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Study on the influence of weather periods on the occurrence of leaf rust and powdery mildew in winter wheat using an interval-based correlation approach

Untersuchung des Einflusses der Witterung auf das Auftreten von Braunrost und Echtem Mehltau an Winterweizen mit Hilfe eines intervallbasierten Korrelationsansatzes Originalarbeit

Abstract

Leaf rust (Puccinia triticina) and powdery mildew (Blumeria graminis f. sp. tritici) are among the most important diseases on winter wheat in Germany. The influence of weather periods on both diseases is little understood. Data on leaf rust and powdery mildew severity from 1976 to 2010 at different sites in the state of Saxony-Anhalt were used in the present study. The "window pane" algorithm was used to analyze and compare the diseaseweather relationships for both pathogens. Over 300,000 possible relationships between climate variables and disease occurrence were analyzed using this approach. The results were displayed as correlograms to gain profound insight into disease-weather relationships and their temporal variability during the epidemic year. Our analysis of the influence of temperature, precipitation sums, radiation and further climatic variables on leaf rust and powdery mildew infestation on winter wheat showed numerous significantly positive and negative effects on the occurrence of both diseases. The occurrence of P. triticina showed positive relationships with mean daily temperatures during spring, winter and autumn. There were significant negative correlations between B. graminis occurrence and mean sunshine duration per day from the beginning of the year until anthesis. Finally, our findings are compared to those in the literature, and new perceptions are discussed.

Key words: *Puccinia triticina, Blumeria graminis* f. sp. *tritici*, weather, climate, correlation analysis

Zusammenfassung

Braunrost des Weizens (Puccinia triticina) und Echter Mehltau des Weizens (Blumeria graminis f. sp. tritici) gehören zu den wichtigsten Schadorganismen an Winterweizen in Deutschland. Der Einfluss von Witterungsperioden auf beide Krankheiten ist bisher wenig verstanden. Daten zur Befallsstärke von Braunrost und echtem Mehltau an Winterweizen der Jahre 1976 bis 2010 konnten für verschiedene Standorte in Sachsen-Anhalt analysiert werden. Ein "window pane" Algorithmus wurde verwendet, um Zusammenhänge zwischen Witterung und Schaderregerauftreten zu analysieren und für beide Schaderreger zu vergleichen. Mit diesem Ansatz war es möglich über 300 000 mögliche Zusammenhänge zwischen klimatischen Parametern und dem Auftreten der agrarischen Schaderreger zu untersuchen. Um tiefer gehende Einblicke in die Zusammenhänge zwischen Witterung und Schaderregerentwicklung und ihre zeitliche Variabilität während der Vegetationszeit zu bekommen, wurden Korrelogramme erstellt. Es wurde der Einfluss von Temperatur, Niederschlagssumme, Globalstrahlung und weiteren Parametern untersucht. Dabei konnten zahlreiche signifikant positive und negative Effekte auf

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Accepted 5 June 2013 das Auftreten der Pilzkrankheiten belegt werden. Zum Beispiel stand das Auftreten von *P. triticina* im direkten positiven Zusammenhang mit der mittleren Temperatur im Frühjahr, Winter und Herbst. Das Auftreten von *Blumeria graminis* f. sp. *tritici* zeigte einen signifikant negativen Zusammenhang mit der täglichen Anzahl an Sonnenstunden von Jahresbeginn bis zur Blüte. Die Ergebnisse werden mit Literaturangaben verglichen und neue Erkenntnisse diskutiert.

Stichwörter: *Puccinia triticina*, *Blumeria graminis* f. sp. *tritici*, Wetter, Klima, Korrelationen

Introduction

Originalarbeit

According to the Intergovernmental Panel on Climate Change (IPCC), climate change will cause global mean temperatures to rise by 2 to 3 K in the next 50 years (IPCC, 2011). Also, the intensity of precipitation events and seasonal precipitation distributions are likely to change. Hence, problems such as early summer drought may worsen and the likelihood of extreme weather events could increase. Consequently, effects on plant disease incidence, pest occurrence and plant protection can be expected. Some modelling approaches and statistical analyses of disease and weather data were conducted and can be found in the literature. JAHN and FREIER (2001) found that, while several fungal diseases and plant pests like leaf rust of wheat (Puccinia triticina) and brown rust of barley (Puccinia hordei) could benefit, others like Rhynchosporium secalis could suffer, and yet others like powdery mildew (Blumeria graminis, f. sp. tritici) could be largely unaffected by a temperature increase of 2 K, assuming that rainfall patterns remain unchanged. In their study, data collected from 1977 to 1990 at 30 sampling dates were compared to the corresponding climate data and future infestation intensities were projected. After performing correlation analyses of long-term data (1977–1990) from the plant protection service of the former German Democratic Republic, JAHN et al. (1996) found that rising mean temperatures would increase the incidence of rusts in cereals and sugar beet, whereas powdery mildew showed a more diverse picture. A mean temperature increase of 1-2 K would be beneficial to powdery mildew on winter barley and sugar beet, and detrimental to powdery mildew on winter wheat. Furthermore, it was shown that a 30% to 60% decrease in rainfall would increase the incidence of rust and mildew diseases (except for powdery mildew on spring barley) and decrease that of Rhynchosporium leaf blotch and eyespot diseases on plants such as cereals.

