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CLIMATE CHANGE AND AGRICULTURE RESEARCH PAPER
Disease–weather relationships for wheat powdery mildew under climate change in China

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SUMMARY

Little is known about the quantitative relationships between wheat powdery mildew (*Blumeria graminis* f.sp. *tritici*) epidemics and climatic variables at the provincial scale in China, particularly under climate change. The present study assesses the actual disease process and corresponding impact on wheat yield and addresses climatic-driven variables that affect a powdery mildew epidemic. Powdery mildew increased in frequency from 1981 to 2010, and wheat yield decreased in most regions. It was clear that differences in disease and yield loss occurred temporally and spatially. Although particular weather variables were positively or negatively related to the disease, multiple stepwise regression analysis indicated that mostly fewer than three variables affected prevalence and severity of powdery mildew in each province. In most cases, some combination of higher temperature, humidity, rainfall and wind led to higher disease severity. These weather factors had different effects on disease development. The influence of climatic variables on powdery mildew tended to decrease from 1981 to 2010, whereas the effect of non-climatic factors increased and was attributed mainly to the use of fungicides and resistant cultivars. Therefore, the results of the current study suggest that wheat powdery mildew in China will not increase consistently in the future. In addition, the quantitative assessment method used in the current study can generally provide a good way to identify disease epidemics under climate change.

INTRODUCTION

Wheat powdery mildew, caused by *Blumeria graminis* f.sp. *tritici*, results in frequent disease damage to wheat worldwide. Initially, the lower leaves are most affected, but powdery mildew appears gradually over the entire crop and produces aggregate damage (Ferrandino 1989). Yield of wheat infected by powdery mildew is often reduced by 10–20%, sometimes up to 40% if the wheat crop is left untreated (Wiese 1987; Bockus *et al.* 2010). In China, ≥0·50 of some wheat fields have been infected (Liu *et al.* 2012). Therefore, it is important to be aware of powdery mildew and its management, as the resulting disease can reduce wheat yield significantly.

Although several excellent studies have been conducted on the spatiotemporal dynamics of wheat

disease populations (Franke *et al.* 2009; Pautasso *et al.* 2012), as well as on the geographic distribution and environmental conditions required for epidemics (Moslonka-Lefebvre *et al.* 2011; Shaw & Osborne 2011; Liu *et al.* 2015), there is a lack of epidemiological studies concerning the empirical quantitative relationship between powdery mildew and climatic conditions. As driving forces for the development of wheat powdery mildew, weather variables are essential for predicting disease during specific parts of the disease cycle, e.g. reproduction and dispersal (De Wolf & Isard 2007; Te Beest *et al.* 2008). Differences in climate and agricultural practices lead to differences in the onset, development and severity of the disease each year. The inter-relationships between powdery mildew and weather factors have been the subject of several studies using statistical models (Te Beest *et al.* 2008; Wiik & Ewaldz 2009); however, most of these studies were conducted to predict

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disease development, not to quantitatively assess the disease response to weather factors. Therefore, it is important to explore the processes involved to effectively forecast and manage the impact of the disease.

Agriculture is changing at an unprecedented pace worldwide due to global climate change (Pretty 2008). It is likely that climatic change has had a significant impact on wheat yield and quality (Bender & Weigel 2011; Lobell *et al.* 2011). As a yield-limiting biotic factor, diseases merely quantitatively account for wheat yield (Barnes *et al.* 2010; Roos *et al.* 2011). Nevertheless, the effect of the environment on epidemic characteristics should be considered. For example, Chancellor & Kubiriba (2006) predicted that the effect of powdery mildew on wheat will increase until 2020 and then decrease before 2080. However, available studies that have considered the likely effect of climate change on powdery mildew have invariably focused on future change and risk, and have depended on simulation models and emission scenarios (Volk *et al.* 2010; West *et al.* 2012), in which uncertainties may exist, rather than considering past climate change.

For timely region-specific prediction of disease severity and effective disease control, a better knowledge of the relationships between climatic factors and the specific disease is fundamental and necessary, especially under climate change. Given the geographic and climatic diversity of wheat production areas in China, it is likely that there are differences in wheat powdery mildew response to climate change; however, studies on this topic are still rare. Therefore, the present study was carried out at provincial and national scales, in order to: (1) assess and compare the actual occurrence of powdery mildew and its impact on wheat yield, (2) identify the key climatic factors driving the variation of wheat powdery occurrence, and (3) quantify and evaluate the disease response to climatic variables under current climate change, which can be applied for better understanding and warning of wheat disease.

MATERIALS AND METHODS

Study area and data

The occurrence of wheat powdery mildew and the disease process varies substantially in different geographic zones. Since the early 1980s, the range and severity of powdery mildew have increased notably due to frequent use of nitrogenous fertilizers, production of semi-dwarf wheat cultivars and expansion of irrigated areas (Wang *et al.* 2005; Luo *et al.* 2009). Before the 1980s, powdery mildew occurred only occasionally in the southwest and coastal areas in Shandong Province, China. In the current study, 'province' was defined as the study unit (Fig. 1) during 1981–2010. Nineteen provinces and cities were included, i.e. Liaoning (LN), Beijing (BJ), Tianjin (TJ), Hebei (HB), Henan (HN), Shandong (SD), Shanxi (SX), Shaanxi (SHX), Gansu (GS), Xinjiang (XJ), Jiangsu (JS), Anhui (AH), Shanghai (SH), Zhejiang (ZJ), Hubei (HUB), Chongqing (CQ), Sichuan (SC), Guizhou (GZ) and Yunnan (YN), as well as the entire wheat region of China (N). Climate conditions in the study area vary from tropical in the southwest to temperate in the north. Annual mean air temperature was 8·4–16·4 °C, total rainfall was evenly distributed throughout the year from 170 to 1150 mm, and annual sunshine duration varied from 1491 to 2810 h.

