^\circ \times 1.9^\circ$
FIO-ESM	The First Institute of Oceanography, SOA, China	$2.8^\circ \times 2.8^\circ$
HadGEM2-AO	National Institute of Meteorological Research, Seoul, South Korea	$1.9^\circ \times 1.2^\circ$
IPSL-CM5A-MR	Institute Pierre-Simon Laplace	$2.5^\circ \times 1.3^\circ$
MIROC5	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology	$1.4^\circ \times 1.4^\circ$
MIROC-ESM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies	$2.8^\circ \times 2.8^\circ$
MIROC-ESM-CHEM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies	$2.8^\circ \times 2.8^\circ$
MPI-ESM-MR	Max Planck Institute for Meteorology (MPI-M)	$1.9^\circ \times 1.9^\circ$
MRI-CGCM3	Meteorological Research Institute	$1.1^\circ \times 1.1^\circ$
NorESM1-M	Norwegian Climate Centre	$2.5^\circ \times 1.9^\circ$

^a Additional information is available at <http://cmip-pcmdi.llnl.gov/cmip5/availability.html>

to construct three climate-PA models, in order to predict Δ PA in response to first differences in climatic variables. Model I included the Δ Ts of the pathogen's oversummering and overwintering periods, since summer and winter temperatures are the key factors that influence the ability of *Blumeria graminis* f. sp. *tritici* to oversummer and overwinter in China (Chen and Xu 2006; Liu and Shao 1994). Meanwhile, model II incorporated the Δ Ts of the pathogen's oversummering, overwintering, and autumn epidemic periods, since autumn temperature has been reported to influence pathogenic reproduction, development speed, and quantity in overwintering seedlings (Chen and Xu 2006; Liu and Shao 1994). In contrast, model III incorporated the Δ Ts of the pathogen's oversummering and overwintering periods and the Δ RH of the early spring period, since RH can affect the pathogen's germination and infection ability in early spring (Chen and Xu 2006; Liu and Shao 1994).

Last, the applicability of the constructed model of Δ PA and first differences in climate were evaluated in regions of winter wheat powdery mildew epidemics in China. We estimated the inferred impact of climate trends on Δ PA since 1970 by redefining each possible disease epidemic period (all possible combinations of starting and ending disease epidemic months) and redeveloping the regression relationship between Δ PA and first differences in climate, with Δ PA as the dependent variable and climatic variable as the independent variable.

Predicted changes in PA with wheat powdery mildew. We estimated changes in PA from the baseline PA (1980 to 2009) for each GCM under each of the representative concentration pathways (RCP2.6, RCP4.5, and RCP8.5) by the 2020s, 2050s, and 2080s using the constructed model and estimated future temperatures (Wang et al. 2015). Sources of uncertainty for the PA projections included GCMs, RCPs, time periods, time periods $\times$ GCMs, time periods $\times$ RCPs, RCPs $\times$ GCMs, and time periods $\times$ RCPs $\times$ GCMs. Thus, analysis of variance (ANOVA) was used to partition the effects of each on the predicted changes in PA. We did not use an ANOVA to make statistical inferences for GCMs, as they are deterministic (Hu et al. 2015; Ziter et al. 2012).

Results

Climate change and trends in regions of powdery mildew epidemics from 1970 to 2012. The mean annual monthly air temperature in China increased significantly from 1970 to 2012 by a mean of 0.329°C per decade over the entire epidemic period (Table 2). The rate of T increase was greatest in the early spring (0.398°C per decade), followed by those of autumn, overwintering, and late spring periods (0.356, 0.336, and 0.316°C per decade, respectively), whereas the rate of T increase was slowest in the oversummering period (0.221°C per decade). However, there were no significant changes in monthly mean precipitation for all epidemic periods. The monthly mean relative humidity decreased significantly by 0.608% per decade over the entire epidemic period (Table 2). The rate of decrease was faster in the early spring and late spring periods than in other epidemic periods, decreasing significantly by 0.616, 0.472, 1.097, and 0.767% per decade in the oversummering, autumn, early spring, and late spring epidemic periods, respectively (Table 2). Monthly mean hours of sunshine also decreased significantly by 4.101 h per decade over the entire epidemic period. Hours of sunshine significantly decreased by 7.893, 3.798, 4.539, and 3.934 h per decade in the oversummering, autumn, overwintering, and late spring periods, respectively (Table 2), with the

greatest decrease occurring in the oversummering period. Various meteorological factors (RH, sunshine, and temperature) changed significantly over the period from 1970 to 2012.