Some plant disease forecasting models were developed by the Central Institution for Decision Support Systems in Crop Protection and Crop Production (German acronym: ZEPP) to predict first outbreaks and seasonal disease development of leaf rust on winter wheat (PUCTRI) and winter rye (PUCREC; RÄDER, 2007), and of Cercospora leaf spot on sugar beet (CERCBET; RACCA et al., 2002). These models contain hourly weather parameters (driving forces), which are used to calculate infection probabilities and infection pressure to make seasonal predictions regarding disease development (RÄDER, 2007). ROSSI et al. (1997) developed another model for leaf rust on winter wheat (RUSTDEP), which is based on the influence of meteorological parameters on urediniospore cycles. The CERCBET model was also used to calculate scenarios for Cercospora leaf spot occurrence under climate change conditions in lower Saxony (RICHERZHAGEN et al., 2011). RICHERZHAGEN et al. (2013) used the decision support system SIG to generate disease development scenarios under a changed climate and found that different diseases benefit while others do not. In their analyses, leaf rust and tan spot on winter wheat gained importance in both scenario periods studied (2021-2050 and 2071-2100), whereas powdery mildew on winter wheat showed no change in infection probabilities for either scenario period. Following another approach, HENZE et al. (2007) used cluster analyses to characterize meteorological events coinciding with an increasing number of Septoria tritici infections on winter wheat in Northern Germany. They found that increasing temperatures during infection and latent periods shortened the latent period of S. tritici significantly, and that increasing precipitation resulted in a slight decrease in the length of the latent period.

Nevertheless, there are not many data available on the influence of changing long-term climatic conditions on plant pathogens (CHAKRABORTY et al., 2010). Different methodological approaches and long-term data from different parts of the crop growing areas are needed and should be combined to elucidate the relationships between climate parameters and fungal diseases. In this context, climate chamber experiments, statistical analysis and modelling approaches with computer simulations are equally important.

Climate chamber experiments have shown that the optimal conditions for leaf rust development are daytime temperatures of around 20–25°C (PRIGGE et al., 2005) and night-time temperatures of 15–22°C with at least 4 hours of leaf wetness (HEITEFUSS et al., 1993; OBST and PAUL, 1993). The optimal temperature for powdery mildew development was found to be around 20°C (YARWOOD et al., 1954), but has a wide range of 12 to 20°C (MERCHÁN VARGAS, 1984; HEITEFUSS et al., 1993; OBST and PAUL, 1993).

One of the statistical modelling approaches is based on analysing relationships between assessed infestation levels of plant pathogens and weather data from past decades to derive models describing corresponding statistical relationships. Subsequently, these models can be driven by climate model output to calculate regional scenarios for pathogen occurrence under expected climate conditions. Long-term data are needed to analyse the influence of weather periods on disease development.

The aim of this study was to build a database by linking data on the occurrence of leaf rust (*P. triticina*) and powdery mildew (*Blumeria graminis* f. sp. *tritici*) on winter wheat, recorded systematically by the federal plant protection service of Saxony-Anhalt from 1976 to 2010 at a different number of sites per year to weather data collected at various weather stations during the corresponding years. The "Window Pane" algorithm (COAKLEY et al., 1988) was used to search for weather periods with a high impact on pathogen development, and the results were graphically displayed. This approach is the basis for deriving impact models and calculating climate change scenarios. It should provide a model study for further analyses using plant pathogen datasets from other German states.

Material and methods

Infestation data

Data on the occurrence of leaf rust (*Puccinia triticina*) and powdery mildew (*Blumeria graminis* f.sp. *tritici*) on winter wheat were collected by the federal plant protection service of Saxony-Anhalt according to methodological specifications of the pest monitoring system (ANONYMOUS, 1982). Following standard monitoring procedure, infestation levels were assessed on 40 plants and the mean infestation level at each monitoring site was documented. The infestation data thus collected from 1976 to 2010 at a different number of sites per year (Tab. 1) was transferred to a special database.