Wheat powdery mildew disease data from 1981 to 2010 were obtained from the National Agro-Technical Extension and Service Center, collected during an annual investigation of a field at the local Plant Protection Station at the municipal (county) level and summed to the wheat occurrence area affected by the disease and a 'precaution' area, which received preventive measures, referred to in ha for each province. Yield loss in the presence of disease was collected and described in units of kg/ha for each province. Wheat yields from 1981 to 2010 were collected from the National Bureau of Statistics of the People's Republic of China, which included annual wheat-planted area (ha) and actual yield after harvesting (kg/ha) at the provincial scale. Annual mean wheat yield from the 19 provinces and cities was calculated to represent N. Dates for each wheat growth stage differ across regions in China based on environmental conditions, climate and agronomic practices (Li *et al.* 2015; Hou *et al.* 2016). For example, wheat in the northern provinces and cities (i.e. LN, BJ, TJ, HB, HN, SD, SX, SHX and GS) experiences a specific overwintering stage in which the wheat merely survives compared with that in the southern provinces and cities (i.e. JS, AH, SH, ZJ, HUB, CQ, SC, GZ and YN). Hence, detailed data were collected from agro-meteorological stations across China where observations, i.e. wheat cultivar, phenological date, height, density, output factors and management including irrigation and fertilization, etc., were taken every 2 days.
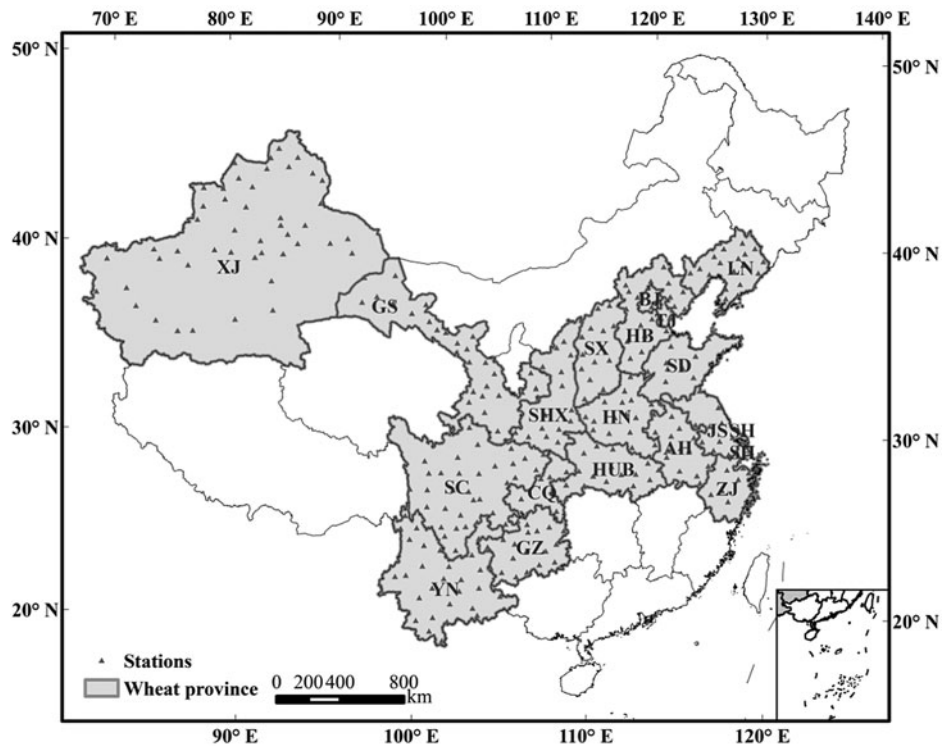
Fig. 1. The location of the study area. LN, Liaoning; BJ, Beijing; TJ, Tianjin; HB, Hebei; HN, Henan; SD, Shandong; SX, Shanxi; SHX, Shaanxi; GS, Gansu; XJ, Xinjiang; JS, Jiangsu; AH, Anhui; SH, Shanghai; ZJ, Zhejiang; HUB, Hubei; CQ, Chongqing; SC, Sichuan; GZ, Guizhou; YN, Yunnan.

Meteorological data from 1981 to 2010 were downloaded from the China Meteorological Data Sharing Service System and included daily mean temperature (T), maximum temperature (T_m), minimum temperature (T_n), precipitation range (P), relative humidity (H), wind speed (W) and sunshine duration (S_d) at 323 stations in the study area (Fig. 1). Wheat powdery mildew epidemics tend to become significant once the wheat begins to grow rapidly (Vechet 2012). Therefore, rapid wheat growth was defined as the period from the beginning of stem elongation (GS 3·0) to early dough (GS 8·3) according to the BBCH growth stage scale (Hess *et al.* 1997), which was selected as the effective 'impact season' for a wheat powdery mildew epidemic. Other growing periods were not considered in the current study. The impact season at each meteorological station was obtained from the observed phenological date, taken from its nearest agro-meteorological station. Annual mean T, T_m and T_n, H, P and heavy rainfall days (i.e. number of days with daily precipitation >25 mm), W and S_d of the impact season for each year were obtained by calculating daily climate parameters. These time-series data from the weather

stations in each province and the entire study region were combined into a panel data set, and the data set was subsequently averaged to reveal provincial and national data (Tao *et al.* 2014).

Disease–weather relationships

The occurrence area ratio (OAR) of wheat powdery mildew was defined as the ratio of occurrence area of wheat powdery mildew to wheat-planted area, so comparisons could be made easily among provinces with clear differences in wheat production. Annual yield loss (ΔYield, as %) was expressed as the yield from wheat exposed to disease divided by the yield not exposed to disease and expressed as a percentage, as follows:

$$\Delta\text{Yield} = \frac{y_d}{y} \times 100$$

where y_d is the yield from wheat exposed to powdery mildew and y is the yield from wheat not exposed to powdery mildew.

The tendency of each climatic variable was defined by a regression coefficient multiplied by 10 using

linear regression analysis as follows:

$$x = ct + d$$

$$tre = c \times 10$$

where *tre* is the tendency of variable, *x* is the climatic variable, *c* is the regression coefficient, *t* is time from 1981 to 2010 and *d* is a regression constant.