Change in the PA with wheat powdery mildew from 1970 to 2012. In regions of winter wheat powdery mildew epidemics, the PA increased gradually from the late 1970s and reached its maximum in 1990 at 46.99% (Fig. 1) and, overall, the PA increased significantly by 8.465% per decade ($P < 0.001$) from 1970 to 2012.

Relationship between climate change and PA with wheat powdery mildew. Across the epidemic periods, there was no significant correlation between Δ T and Δ PA (Table 3). However, Δ T of the pathogen overwintering period was significantly correlated to Δ PA, with a correlation value of 0.370 ($P = 0.016$). The regression coefficient of Δ T and Δ PA indicated a negative relationship, although not significant, for oversummering and late spring periods, whereas positive relationships were observed for the rest of the epidemic periods.

No significant correlation was observed between Δ P and Δ PA. Positive linear relationships were observed for overwintering and early spring periods, whereas negative relationships were observed for the rest of the epidemic periods. First differences in RH (i.e., Δ RH) were significantly correlated with Δ PA in the early spring period, with a correlation coefficient of 0.548 ($P < 0.001$), whereas the relationship was not significant for the other periods (Table 3). No significant correlation was observed between Δ SH and Δ PA. However, a positive linear relationship was observed during the autumn, whereas negative correlations were observed in the rest of the epidemic periods (Table 3).

Predictions of changes in epidemics of powdery mildew in the future. *Model construction for the relationship between temperature and PA with wheat powdery mildew.* Based on the aforementioned

Fig. 1. Time series of percent acreage (PA) with wheat powdery mildew in regions of powdery mildew epidemics in winter wheat in China from 1970 to 2012. In 1990 and 1991, severe wheat powdery mildew epidemics occurred in China due to disease-favorable weather conditions (Cao et al. 2011).

Table 2. Trends in climate change over time in regions of powdery mildew epidemics in winter wheat in China from 1970 to 2012^a

Periods of epidemics	T (°C)			P (mm)			RH (%)			SH (h)		
	Trend	R ²	P value	Trend	R ²	P value	Trend	R ²	P value	Trend	R ²	P value
Oversummering (Jul–Aug)	0.221	0.361	<0.001	1.050	0.010	0.544	−0.616	0.257	<0.001	−7.893	0.451	<0.001
Autumn (Sep–Nov)	0.356	0.496	<0.001	−2.214	0.077	0.073	−0.472	0.109	0.031	−3.798	0.201	0.003
Overwintering (Dec–Feb)	0.336	0.239	<0.001	0.980	0.028	0.286	−0.306	0.024	0.320	−4.539	0.208	0.002
Early spring (Mar–Apr)	0.398	0.337	<0.001	−0.839	0.008	0.582	−1.097	0.294	<0.001	−0.285	0.001	0.825
Late spring (May–Jun)	0.316	0.607	<0.001	0.409	0.002	0.786	−0.767	0.212	<0.001	−3.934	0.217	<0.001
Entire period (Jul–Jun)	0.329	0.671	<0.001	−0.201	0.003	0.731	−0.608	0.321	<0.001	−4.101	0.457	<0.001

^a Trends per decade in monthly mean air temperature (T), precipitation (P), relative humidity (RH), and hours of sunshine (SH).

results, three constructed models were examined using *t*-test and F-test methods (Table 4). The intercepts of the regressions that represented the average change in PA with climate were constant. Model I included the first-differences time series of temperature (ΔT) in the pathogen's oversummering and overwintering periods, where ΔT s for oversummering (-3.873 ; $P = 0.027$) and overwintering (2.817 ; $P = 0.003$) periods had a larger effect on ΔPA . Meanwhile, model II incorporated the ΔT s of the oversummering, overwintering, and autumn epidemic periods, and the very small increase in ΔT from the autumn period produced little change in ΔPA (0.985 ; $P = 0.486$). Model III incorporates ΔT s in pathogen oversummering and overwintering periods and ΔRH in the early spring period, where the ΔT s for the oversummering (-2.668 ; $P = 0.103$) and overwintering (1.726 ; $P = 0.065$) periods and the ΔRH of early spring period (1.166 ; $P = 0.005$) each had effects on ΔPA .