Because the maximum infestation level of fungal diseases is the best indicator of disease-related damage, only data from the beginning of anthesis until early ripening (Feekes 16 or BBCH 60 to 70) was included in the analyses. If more than one measurement was performed during anthesis, the value from the last monitoring date was used. The mean monitoring date for leaf rust (Fig. 2) and powdery mildew (not shown) was June 16th to 17th.

Weather data

Weather data consisted of daily measurement data from 1,218 German Weather Service (DWD) weather stations. Missing or inhomogeneous data were, respectively, replaced or corrected by interpolation by the Potsdam Institute for Climate Impact Research. The following daily variables for Saxony-Anhalt were analyzed: mean, minimum and maximum temperature, precipitation, relative humidity, sunshine, wind speed, and air pressure corrected to sea level (collected by 61 weather stations). The number of days with precipitation (daily precipitation sum above 0 mm), freezing days (daily minimum temperature under 0°C), days with snowfall (daily precipitation sum above 0 mm and daily mean temperature under 0° C), and days with a mean temperature between 17 and 23°C (the optimal temperature range for powdery mildew development) were calculated as additional variables for all weather stations used.

Monitoring sites (Fig. 1) were connected with weather data from the corresponding weather stations using Thiessen polygons calculated with the ArcGIS software package. Briefly, the monitoring sites were linked to weather data from the nearest weather station by calculating Voronoi fields through inverse distance weighting to interpolate the climatic data between weather stations (SHEPARD, 1968). Because monitoring sites from 1976 to 1990 could not be linked to municipalities, district capitals of the former German Democratic Republic were taken as substitute monitoring sites. From 1991 to 2010, the municipalities linked to the monitoring sites were known, and the capitals of the municipalities were defined as the monitoring sites.

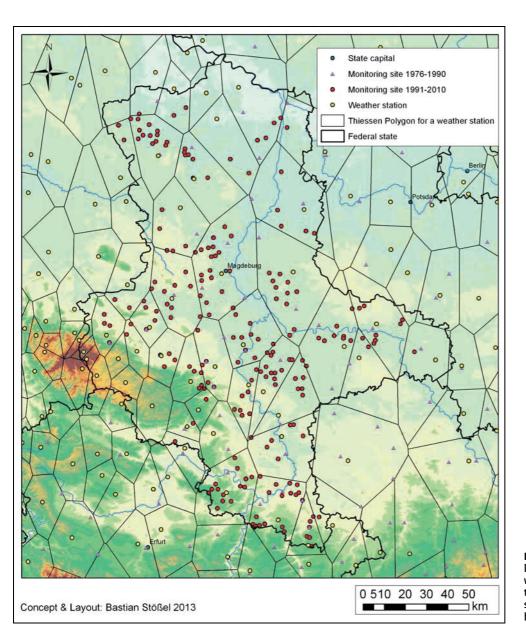
Correlograms

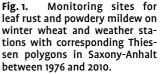
Kendall correlation coefficients between daily weather variables and infestation levels at BBCH 60 to 70 per year

Leaf rust (P. triticina)							Powdery mildew (B. graminis f.sp. tritici)					
Year	N	Year	Ν	Year	Ν	Year	Ν	Year	Ν	Year	Ν	
1976	48	1989	44	2000	31	1976	50	1987	26	1999	35	
1977	43	1990	39	2001	35	1977	45	1988	43	2000	31	
1978	31	1992	28	2002	37	1978	33	1989	34	2001	35	
1979	40	1993	38	2003	30	1979	41	1990	34	2002	37	
1981	20	1994	39	2004	29	1980	47	1992	28	2003	30	
1984	26	1995	34	2005	29	1981	47	1993	38	2004	30	
1985	28	1996	19	2006	30	1982	38	1994	39	2005	30	
1986	13	1997	37	2007	30	1983	42	1995	34	2006	30	
1987	24	1998	17	2008	19	1984	20	1996	19	2007	30	
1988	43	1999	37	2009	36	1985	45	1997	37	2008	19	
				2010	35	1986	45	1998	17	2009	36	
										2010	35	

Tab. 1. Number of monitoring sites for leaf rust and powdery mildew on winter wheat per year in Saxony-Anhalt from 1976 to 2010







and site were calculated in order to identify important weather periods influencing the occurrence of leaf rust and powdery mildew in winter wheat. The analyses were limited to weather periods from days 1 to 300 before the monitoring date, corresponding to the earliest sowing date for winter wheat in the study region. The number of correlation coefficients to be calculated was about 45,000 per plant disease and weather variable. SAS statistical analysis software was used to perform these time-consuming calculations.