The time-series data were converted to differences in OAR and climate parameters, i.e. differences (Δfactors) in values from one year to the next, to analyse the disease–weather relationships in the study regions. The significance of time trends in changes in the OAR and climate variables were determined using Student's *t* test at $P < 0.05$. The relationships between trends in OAR and climatic parameters were evaluated by Pearson's correlation analysis. Next, multiple stepwise regressions were performed for each province to observe trends in climatic parameters and to estimate the role of climate in recent OAR trends using the difference in OAR (ΔOAR) as the dependent variable and the differences in mean temperature (ΔT), maximum temperature (ΔT_m), minimum temperature (ΔT_n), relative humidity (ΔH), precipitation (ΔP), number of rainy days (ΔR_d), number of heavy rainfall days (ΔH_{rd}), wind speed (ΔW) and sunshine duration (ΔS_d) as the independent variables, as follows:

$$\Delta OAR = a + b_i \Delta x_i + \varepsilon$$

where ΔOAR is the observed trend in OAR, *a* is the averaged variation in OAR due to non-climatic factors, i.e. structure of cropping and management during wheat growth, b_i is the OAR change response to each independent element, Δx_i is the difference in *T*, *H*, *W*, *P*, R_d and S_d and ε is residual error.

Next, the contribution of OAR change response to climate change (*h*, as %) was quantified as follows:

$$h = \frac{b_i \Delta x_i}{\Delta OAR} \times 100$$

where $b_i \Delta x_i$ is the variation of OAR induced by climate change, ΔOAR is the observed change in OAR during specific time series.

Given that OAR varied following climate change, the study period was divided into three individual time periods, 1981–1990, 1991–2000 and 2001–2010, to trace the climate–disease relationships under climate change. To compare, the response of the OAR to the climate trends over the whole study period from 1981 to 2010 was also investigated in each unit and over the whole study area.

## RESULTS

Occurrence area rate trend and climate change

Obvious differences in mean OAR were observed in the study regions, ranging from 0·06 in XJ to 0·73 in SH during 1981–2010 (Fig. 2). Mean OAR values decreased successively in SH, JS, BJ, GZ, CQ, HB, SHX, SD, HN, GS and LN, corresponding to values of 0·73, 0·49, 0·41, 0·33, 0·32, 0·31, 0·30, 0·30, 0·26 and 0·25, respectively, which were above that for N (0·24). During the inter-decadal periods, i.e. 1981–1990, 1991–2000 and 2001–2010, mean OAR values in SH, JS, BJ, CQ, SD, HN, HB and GZ were all larger than that of N which were 0·16, 0·25 and 0·31 during each period, respectively. In contrast, XJ had the smallest mean OAR value, which was 2·16, 3·96 and 3·87 times smaller than that of N during each decade from 1981 to 2010, respectively. Tracing the development of mean OAR during the three periods, mean OAR for BJ, HN, TJ and AH was larger in 1991–2000 than that in 1981–1990 and 2001–2010. A decrease of mean OAR was detected in ZJ for the periods 1981–1990, 1991–2000 and 2001–2010. In contrast, clear increases were observed in the other provinces, with the biggest increase recorded in GZ and the smallest in XJ.

All climatic variables tended to vary at the provincial scale during the past three decades (Fig. 3). Daily mean temperature, T_m and T_n tended to increase from 0·14 to 1·03 °C/decade, whereas *H*, R_d and *W* decreased by 0·37%/decade, 3·47 days/decade and 0·29 m/s/decade. Precipitation range, H_{rd} and S_d tended to differ among provinces and cities, ranging from −30·82 to 14·95 mm/decade, −0·40 to 0·30 day/decade and 44·02 to 39·57 h/decade, respectively.

Wheat yield loss trend

Wheat yields in the study regions decreased significantly due to the impact of OAR during the entire study period (Fig. 4). Annual yield loss caused by OAR differed at the provincial scale, with the greatest change in GZ (1·88%), followed by YN, JS, CQ, LN, SH, HUB, AH, TJ, SD, BJ, HN and GS, which exceeded the 0·39% in N. The smallest value was observed in XJ (0·12%). The ΔYield values during 1981–1990 in SH, GZ, TJ, JS, AH, BJ, CQ, HN, SD, YN and HUB were >0·50%, whereas that in SX was <0·10%. As time passed, the ΔYield values during 1991–2000 in YN, GZ, CQ and AH were >0·50%,
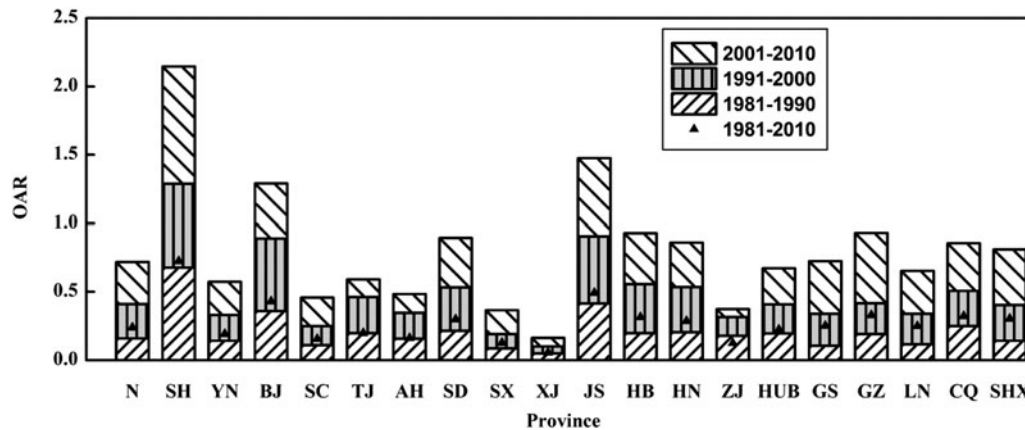
Fig. 2. The mean occurrence area rate for the study regions during the study period. N, entire wheat region of China; SH, Shanghai; YN, Yunnan; BJ, Beijing; SC, Sichuan; TJ, Tianjin; AH, Anhui; SD, Shandong; SX, Shanxi; XJ, Xinjiang; JS, Jiangsu; HB, Hebei; HN, Henan; ZJ, Zhejiang; HUB, Hubei; GS, Gansu; GZ, Guizhou; LN, Liaoning; CQ, Chongqing; SHX, Shaanxi.
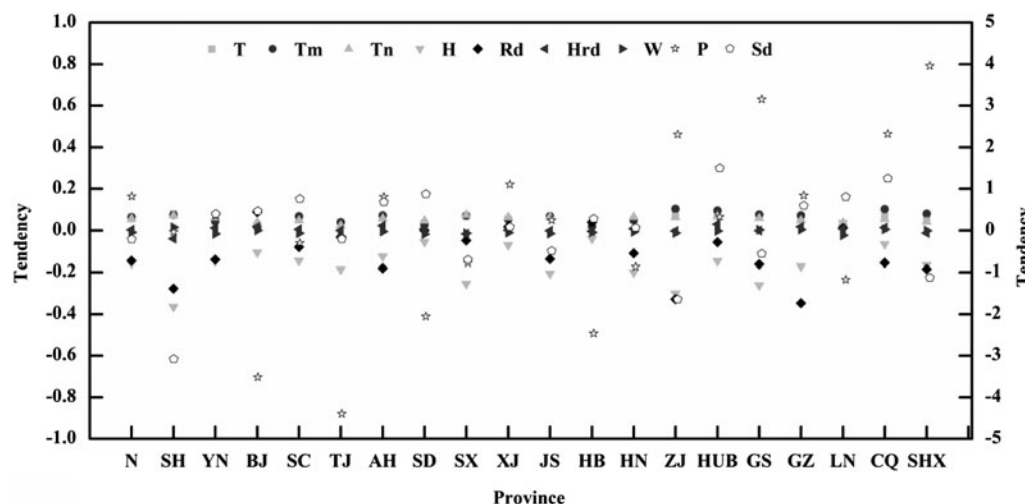
Fig. 3. The climate tendency for the study regions during the whole study period. T, daily mean temperature; T_m, maximum temperature; T_n, minimum temperature; H, relative humidity; R_d, number of rainy days; H_{rd}, number of heavy rainfall days; W, wind speed; P, precipitation range; S_d, sunshine duration; N, entire wheat region of China; SH, Shanghai; YN, Yunnan; BJ, Beijing; SC, Sichuan; TJ, Tianjin; AH, Anhui; SD, Shandong; SX, Shanxi; XJ, Xinjiang; JS, Jiangsu; HB, Hebei; HN, Henan; ZJ, Zhejiang; HUB, Hubei; GS, Gansu; GZ, Guizhou; LN, Liaoning; CQ, Chongqing; SHX, Shaanxi.