However, the climatic variables were closely correlated. The change in T during the autumn was significantly correlated to that during the overwintering period, with a correlation coefficient of 0.274 . Year-to-year changes in RH during the early spring epidemic period had a correlation coefficient of 0.36 with first differences in T of the overwintering period. If partial correlations were calculated between the first differences of PA and each of the climatic variables, thereby removing the influences of ΔT from the autumn period and ΔRH from early spring, then the two important underlying influences of ΔT s in the oversummering and overwintering periods were revealed. The partial correlations of first differences of PA with the first differences of T in oversummering, autumn, and overwintering periods were -0.351 , 0.113 , and 0.415 , respectively. The strong

underlying relationships between ΔPA and ΔT s from oversummering and overwintering periods were reflected by the coefficients of the multiple regression of PA against the climate variables. Changes in T from the autumn period had only a weak effect on PA , once the cross-correlations among ΔT s from autumn, oversummering, and overwintering periods were taken into account through multiple regression or partial correlation. First-differences time series of RH (ΔRH) in the early spring also had only minor effects on PA (data not shown).

An applicability test was performed to evaluate how the results varied with epidemic period. For each possible epidemic period definition (e.g., range of months), a regression between climate and ΔPA was developed and applied to the observed climate trend. Models with high R^2 values were assumed to represent the most plausible epidemic period for wheat powdery mildew. The results were fairly insensitive to the choice of epidemic period in models that had the highest R^2 value. Thus, the particular choice of epidemic period failed to significantly affect the inferred effect of climate on the ΔPA of winter wheat powdery mildew epidemics in China (Fig. 2).

Prediction of future change in PA with wheat powdery mildew. Changes in the PA values for the 15 GCMs under the three RCPs and three time periods were calculated according to the constructed model. Based on model I, PA would increase for all representative concentration pathways (RCP2.6 [Fig. 3], RCP4.5 [Fig. 4], and RCP8.5 [Fig. 5]), and, related to the baseline data from 1980 to 2009, PA was predicted to increase by 14.43% (9.46 to 20.86%), 14.51% (9.77 to 20.92%), and 14.37% (8.80 to 21.99%) for RCP2.6, RCP4.5, and RCP8.5, respectively, by the 2020s; 14.21% (9.00 to 21.15%), 13.28% (7.88 to 19.69%), and 12.62% (6.50 to

Table 3. Correlation and regression analyses of climate change and powdery mildew epidemics in wheat based on first differences of meteorological variables and first differences of percent acreage (PA) with wheat powdery mildew in China from 1970 to 2012^a

Epidemic period	ΔT ($^{\circ}C$)			ΔP (mm)			ΔRH (%)			ΔSH (h)		
	Slope ($^{\circ}C$)	R	P value	Slope ($^{\circ}C/mm$)	R	P value	Slope ($^{\circ}C/\%$)	R	P value	Slope ($^{\circ}C/h$)	R	P value
Oversummering (Jul–Aug)	−2.641	−0.225	0.153	−0.031	−0.077	0.626	0.205	0.049	0.760	−0.028	−0.069	0.663
Autumn (Sep–Nov)	1.725	0.180	0.253	−0.096	−0.194	0.218	−0.284	−0.100	0.528	0.129	0.227	0.149
Overwintering (Dec–Feb)	2.331	0.370	0.016	0.021	0.038	0.812	0.284	0.159	0.315	−0.033	−0.088	0.581
Early spring (Mar–Apr)	0.550	0.076	0.632	0.074	0.210	0.183	1.535	0.548	<0.001	−0.114	−0.212	0.178
Late spring (May–Jun)	−1.591	−0.115	0.467	−0.021	−0.057	0.719	0.370	0.129	0.417	−0.051	−0.113	0.477
Entire period (Jul–Jun)	4.360	0.271	0.083	−0.034	−0.035	0.826	1.530	0.291	0.061	−0.064	−0.078	0.623

^a First-differences time series of temperature (ΔT), precipitation (ΔP), relative humidity (ΔRH), and hours of sunshine (ΔSH). Slope = regression coefficient of first differences in meteorological variable and PA ; R = correlation coefficient of first differences in meteorological variable and PA .