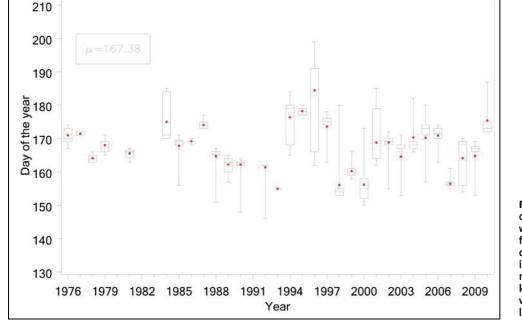
Time intervals with the highest correlation coefficients were calculated using the "Window Pane" algorithm proposed by COAKLEY and colleagues (COAKLEY et al., 1988; COAKLEY, 1989). In this study, the algorithm was applied with time intervals ranging from day 1 to day 300 before disease monitoring, and window lengths of 5 to 300 days. The results were presented as correlograms (GOLDWIN, 1982), which are perfectly suited for presenting the results of the "Window Pane" algorithm in its entirety. In contrast to the aforementioned publications describing the "Window Pane" and Goldwin's correlogram methods, Kendall correlation coefficients were calculated to derive the correlation matrices. Moreover, Kendall's correlation coefficient was used to account for non-normality of the pathogen data, and non-parametric tests were performed to derive distributionally independent results (HARTUNG, 2009).

Results

Leaf rust

The results of our analysis of the influence of selected weather parameters on leaf rust occurrence are presented in Fig. 3 and 4. There was a positive correlation between daily mean temperature and leaf rust infestation level over most investigated time intervals, whereby the highest correlation coefficients were found for longer periods

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26 28 13 24 43 44 39 28 38 39 34 19 37 17 37 31 35 37 30 29 29 30 30 19 36 35

Fig. 2. Monitoring day as "day of the year" (1976 to 2010) for winter wheat at monitoring sites for leaf rust: The mean value (red dot), median (crossbar in box), interquartile range (box height), minimum and maximum (whiskers) are shown. Overall mean values are shown in the upper left box.

(e.g., from day 1 to day 300 before the monitoring date) (Fig. 3a). An interesting finding is that correlation coefficients for short 5- to 20-day periods around 120, 150, 200, 240 and 260 days before monitoring were lower than those obtained averaging over these periods.

N

48 43 31 40

Correlations between precipitation sums and leaf rust infestation showed rather short- to medium-term relationships (Fig. 3b). Positive correlations were observed from days 90 to 150 (mid-March to mid-January), around days 230 and 295, and in the first 20 to 40 days before monitoring. Short-term negative correlations were found around 60, 170 and 210 days before field monitoring.

Our correlation analyses of sunshine duration and leaf rust infestation revealed some interesting findings (Fig. 3c). First, sunshine duration had a significantly positive influence on leaf rust severity when averaged over 300 days. In contrast to Fig. 3a, correlations on shorter time scales were higher than those for longer time periods. Furthermore, there were significant positive correlations from days 30 to 60 (mid-May to mid-April) and 160 to 270 before monitoring (end of January to mid-September). No significant positive correlations were found from early spring to mid-winter (day 80 to 150), and significant negative correlations were observed between days 90 and 120 (March to February). There were no significant correlations during the first 30 days before disease monitoring. Between days 290 and 300, significant negative correlations with leaf rust infestation were observed.

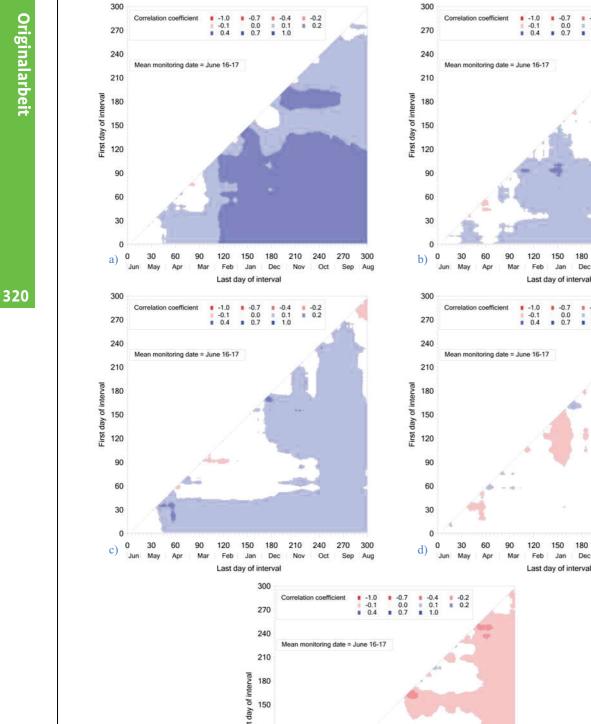
Correlations between leaf rust infestation and relative humidity showed mainly short-term relationships, except during the period from day 140 to 270 (end of January to mid-September), when significant negative mid- to longterm correlations were observed (Fig. 3d). From days 30 to 60 (mid-May to mid-April), another noteworthy negative correlated period was observed. Analysis of correlations between wind speed and leaf rust infestation showed nearly exclusively negative relationships (Fig. 3e). Significant negative correlations were found for mean wind speed in autumn (days 240 to 270 before monitoring), late autumn and winter (days 150 to 180), and during the first 60 days before monitoring (spring to early summer).