whereas ΔYield values in the other provinces were 0·08–0·47%. The ΔYield value during 2001–2010 in GZ reached 3·12%, which was 2·02, 3·28, 3·60, 4·04, 4·23, 5·30 and 5·40 times greater than that in LN, YN, HUB, GS, CQ and JS, respectively, with values >0·50%. The ΔYield values decreased by 0·73, 0·61, 0·37, 0·30, 0·22 and 0·08% in TJ, AH, ZJ, HN, SD and N, respectively, but increased by 0·40% in SD during the past three decades.

Disease–weather relationships at the provincial and national levels

The correlations between the impact-season ΔOAR and the differences in the climatic factors in the study regions are given in Table 1. The impact-season ΔOAR value was positively correlated with ΔT in SC but negatively correlated with ΔT in SX during the entire study period, and no associations were found in the other provinces and cities. An

Fig. 4. The mean yield loss (%) of wheat caused by occurrence area rate for the study regions during the study period. N, entire wheat region of China; SH, Shanghai; YN, Yunnan; BJ, Beijing; SC, Sichuan; TJ, Tianjin; AH, Anhui; SD, Shandong; SX, Shanxi; XJ, Xinjiang; JS, Jiangsu; HB, Hebei; HN, Henan; ZJ, Zhejiang; HUB, Hubei; GS, Gansu; GZ, Guizhou; LN, Liaoning; CQ, Chongqing; SHX, Shaanxi.
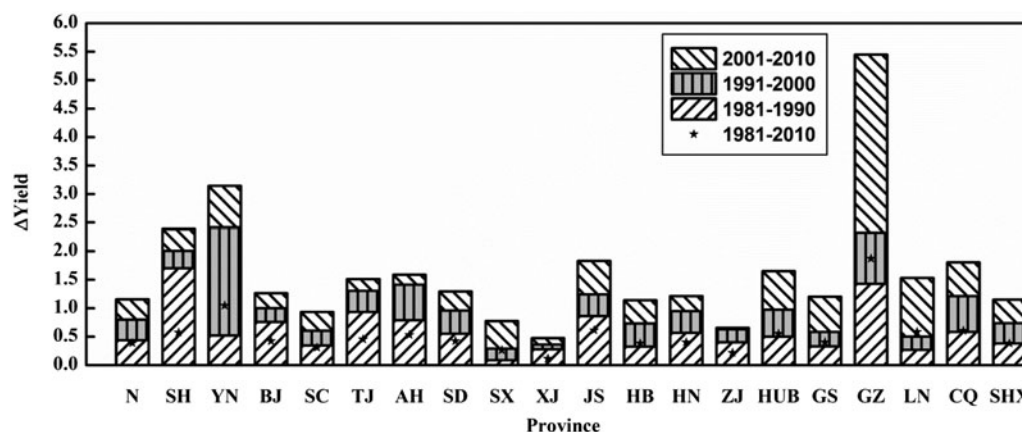
observed trend in OAR was positively correlated with ΔT_m at SC but negatively correlated with ΔT_m in AH, SX and HUB. A significant positive correlation was observed between ΔOAR and ΔT_n in SC, JS and CQ. The correlation between ΔOAR and ΔH was positive in BJ, AH, SD, SX, HB, HN, GS and SHX but negative in SC. A positive correlation was observed between ΔOAR and rainfall factors, including ΔP, ΔR_d and ΔH_{rd} in BJ, TJ, AH, SD, SX, HB, HN, LN and SHX. Observed trend in OAR was negatively correlated with ΔW in BJ, SX, ZJ and HUB, but was positively correlated with ΔW at SC. Observed trend in OAR and ΔS_d were negatively correlated in AH, SD, SX, HN, HUB and SHX. The correlation between ΔOAR and humidity and rainfall factors was more significant than that of the other climate variables. The impact-season ΔOAR was positively correlated with ΔT_n, ΔH, ΔP, ΔR_d and ΔH_{rd} but negatively correlated with ΔS_d at the national scale; impact-season ΔOAR was not associated with ΔT, ΔT_m or ΔW.

Such relationships were complex during the inter-decadal periods. Overall, the ΔOAR was positively correlated with ΔT_n, ΔH, ΔP and ΔR_d but negatively correlated with ΔW and ΔS_d in specific provinces. The relationships between ΔOAR and the climate variables weakened gradually over time in most provinces and cities.