Table 4. Results of multivariate linear regression models between first differences in the percent acreage with wheat powdery mildew and climate conditions in China from 1970 to 2012

Models	Estimate	S.E. ^a	<i>t</i> Test	P value	95% CI ^b
Model I					
Intercept ^c	0.646	0.916	0.705	0.485	−1.207, 2.498
ΔT of oversummering period	−3.873	1.689	−2.293	0.027	−7.290, −0.456
ΔT of overwintering period	2.817	0.905	3.113	0.003	0.987, 4.648
R^2 : 0.239, F = 6.139, Sig. F = 0.005 < 0.01					
Model II					
Intercept	0.612	0.923	0.662	0.512	−1.258, 2.481
ΔT of oversummering period	−3.935	1.702	−2.311	0.026	−7.381, −0.488
ΔT of autumn period	0.985	1.399	0.704	0.486	−1.847, 3.817
ΔT of overwintering period	2.648	0.942	2.81	0.008	0.740, 4.555
R^2 : 0.249, F = 4.205, Sig. F = 0.012 < 0.05					
Model III					
Intercept	0.708	0.838	0.845	0.403	−0.988, 2.404
ΔT of oversummering period	−2.668	1.597	−1.671	0.103	−5.902, 0.565
ΔT of overwintering period	1.726	0.907	1.904	0.065	−0.110, 3.561
ΔRH of early spring period	1.166	0.396	2.945	0.005	0.364, 1.968
R^2 : 0.381, F = 7.788, Sig. F = 0.04 < 0.05					

^a Standard error.

^b Confidence interval.

^c Intercept = the parameter of multiple liner regression model of climate change and powdery mildew epidemic; first differences in temperature (ΔT) and relative humidity (ΔRH).

20.48%), respectively, by the 2050s, and by 13.55% (8.24 to 20.83%), 12.81% (7.05 to 20.48%), and 10.48% (3.99 to 19.19%), respectively, by the 2080s.

Uncertainties in predicting future changes in PA with wheat powdery mildew. When we examined the influence of three factors (3 time periods $\times$ 15 GCMs $\times$ 3 RCPs) on PA, we obtained 135 predictions. The results of the variance portioning analysis indicated that the uncertainty in GCMs explained 60.228% of the total variability across predictions, whereas the variance accounted for by time periods, RCPs, and time periods $\times$ RCPs were 22.354, 12.315, and 4.143%, respectively. Variance explanations for the remaining factors (time periods $\times$ GCMs, RCPs $\times$ GCMs, and time periods $\times$ RCPs $\times$ GCMs) accounted for less than 1.000% (Table 5).

Fig. 2. The inferred impact of climate trends for 1970 to 2012 on percent acreage (PA) with wheat powdery mildew in China versus the R^2 value of the regression model used to estimate impacts. Each point represents a different definition of powdery mildew epidemic period, with all possible combinations of starting and ending months. Models with high R^2 values are assumed to represent the most plausible epidemic period. The red point indicates the epidemic period reported in the present study.

Fig. 3. Increases in percent acreage (PA) with powdery mildew in China generated for 15 general circulation models for representative concentration pathways (RCP2.6, RCP4.5, and RCP8.5) by the 2020s, relative to the period from 1980 to 2009 (baseline).

Discussion

The present study analyzed the change in climate from 1970 to 2012 using monthly mean climate data to consider the epidemics of wheat powdery mildew in winter wheat-growing regions of China. During this period, we found that T increased, whereas RH and SH decreased significantly. In China, the mean temperature has increased in the last several decades, especially since the 1980s (Tao et al. 2003). Our study demonstrated that T rose faster during the overwintering epidemic period than the oversummering period, similar to previous findings (Zhai et al. 1999), which is generally conducive to powdery mildew epidemics (Chen and Xu 2006; Liu et al. 2015). Meanwhile, precipitation trends varied over different epidemic periods. We found that the increased precipitation of autumn, winter, and early spring were conducive to powdery mildew epidemics; however, too much rain can also reduce the density of conidia (spores) in the air (Huo et al. 2012; Zhang et al. 2013). Furthermore, the trends observed in SH were consistent with the results reported by Yu et al. (2011), who found that, over the past 59 years in China, SH decreased significantly in all seasons, which provides a conducive environment for the development of wheat powdery mildew (Qian et al. 2005). Thus, the results of the present study demonstrate that changes in climate contributed to the increase in wheat powdery mildew. Thereafter, we analyzed the possible effects of climate change on powdery mildew epidemics.