Analysis of correlations between leaf rust infestation and the number of days with precipitation (Fig. 4a) showed significant positive correlations from day 90 to day 150 (March to January), day 190 to day 240 (end of November to mid-October), and day 290 to day 300. Significant negative correlations occurred during the interval from days 35 to 60 and around day 170 before monitoring.

The influence of freezing days on leaf rust infestation in spring was mainly negative (Fig. 4b), especially during the winter to early spring, from the beginning of November (day 225) until mid-March (day 90). Our analysis of correlations between the number of days with snowfall and leaf rust occurrence revealed the most negative correlation coefficients in the interval between days 90 and 210 (mid-March to mid-November), and further negative correlations during shorter time periods around day 210 (Fig. 4c).

Powdery mildew

The results of our analysis of the influence of selected weather parameters on powdery mildew occurrence are shown in Fig. 5 and 6. Powdery mildew infestation was not clearly affected by mean temperature over the whole vegetation period (Fig. 5a). Rather short intervals with significant correlation coefficients were observed. Periods with the most negative correlations were around days 230 and 290 and during the first two to three months



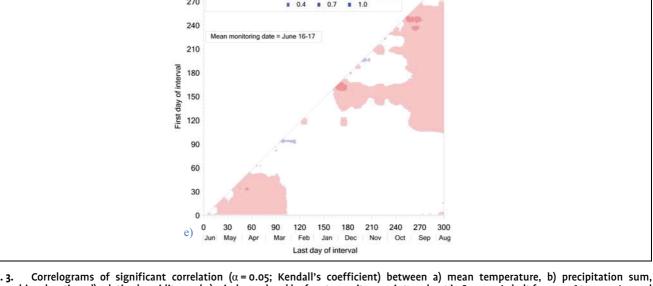


Fig. 3. c) sunshine duration, d) relative humidity, and e) wind speed and leaf rust severity on winter wheat in Saxony-Anhalt from 1976 to 2010. Legend elements represent the median of the interval of correlation coefficients. Day zero represents the monitoring day.

-0.7 0.0 0.7

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180 210 240 270 300

Dec Nov Oct Sep Aug

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180 210 240 270 300

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1

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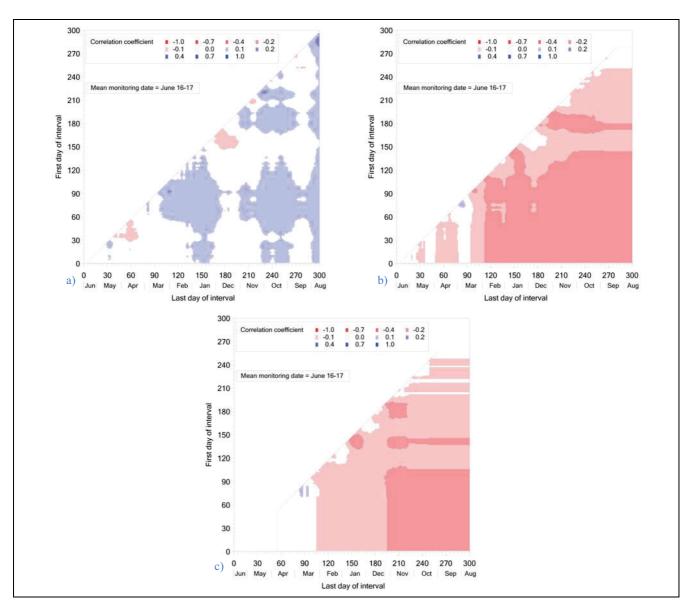


Fig. 4. Correlograms of significant correlation (α = 0.05; Kendall's coefficient) between a) number of precipitation days, b) number of freezing days and c) number of days with snowfall and leaf rust severity on winter wheat in Saxony-Anhalt from 1976 to 2010. Legend elements represent the median of the interval of correlation coefficients. Day zero represents the monitoring day.

before monitoring. Negative correlations were found for days 130 to 210 before disease monitoring.

Regarding relationships between minimum temperatures and powdery mildew infestation levels, there were significant positive correlations in the period from day 70 to day 110 (beginning of April until end of February) and during the winter months (February to December) (Fig. 5b). Conversely, significant negative correlations were observed from mid-November to mid-October.