Disease response to recent climate change

At least 23·3% of the variance in OAR was explained by climate variables at both the provincial and national scales during 1981–2010, except in SH, YN

and GZ, and the most significant was 75·6% at SHX (Table 2). The OAR response patterns to climate change differed across the study regions. At the national scale, 50·4% of the variance in OAR was explained by T_m and H, and OAR increased by 0·07 for every 1 °C rise in T_m and decreased by 0·02 for every 1% decrease in H. Occurrence area rate increased by 0·18 for each 1 °C rise in T_m during 1981–1990, but declined 0·04 for each 10 mm decrease in P. No clear OAR response to climate factors was detected during 1991–2000 or 2001–2010.

The impact of climate change on OAR varied at the provincial scale during the study period. The variations in climatic factors affected the variations in OAR significantly ($P < 0.05$) during 1981–1990 and 1991–2000 in BJ, TJ, SD, HN, ZJ, HUB and SHX, but not during 2001–2010. The variance in OAR was explained by climatic variables only during 1981–1990 in HB. The effect of climatic factors on the variation in OAR in SC and SX was evident in 1991–2000 and 2001–2010 but not in 1981–1990. The climate factors had measurable impacts on OAR in GS during all time periods when OAR was determined by different variables. Occurrence area rate at GS increased by 0·04 in response to a 1% decrease in H during 1981–1990, and strengthened as time went on, with magnitudes of increase of 0·08 and 0·07 for a 1% increase in H and a 1 day decrease in R_d during 1991–2000, as well as increases of 0·05 and 0·28 for a 1% increase in H and a 1 day decrease in H_{rd}, respectively during 2001–2010. Consequently, the number of provinces and cities with a significant

Table 1. *Correlation coefficients between the first differences value of yield and climatic factors at $P < 0.05$ during the whole study period (1981–2010) and each individual time period (1981–1990, 1991–2000 and 2001–2010)*

Time period	Study regions	ΔOAR v.								
		ΔT	ΔT_m	ΔT_n	ΔH	ΔP	ΔR_d	ΔH_{rd}	ΔW	ΔS_d
1981–2010	N	–	–	0·466	0·530	0·490	0·352	0·386	–	
	BJ	–	–	–	0·424	0·436	0·350	0·544	−0·562	–
	SC	0·630	0·600	0·647	−0·430	–	−0·363	–	0·452	–
	TJ	–	–	–	–	0·342	0·422	–	–	–
	AH	–	−0·407	–	0·442		0·417	–	–	−0·483
	SD	–		–	0·644	0·433	0·403	–	–	−0·355
	SX	−0·365	−0·396	–	0·734	0·504	0·722	–	−0·369	−0·462
	XJ	–	–	–	–	–	0·457	–	–	–
	JS	–	–	0·334	–	–	–	–	–	–
	HB	–	–	–	0·592	0·560	0·625	0·338	–	–
	HN	–	–	–	0·560	0·571	0·649	0·406	–	−0·338
	ZJ	–	–	–	–	–	–	–	−0·515	–
	HUB	–	−0·351	–	–	–	–	–	−0·374	−0·415
	GS	–	–	–	0·525	0·401	–	–	–	–
	LN	–	–	–	–	0·365	–	–	–	–
	CQ	–	–	0·521	–	–	–	–	–	–
	SHX	–	–	–	0·656	0·453	–	–	–	−0·392
1981–1990	N	–	–	0·650	0·627	0·733	0·605	0·666	–	–
	BJ	–	–	–	0·781	0·687	–	0·661	–	–
	TJ	−0·759	–	−0·799	0·849	0·893	0·839	0·825	–	–
	SD	–	–	–	0·789	0·585	0·609	–	–	–
	HB	–	−0·635	–	0·935	0·907	0·905	–	0·651	−0·634
	HN	–	–	–	0·648	0·640	0·705	0·608	–	–
	ZJ	–	–	0·583	–	–	–	–	−0·672	–
	YN	−0·601	−0·648	–	0·656	–	0·626	–	–	−0·623
	HUB	–	–	–	–	–	–	–	−0·759	–
	GS	–	–	–	−0·756	–	−0·693	–	–	–
	SHX	–	–	0·998	–	–	−0·996	–	–	–
1991–2000	BJ	–	–	–	0·623	–	–	–	−0·893	–
	SC	0·831	0·749	0·841	−0·666	–	−0·591	–	0·729	–
	TJ	–	–	0·724	–	–	–	–	–	–
	AH	–	–	–	–	–	0·618	–	–	−0·641
	SD	–	–	–	0·811	–	0·632	–	–	–
	SX	–	–	–	0·642	0·711	0·821	–	–	–
	HN	–	–	–	0·851	–	0·718	–	–	−0·592
	ZJ	–	–	–	–	−0·732	–	−0·614	–	–
	HUB	–	–	–	–	–	0·654	–	–	–
	GS	–	–	–	0·717	0·636	–	0·654	–	–
	LN	–	–	–	–	–	0·618	–	–	–
	SHX	–	–	–	0·827	0·644	0·586	–	–	–
2001–2010	SH	–	–	–	–	–	–	–	–	−0·725
	SC	0·864	0·905	0·855	−0·754	–	–	–	–	–
	SX	−0·623	–	–	0·868	–	0·846	–	−0·657	−0·622
	XJ	–	–	–	0·697	0·647	0·729	–	–	−0·706
	JS	–	–	0·625	–	–	–	–	–	–
	ZJ	0·654	–	0·699	–	–	–	–	–	–

Table 1. (*Cont.*)

| Time period | Study regions | ΔOAR v. | | | | | | | | |
		ΔT	ΔT_m	ΔT_n	ΔH	ΔP	ΔR_d	ΔH_{rd}	ΔW	ΔS_d
	GS	–	–	–	–	–	–	−0·743	–	–
	GZ	–	–	0·646	–	–	–	–	–	–

ΔOAR, difference in occurrence area rate; ΔT, difference in mean temperature; ΔT_m, difference in maximum temperature; ΔT_n, difference in minimum temperature; ΔH, difference in relative humidity; ΔP, difference in precipitation; ΔR_d, difference in number of rainy days; ΔH_{rd}, difference in number of heavy rainfall days; ΔW, difference in wind speed; ΔS_d, difference in sunshine duration; N, entire wheat region of China; BJ, Beijing; SC, Sichuan; TJ, Tianjin; AH, Anhui; SD, Shandong; SX, Shanxi; XJ, Xinjiang; JS, Jiangsu; HB, Hebei; HN, Henan; ZJ, Zhejiang; HUB, Hubei; GS, Gansu; LN, Liaoning; CQ, Chongqing; SHX, Shaanxi; SH, Shanghai.

response to climatic factors decreased as time went on.