Plant growth at high nitrogen availability may result in increased disease severity (Mitchell et al. 2003). For instance, the use of nitrogen fertilizer could result in a denser canopy and a more humid microclimate (Bremner 1995). This issue should also be considered to determine the relationship between wheat powdery mildew epidemics and climate change under the nitrogen circumstances. However, deficiency of corresponding information in our dataset had impeded such analysis. Further study is needed to study this issue. During the studied period of time from 1970 to 2012, some resistant cultivars were used in production, such as those with the resistance gene *Pm8*. However, large-area applications of these resistant cultivars in short periods of time resulted in quick losses of resistance, due to the increases in frequency of races or genotypes with corresponding virulence to these resistant genes. Thus, most cultivars currently used in production are most likely susceptible to powdery mildew.

Global warming has the potential to change the severity of disease epidemics (Evans et al. 2008; Juroszek and von Tiedemann 2013). Therefore, our study focused on the relationships between climate changes and disease epidemics, and we assumed that climatic variations

Fig. 4. Increases in percent acreage (PA) with powdery mildew in China generated for 15 general circulation models for representative concentration pathways (RCP2.6, RCP4.5, and RCP8.5) by the 2050s, relative to the period from 1980 to 2009 (baseline).

caused changes in disease epidemics and not vice versa. The relationship between ΔT and ΔPA , represent a more accurate reflection of the impacts of climate change on wheat powdery mildew epidemics. ΔT was significantly and positively correlated to ΔPA during the overwintering period. However, ΔT was negatively correlated to ΔPA during the oversummering and late spring periods, suggesting that high temperature inhibited the development of powdery mildew epidemics in these two periods (Chen and Xu 2006; Zhang et al. 2013). Changes in RH were positively correlated with powdery mildew epidemics in all epidemic periods except autumn, meaning that high relative humidity was conducive to epidemics (Cao et al. 2015; Chen and Xu 2006; Liu et al. 2015). In agreement with previous findings (Chen and Xu 2006; Liu et al. 2015), we also found that ΔSH were negatively correlated with epidemics over all epidemic periods except autumn, meaning that cloudy conditions and less sunlight are conducive to infection by powdery mildew (Liu et al. 2015).

The approach adopted here was to remove the effects of trends in the PA and climate time series by calculating the first differences of the variables and subsequently calculating the relationships between them. The use of the first-differences time-series method, which assumed that changes in year-to-year disease management practices were uncorrelated with climate (Kaufmann and Snell 1997; Peterson et al. 1998), prevented the confounding influence of long-term variation, such as changes in crop management (resistant varieties, irrigation, fertilization, and pesticide use) (Lobell and Field 2007; Nicholls 1997). This method has the advantage of making use of all the available data to calculate long-term changes, even in the face of missing climatic data (Vuille and Bradley 2000), and can also be used to estimate which key meteorological factors are related to disease epidemics (Lobell and Field 2007; Lobell et al. 2005; Nicholls 1997).

The model developed in the present study involves the removal of trends in PA and temperature, a regression calculation of the detrended variables, and the use of the regression to estimate the effect of trend on PA. This simple approach can estimate the impact of recent climate trends, with the assumption that a certain climate variation will have the same impact regardless if the climate variation occurred from one year to the next. We predicted the impacts of future climate change on disease epidemics, using a combination of the constructed temperature-PA model and downscaled GCM outputs. The increase in PA for the RCP2.6 would be lower than that for the RCP4.5 by the 2020s and would be higher by the 2050s and 2080s. The increased PA value for RCP8.5 would be lower than that for RCP2.6 and RCP4.5 in the future. This could be a result of the fact

that, when temperature elevates very rapidly for RCP8.5, the over-summering of pathogens could be inhibited, thereby affecting incidences of epidemics (Li et al. 2013).