Two distinct patterns could be seen when looking at the correlograms between precipitation sums and powdery mildew occurrence (Fig. 5c). Firstly, precipitation sums from February to September and from days 20 to 40 before monitoring were negatively correlated with disease severity. Secondly, time windows around 300 days before monitoring and during the first 10 to 15 days before monitoring showed significant positive correlations. Analysis of correlations between relative humidity and disease infestation level showed significant negative correlations from days 90 to 230 (mid-March to the beginning of November) and positive relationships in April and during the first 10 to 15 days before disease monitoring.

There were significant negative correlations between sunshine duration and disease occurrence for the time window from December until the monitoring date (Fig. 5e). The strongest correlations were observed in the first 10 to 15 days before monitoring.

The correlogram for maximum temperatures and severity of *B. graminis* f. sp. *tritici* showed significant negative correlations in late summer (end of August) and from the beginning of February until monitoring (Fig. 5f). Between the end of January and the beginning of December, there were significant positive correlations during interval lengths of 10 to 20 days.

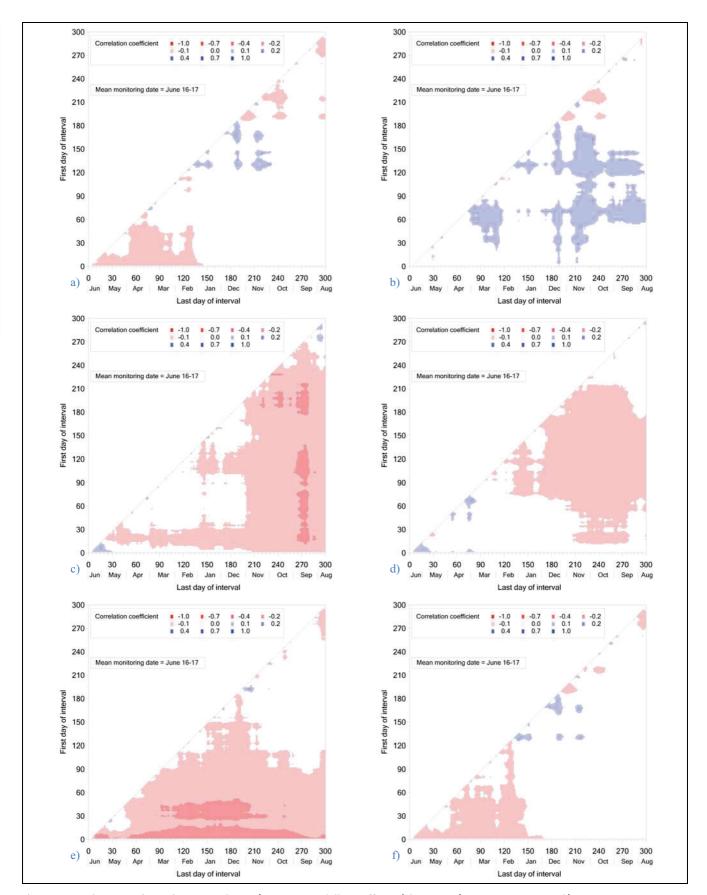


Fig. 5. Correlograms of significant correlation (α = 0.05; Kendall's coefficient) between a) mean temperature, b) minimum temperature, c) precipitation sum, d) relative humidity, e) sunshine duration, and f) maximum temperature and powdery mildew severity on winter wheat in Saxony-Anhalt from 1976 to 2010. Legend elements represent the median of the interval of correlation coefficients. Day zero represents the monitoring day.

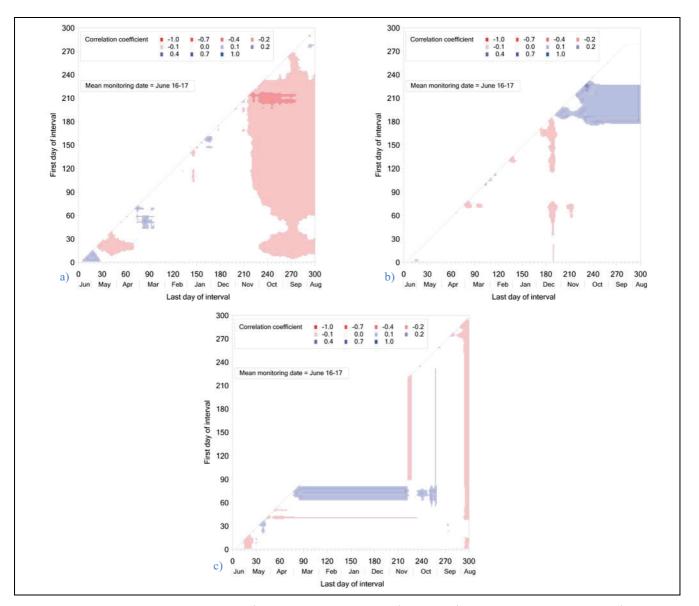


Fig. 6. Correlograms of significant correlation (α = 0.05; Kendall's coefficient) between a) number of precipitation days, b) number of freezing days, and c) number of days with temperatures between 17 and 23°C and powdery mildew severity on winter wheat in Saxony-Anhalt from 1976 to 2010. Legend elements represent the median of the interval of correlation coefficients. Day zero represents the monitoring day.