Climate change in the past three decades had a discernible effect on OAR in the study regions, and its contribution was determined from the observed relationships between OAR and the climate variables (Table 3). A 0·18 increase in OAR was detected during 1981–2010 on a national scale, and the contribution of climate change was −8%, while that of non-climate elements was 108%. When the study was divided into three periods, the contribution of climate change to the OAR tended to decline from 25% during 1981–1990 to 0% during 1991–2000 and 2001–2010.

The contribution of climate change to OAR was determined during each study period at the provincial scale. A very slight effect of climate on OAR was observed in SH, YN, GZ and CQ, where the influence was detected only during one specific period. The climate variables changed the OAR trend during one period from 22 to 44% in JS, HB, AH, LN and XJ, but the contribution in TJ and ZJ was lower. An increase in the contribution of climate was apparent during the first two periods in BJ, ranging from −25 to 53%, and the contribution increased to 74% during 1981–2010. The contribution of climate to changes in OAR at SC decreased from 60% during 1991–2000 to −52% during 2001–2010. The contribution of climate to changes in OAR decreased successively from 1981 to 1990, 1991 to 2000 and 1981 to 2010 in SD and SHX, but increased in HN and HUB. The contribution of climate change to OAR varied frequently in GS with magnitudes of 1, 32, −17 and −10% during each decade from 1981 to 2010 and the entire period. Overall, the contribution of climate change to OAR declined gradually at both the national and provincial scales. Meanwhile, the contribution of climate change to OAR increased gradually from the southern to the northern provinces and cities.

DISCUSSION

In the present study, the occurrence of powdery mildew and its impact on wheat yield was identified over the past three decades. Clear increases of OAR were detected in the major provinces and cities, suggesting that powdery mildew tended to be severe. This was in agreement with simulated results of a similar increase conducted by previous researchers (Chancellor & Kubiriba 2006). Considering the disease effect, wheat yield loss ranged from 0·02 to 3·12% at the provincial scale, being smaller than such observations in some specific fields (Liu *et al.* 2012). However, through analysis of differences in actual wheat yield from one year to the next in each unit, values of wheat yield loss were mostly <10%, implying the yield loss induced by powdery mildew played a significant role and should not be ignored in future wheat yield analysis. Of course, OAR and yield loss generally differed at the temporal and spatial dimension across the study regions, and such information will help to discriminate the infectious severity of powdery mildew.

Although the incidence of wheat powdery mildew was determined mainly by T, H, P, R_d, W and S_d, clear differences and even opposite correlations were detected in the different provinces and cities, except in SH, YN and GZ. This discrepancy may result largely from the different climates in the different regions of China, which produced different effects on powdery mildew development. Several factors were

Table 2. *Multiple linear regressions analysis of the first differences in occurrence area rate and climate factors at $P < 0.05$ during the whole study period and each individual time period*

Time period	Study regions	ΔT	ΔT_m	ΔT_n	ΔH	ΔP	ΔR_d	ΔH_{rd}	ΔW	ΔS_d	Model R^2
											(Estimate coefficients)
1981–2010	N	–	–	0·071	0·019	–	–	–	–	–	0·504
	BJ	–	–	–	–	–	–	–	−0·531	–	0·580
	SC	–	–	0·088	–	–	–	–	–	–	0·419
	TJ	–	–	–	–	0·029	–	–	–	–	0·312
	AH	–	–	–	–	–	–	–	–	−0·001	0·234
	SD	–	–	–	0·016	–	–	–	–	–	0·415
	SX	–	–	–	0·013	–	–	–	–	0·001	0·539
	XJ	–	–	–	–	–	0·142	–	–	–	0·309
	JS	–	–	0·005	–	–	–	–	–	–	0·312
	HB	–	–	–	–	–	0·023	–	–	–	0·391
	HN	–	–	0·076	–	–	0·019	–	–	–	0·422
	ZJ	–	–	–	–	–	–	–	−0·289	–	0·265
	HUB	–	–	–	–	–	–	–	–	−0·001	0·272
	GS	–	–	–	0·03	–	−0·022	–	–	0·001	0·411
	LN	–	–	–	–	0·001	–	–	–	–	0·233
	CQ	–	–	0·053	–	–	–	–	–	–	0·273
	SHX	–	–	–	0·029	–	−0·021	–	–	–	0·756
1981–1990	N	–	–	0·177	–	0·004	–	–	–	–	0·537
	BJ	–	0·759	–	0·085	–	–	–	–	–	0·908
	TJ	–	–	–	–	0·002	–	–	–	–	0·797
	SD	–	–	–	0·030	–	–	–	–	–	0·619
	HB	–	–	–	0·042	–	–	−0·157	–	–	0·875
	HN	–	–	–	–	–	0·018	–	–	–	0·498
	ZJ	–	–	–	–	–	–	–	−0·503	–	0·452
	YN	–	−0·036	–	0·013	–	–	–	–	–	0·564
	HUB	–	–	–	–	–	–	–	−1·313	–	0·576
	GS	–	–	–	−0·036	–	–	–	–	–	0·571
	SHX	–	–	0·800	–	–	–	–	–	–	0·955
1991–2000	BJ	–	–	–	–	–	–	–	−0·686	−0·001	0·798
	SC	–	–	0·081	–	–	–	–	–	–	0·707
	TJ	–	–	0·142	–	–	–	–	–	–	0·525
	AH	–	–	–	–	–	0·011	–	–	–	0·641
	SD	–	–	–	0·015	–	–	−0·077	–	–	0·658
	SX	–	–	–	0·007	–	–	–	–	0·001	0·692
	HN	–	–	–	0·012	–	–	–	–	–	0·725
	ZJ	–	–	–	–	0·001	–	–	–	–	0·512
	HUB	–	–	–	–	–	0·012	–	–	–	0·632
	GS	–	–	–	0·076	–	−0·070	–	–	–	0·854
	LN	–	–	–	–	–	0·018	–	–	–	0·675
	SHX	–	–	–	0·030	–	−0·021	–	–	–	0·911
2001–2010	SH	–	–	–	–	–	–	–	–	−0·003	0·525
	SC	–	0·129	–	–	–	–	–	–	–	0·819
	SX	–	0·185	–	0·057	–	–	–	0·489	–	0·982
	XJ	–	–	–	–	–	0·005	–	–	–	0·513
	JS	–	–	0·089	–	–	–	–	–	–	0·532