It is important to identify the various sources of uncertainty in climatic prediction. Uncertainties in global warming are related to shortcomings of the data used to establish the global temperature series, the mechanism of climate change, and the lack of scientific understanding of the observed climatic elements (Gong and Wang 2002; Pachauri et al. 2014). Lobell et al. (2006) indicated that the uncertainty of climate change generally had a large impact on predictions. Gouache et al. (2013) also pointed out that there might be inevitable uncertainties in statistical predictions associated with future weather. The results of the present study were dependent on GCM outputs, which vary substantially, both temporally and spatially, owing to the properties of gridded data, model biases, and uncertainties from a range of sources (Gouache et al. 2013; Hu et al. 2015; Ziter et al. 2012). In general, a projection of the potential response of powdery mildew epidemics to future climate change relies on the developed emission scenarios, climate models, and disease epidemic simulation models (Ceglar and Kajfež-Bogataj 2012). For changes in PA, uncertainty in climate model selection explained the most variance (>60%), followed by time period (>22%). This result is reasonable, since the mechanism of climate models are complicated and global warming is a temporally connected process (Hu et al. 2015; Juroszek and von Tiedemann 2013; Pachauri et al. 2014).

The sensitivity of disease epidemics in response to temperature change is also influenced by changes in other climate parameters, such as precipitation and relative humidity. Furthermore, changes in temperature significantly affect both pathogen and host as well as host-pathogen interactions (Coakley et al. 1999; Garrett et al. 2006, 2011; Huang et al. 2006; Jönsson et al. 2009; Tao et al. 2006), and variation in daily temperature range could be more important than average temperature on disease development (Scherin and van Bruggen 1994a, b; Shakya et al. 2015). The temperature-PA model ($R^2 = 0.239$) reflects the importance of variables omitted from this analysis, which are likely to include regional variations in epidemic periods and climate responses, as well as other conditions that influence disease epidemics (Robinson et al. 2012). Consideration of these factors would likely improve model performance, although the temperature-PA model is meant to simplify the natural process in order to capture a few essential features (Hu et al. 2015).

According to our analysis, growers could adapt crop production systems as the climate changes, thus, minimizing or possibly reversing the adverse effects of global warming. Therefore, the magnitude of PA would be reduced when management practices, wheat cultivars, and use of nitrogen fertilizer are taken into account, and our estimates of climate impacts can be viewed as an upper limit (Chakraborty et al. 1998; Garrett et al. 2006). Furthermore, the statistical model used in the present study is large scale. For example, the conclusion that climatic trends have increased the PA in all winter wheat regions of China does not preclude the possibility that the PA will actually decrease in some regions, owing to cultivar sensitivity, different management practices,

Fig. 5. Increases in percent acreage (PA) with powdery mildew in China generated for 15 general circulation models for representative concentration pathways (RCP2.6, RCP4.5, and RCP8.5) by the 2080s, relative to the period from 1980 to 2009 (baseline).

Table 5. Descriptive statistics of the variation in predicted increases in percent acreage with wheat powdery mildew, explained by various sources of uncertainty, across winter wheat growing regions of China^a

Sources of uncertainty	Variance	df	Contribution rate of variance %
Time periods	52.333	2	22.354
GCM	141.002	14	60.228
RCP	28.83	2	12.315
Time periods × GCM	1.035	28	0.442
Time periods × RCP	9.699	4	4.143
RCP × GCM	0.862	28	0.368
Time periods × RCP × GCM	0.352	56	0.150
Total	234.113	134	100

^a df = degrees of freedom. Time periods: 2020s (2010–2039), 2050s (2040–2069), and 2080s (2070–2099); GCM = general climate models (15 models); RCP = representative concentration pathways (RCP2.6, RCP4.5, and RCP8.5).

or local climate conditions in the various regions. However, the results of the present study provide insight for managers of agricultural systems into the importance of considering climate change when developing agricultural management practices and the need to be prepared to address a variety of disease conditions (Cao et al. 2015; Liu et al. 2015; Shen et al. 2015; Xue et al. 2009) as well as considering nitrogen fertilizer conditions (van Bruggen et al. 2015a).

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