In late spring (days 20 to 60) and especially in autumn (days 210 to 270), the number of days with precipitation had a significantly negative effect on powdery mildew occurrence at anthesis (Fig. 6a). Significant positive correlations were observed during the first 20 days before monitoring.

Regarding correlations between freezing days and powdery mildew occurrence (Fig. 6b), significantly positive correlations were observed from mid-October to the end of November (days 240 to 200).

Furthermore, we observed significant positive correlations between the number of days with mean temperatures of 17 to 23°C and powdery mildew occurrence for periods in beginning April, from days 70 to 80 and around mid-October. There were significant negative correlations around 15 and 300 days before monitoring (Fig. 6c).

Discussion

Long-term data on fungal infestation levels in cereals and site-related weather data can be used to determine the influence of different weather periods on infestation levels. This approach was also used by different authors (COAKLEY et al., 1988; COAKLEY, 1989; CALVERO Jr. et al., 1996, JAHN et al., 1996, JAHN and FREIER, 2001, PIETRAVALLE et al., 2003; TE BEEST et al., 2008, 2009). Simulation models often lack sufficient temporal and/or spatial resolution of monitoring data for proper evaluation (e.g. RÄDER, 2007). The German state monitoring systems provide an excellent database for studies on plant diseases in cereals. They have been supported by a consistent computer-aided data acquisition system for plant disease infestation called ISIP since 2004 (KLEINHENZ and RÖHRIG, 2003). The present study showed that a sufficient number

Analyses of daily weather variables provide evidence of important time intervals during the growing period. However, the identification of periods of greatest influence is not possible using daily weather data because the explanatory power of correlations between daily weather variables and disease data is very limited and may contain many spurious relationships. Furthermore, there is no evidence that daily weather a few months before the monitoring date for a fungal disease could possibly influence disease severity similarly every year. How often days with favorable or unfavorable conditions occurred in a specific time interval and how favorable or unfavorable those conditions were is much more important (BURLEIGH et al., 1972a). Therefore, daily weather data must be accumulated on different time scales to gain further insight into disease-weather relationships.

The "Window Pane" algorithm produced reasonably good results and is a useful tool for investigating diseaseweather relationships because all time intervals that could possibly explain variations in disease levels can be evaluated rather than only a few selected intervals. This method can be used for preliminary variable selection before regression modeling when a large number of possible explanatory variables must be processed. The explanatory variables must then be condensed to those explaining the biggest part of variability of the predictand. CALVERO Jr. et al. (1996), PIETRAVALLE et al. (2003) and TE BEEST et al. (2008, 2009) mentioned only the "best" correlations for each variable but provided no overview of the calculated results.

The Goldwin correlogram (GOLDWIN, 1982) is an excellent method for displaying the results of the variable selection process, obtaining an impression of all significantly correlated time windows, and comprehending the basis on which some correlations are selected and others dropped. The use of correlograms allowed us to show not only significance or non-significance, but also the strength of correlation between infestation data and weather parameters for over 350,000 correlations analyzed per disease.

However, the suitability of different correlation coefficients to analyze data with heavily skewed probability distributions must be further investigated to improve the results. Partial correlation coefficients could produce better variable selection results than simple correlation coefficients, but are much more costly in terms of computing capacity and the expenditure of time. Furthermore, proper interpretation of the correlograms is not possible without a solid background in phytopathology. Definition of the minimum window length to extract the "best" correlations requires a deep understanding of the subject matter as well. Therefore, new statistical models must be developed to gain further insight into diseaseweather relationships. These models should make it possible to run climate change scenarios for future leaf rust and powdery mildew development and to perform climate impact assessments for future agricultural production and plant disease management based on these plant pathogen scenarios.

Leaf rust

Leaf rust, caused by *Puccinia triticina*, is one of the four most important diseases in winter wheat in Germany (FREIER et al., 2012). The infestation level mainly depends on the weather conditions, wheat variety, and use of fungicides. The present study included only fields not treated with fungicides to ensure that, besides weather, mainly the cultivar and its resistance influenced disease severity. Analysis of the cultivars used in the study showed degrees of resistance between 2 and 9 with 9 indicating the highest degree of susceptibility (Federal Plant Variety Office, 1976 to 2010). Seventy percent of the data showed a degree of resistance between 3 and 5 with a tendency towards higher susceptibility after the year 1990.