Table 2. (*Cont.*)

| Time period | Study regions | Estimate coefficients | | | | | | | | | Model R^2 |
		ΔT	ΔT_m	ΔT_n	ΔH	ΔP	ΔR_d	ΔH_{rd}	ΔW	ΔS_d	
	GS	–	−0·046	–	–	–	–	−0·281	–	–	0·827
	GZ	–		0·298	–	–	–		–	–	0·647

ΔT, difference in mean temperature; ΔT_m, difference in maximum temperature, ΔT_n, difference in minimum temperature; ΔH, difference in relative humidity; ΔP, difference in precipitation; ΔR_d, difference in number of rainy days; ΔH_{rd}, difference in number of heavy rainfall days; ΔW, difference in wind speed; ΔS_d, difference in sunshine duration; N, entire wheat region of China; BJ, Beijing; SC, Sichuan; TJ, Tianjin; AH, Anhui; SD, Shandong; SX, Shanxi; XJ, Xinjiang; JS, Jiangsu; HB, Hebei; HN, Henan; ZJ, Zhejiang; HUB, Hubei; GS, Gansu; LN, Liaoning; CQ, Chongqing; SHX, Shaanxi; SH, Shanghai.

absent from the relationships, and fewer than three of factors (i.e. T_m, T_n, H, P, R_d, H_{rd}, W and S_d) had notable roles in disease development in each province. Powdery mildew generally grows well in highly humid environments with moderate temperatures (Huang *et al.* 2000). In the current study, higher H favoured development of powdery mildew infection, which agreed with results of previous studies (Wiese 1987; Liu *et al.* 2015). The positive correlation between OAR and P might be explained by the increase in H favouring disease development, as confirmed by Wiik & Ewaldz (2009) who found that P during the spring is important for disease epidemics. However, H_{rd} can affect disease severity negatively, as high P can wash spores away (Merchan & Kranz 1986), which would decrease the quantity of disease inoculum.

Temperature during the impact season affects the developmental rate and severity of the disease. As the optimal range for powdery mildew is 15–22 °C (Wiese 1987), the minimum and maximum temperatures are restrictive factors. The key factor affecting powdery mildew severity in the current study was T_n; it was <12 °C in the study area. Since this is the minimal T_n required for a damaging powdery mildew epidemic (Te Beest *et al.* 2008), any increase in T_n would provide a more favourable environment for a disease epidemic. No clear association was found in the current study between OAR and T_m; therefore, T_m may be a more limiting factor for disease development. In the current study, it was near 20 °C and as high as 24 °C in most provinces; powdery mildew cannot tolerate temperatures >25 °C (Jones & Clifford 1983). However, no relationship was found between T and epidemic development, probably because the effect of temperature was integrated into T_n. The current study used only

mean temperature, but a detailed study by Te Beest *et al.* (2008) emphasized that cumulative minimum temperatures >12 °C and the number of days with maximum temperature exceeding 20 °C resulted in a damaging epidemic, so these factors need to be carefully elucidated in further studies.

Powdery mildew disease severity is also influenced by W because conidia are transported by high W. A higher W was correlated with higher disease severity, which might be due to the humid environment created by W (Te Beest *et al.* 2008). These results were similar to Friedrich (1995), who concluded that higher W increased the probability of infection. Moreover, wind direction was another factor determining dispersal of wheat powdery mildew (Liu *et al.* 2015), and is therefore suitable for studies on its effect on disease spread; however, studies might be limited due to shortage of detailed data. Mildew infections proceed under low-light intensity (Wiese 1987), but the effects of S_d were inconsistent in different regions, probably because of differences in prevailing climatic conditions (Juroszek & von Tiedemann 2013). However, they should be further investigated.

The impacts of climate change on powdery mildew disease prevalence are complex due to the different relationships among the climatic variables and variations in disease (Verreet *et al.* 2000; Savary *et al.* 2011*b*). A quantitative understanding of these relationships between disease occurrence and climatic variables is critical to determine the factors that affect the development of powdery mildew. In the current study, although the between-year variance in OAR explained by climate variables increased under climate change, the number of provinces where powdery mildew was affected by climatic variables decreased, and only five provinces (i.e. SH, SC, SX, XJ and GS) were predominantly affected by climatic

Table 3. *Occurrence area rate (OAR) change, the contribution of climate driven and non-climate driven OAR changes during the whole study period and each individual time period*

Study regions		Time period				Study regions		Time period			
		1981–2010	1981–1990	1991–2000	2001–2010			1981–2010	1981–1990	1991–2000	2001–2010
N	OAR change	0·18	0·28	−0·17	0·03	JS	OAR change	0·31	0·50	0·19	−0·09
	Climate driven	−8·36	25·28	0·00	0·00		Climate driven	−1·93	0·00	0·00	35·48
	Non-climate driven	108·36	74·73	100·00	100·00		Non-climate driven	101·93	100·00	100·00	64·52
SH	OAR change	1·08	0·39	0·04	0·58	HB	OAR change	0·41	0·69	−0·43	0·11
	Climate driven	0·00	0·00	0·00	6·84		Climate driven	27·49	42·86	0·00	0·00
	Non-climate driven	100·00	100·00	100·00	93·16		Non-climate driven	72·51	57·14	100·00	100·00
YN	OAR change	−0·07	−0·11	0·05	−0·02	HN	OAR change	0·20	0·50	−0·37	0·04
	Climate driven	0·00	−2·07	0·00	0·00		Climate driven	96·14	36·00	65·09	0·00
	Non-climate driven	100·00	102·07	100·00	100·00		Non-climate driven	3·86	64·00	34·91	100·00
BJ	OAR change	0·43	0·44	−0·50	0·08	ZJ	OAR change	−0·47	−0·33	−0·07	−0·08
	Climate driven	73·55	−24·93	52·98	0·00		Climate driven	−9·84	−3·05	0·00	59·61
	Non-climate driven	26·45	124·93	47·02	100·00		Non-climate driven	109·84	103·05	100·00	40·39
SC	OAR change	−0·10	−0·10	−0·08	−0·02	HUB	OAR change	−0·05	−0·29	0·05	0·2
	Climate driven	−44·88	0·00	59·74	−51·60		Climate driven	−7·94	−16·99	−9·30	0·00
	Non-climate driven	144·88	100·00	40·26	151·60		Non-climate driven	107·94	116·99	109·3	100
TJ	OAR change	0·04	0·29	−0·12	−0·06	GS	OAR change	0·36	0·3	−0·07	0·11
	Climate driven	60·00	56·90	−43·60	0·00		Climate driven	−10·11	0·72	31·94	−17·09
	Non-climate driven	40·00	43·10	143·60	100·00		Non-climate driven	110·11	99·28	68·06	117·09
AH	OAR change	−0·03	0·32	−0·37	−0·05	GZ	OAR change	0·28	0·21	−0·08	0·06
	Climate driven	−26·40	0·00	21·51	0·00		Climate driven	0·00	0·00	0·00	−4·70
	Non-climate driven	126·40	100·00	78·49	100·00		Non-climate driven	100·00	100·00	100·00	104·7
SD	OAR change	0·18	0·40	−0·26	−0·08	LN	OAR change	0·28	0·29	−0·29	0·11
	Climate driven	48·80	84·68	65·21	0·00		Climate driven	22·6	0·00	44·07	0·00
	Non-climate driven	51·20	15·33	34·79	100·00		Non-climate driven	77·4	100·00	55·93	100·00
SX	OAR change	0·13	0·28	−0·25	0·13	CQ	OAR change	0·10	0·00	−0·02	0·11
	Climate driven	−16·55	0·00	44·91	−21·02		Climate driven	−19·61	0·00	0·00	0·00
	Non-climate driven	116·55	100·00	55·09	121·02		Non-climate driven	119·61	100·00	100·00	100·00
XJ	OAR change	0·10	0·06	0·00	0·08	SHX	OAR change	0·38	0·22	−0·08	0·14
	Climate driven	14·20	0·00	0·00	30·00		Climate driven	17·57	36·36	20·75	0·00
	Non-climate driven	85·80	100·00	100·00	70·00		Non-climate driven	82·43	63·64	79·25	100·00

N, entire wheat region of China; SH, Shanghai; YN, Yunnan; BJ, Beijing; SC, Sichuan; TJ, Tianjin; AH, Anhui; SD, Shandong; SX, Shanxi; XJ, Xinjiang; JS, Jiangsu; HB, Hebei; HN, Henan; ZJ, Zhejiang; HUB, Hubei; GS, Gansu; GZ, Guizhou;LN, Liaoning; CQ, Chongqing; SHX, Shaanxi.

variables. This finding indicated that the mean effects of climate gradually weakened in most units and across the entire wheat-growing region, which was consistent with reports suggesting that the significance of wheat diseases might not consistently increase in the future on a global or national scale (Juroszek &

von Tiedemann 2013) and that the overall risk of wheat powdery mildew would decrease (Savary *et al.* 2011*a*). A similar result was reported by Cao *et al.* (2015), who observed that climate variables only slightly increase the severity of wheat powdery mildew. Of course, inverse responses of disease to climate change occurred at XJ and SH, where the effects of climate increased disease severity. This was in accordance with studies reporting that climate change might modify the range of prevalent diseases in some regions in the future (Duveiller *et al.* 2007). Overall, the correlations between climatic variables and disease incidence provide a basis to explore disease progression based on weather conditions.

The current results suggest that the effect of climate change on OAR tended to weaken, while the effect of non-climatic factors was enhanced. Disease severity is frequently associated with the presence of the pathogen and resistance of the cultivar, regardless of conducive climatic circumstances (Chakraborty *et al.* 2000). Therefore, a disease epidemic can be controlled by non-climate factors, i.e. use of fungicides and resistant cultivars (Ransom & McMullen 2008). Fungicides are likely to be the most effective way to control disease in agriculture (Van Drooge *et al.* 2001; Lackermann *et al.* 2011), and their use has increased gradually with an increase in occurrence of powdery mildew in China. Widely cultivated in China, wheat is classified into resistant, moderately resistant and susceptible host cultivars, which reveal different resistance levels to diseases (Babosha 2009; Li *et al.* 2012). Khan *et al.* (1997) postulated that particular wheat cultivars in Mississippi, USA develop significant diseases, and that there was a twofold difference in the response of different wheat cultivars to powdery mildew (Lopez *et al.* 2015) in one specific region. As fungicides usually reduce OAR, cultivar resistance is a main non-climate factor determining variations in OAR. Resistant cultivars are better choice with potentially high durable resistance to powdery mildew (Troch *et al.* 2013; Asad *et al.* 2014). However, although weather conditions could occasionally reduce disease severity, such as in SX and CQ in the study area of the current work, the extent of powdery mildew occurrence would not decrease because of the presence of susceptible wheat cultivars in regions receiving greater threats from disease.

In the current study, there may be some uncertainties that should be noted. First, the work was based on the assumption that means wheat phenology was used for 1981–2010. Since previous reporters (Tao *et al.* 2014; He *et al.* 2015) had argued that the wheat growth period would change in most zones, i.e. advancement of wheat anthesis and maturity date, and reduced growth period, these variations should be incorporated into further studies to investigate a more accurate response of OAR to climate change in the future, once detailed phenology data can be obtained from multiple observations. Next, the analysis period focused on the impact season in wheat production, providing an appropriate knowledge of climate–disease relationship at the wide temporal scale. However, further work is also needed to assess and determine whether there are critical times for powdery mildew epidemics, if reliable and timely assessments and prediction of disease occurrence are conducted to implement wheat protection activities. Comparatively investigating the relationship between OAR and climate variables at the provincial scale over the last few decades, associated with weather patterns, disease risk will change, requiring strategies for management be updated according to new climatic conditions, which can help farmers and policy makers optimizing disease management.

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