The clearly positive influence of higher temperatures on all developmental stages of leaf rust on winter wheat and on disease severity at anthesis found in our analyses agree with the findings of laboratory studies (CHESTER, 1946; HASSEBRAUK, 1959; ZADOKS, 1965) and statistical analyses of monitoring data (CHESTER, 1946; HOGG, 1969; BURLEIGH et al., 1972a, b; DAAMEN et al., 1992; JAHN et al., 1996; EVERSMEYER and KRAMER, 1998; MOSCHINI and PÉREZ, 1999; WIIK and EWALDZ, 2009). Especially in winter and spring, temperatures play a major role in determining the amount of urediniospores managing to overwinter and increasing the amount of initial inoculum available for epidemic development on host plants in spring (BURLEIGH et al., 1969; EVERSMEYER and KRAMER, 1994, 1995, 1996, 1998).

Higher spring temperatures can accelerate uredia and urediniospore development and shorten latency and incubation times, thus increasing the number of leaf rust generations until anthesis of wheat. Lower temperatures slow down the development of leaf rust and decrease the amount of disease cycles until anthesis (RoELFS and BUSHNELL, 1985; EVERSMEYER and KRAMER, 1996). The identified correlations show the importance of air temperatures during the transition from autumn to winter and from winter to spring, when temperatures are at the lower limit of leaf rust development (CHESTER, 1946).

The influence of precipitation on the development of leaf rust on winter wheat has already been the topic of many studies (DAAMEN et al., 1992; HEITEFUSS et al., 1993; WIIK and EWALDZ, 2009). As an important source of humidity, precipitation is essential for urediospore germination and infection. This becomes obvious when looking at the positive correlation periods in August, October and May. The findings in August agree with those of WIIK and EWALDZ (2009). In late summer, humidity is an important prerequisite for leaf rust survival throughout the crop-free period as it provides moisture for volunteers. Furthermore, precipitation in late summer results in lower inso-

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lation, which makes it easier for leaf rust to over-summer (ZADOKS, 1965; EVERSMEYER and KRAMER, 1998).

In autumn, leaf rust infects newly sown winter wheat, and its population size and spatial distribution can expand if weather conditions are good enough. Sufficient precipitation is needed as a source of moisture for leaf wetness, a major determinant of optimal infection and germination. These conditions seem similarly important in spring, especially in May, when leaf rust is in the crucial phase that determines disease severity during anthesis. The wetter and warmer the conditions during this time, the shorter the latency and infection periods and the more generations produced (Hogg, 1969). The above-mentioned findings contradict those of JAHN et al. (1996), who found that leaf rust infestation on winter wheat increases under drier future conditions.

The positive relationships between precipitation in January and February and leaf rust severity cannot be completely explained as a result of the presence of the necessary humidity, but rather with the isolation effect of snowfall at lower temperatures in contrast to freezing temperatures without snowfall. However, this isolation effect was not seen in the correlogram for snowfall days. Our results showed the exact opposite of an isolation effect by snow cover. Snow-free periods during winter are needed for re-infection of host material and are thus important for leaf rust survival (Eversmeyer and KRAMER, 1998). Caution is advised when interpreting findings on the influence of snow cover on urediniospores because the results only show correlograms for snowfall and disease severity. The fact that no snow is falling does not necessarily mean that there is no snow cover. Additionally, the calculated variable snowfall seem to be dominated by low temperatures, and the expected precipitation signal is mainly absent. Further studies are needed to determine whether this method for calculating days with snowfall makes sense or must be changed.

The effects of sunshine duration and radiation on the development of fungal pathogens are known (DE VALLA-VIEILLE-POPE et al., 2002). This knowledge is also valid for leaf rust on winter wheat where urediniospores are exposed to intense solar radiation during transport (SACHE, 2000), germination, infection, reproduction and sporulation. As expected, correlations between sunlight hours and leaf rust severity show patterns similar to those between disease severity and mean temperatures over long periods of time. During winter, the correlation structures for sunlight duration are contrary to those for mean temperature. This can be explained by the decoupling of radiation and temperature during winter months. Sunny days and high radiation are common during winter weather situations with persistent high-pressure systems, which generally bring relatively cold rather than warm temperatures to Central Europe. However, it is surprising that sunshine duration shows no significant correlations regarding the conditions in March and early April. The negative correlated period around day 290 corresponds with the findings of the correlograms for precipitation. If there were a positive correlation for precipitation sums in this interval, sunshine duration would naturally show a negative relationship because more precipitation would mean more cloudiness and less sunshine hours, and that, in turn, would increase the possibility of leaf rust urediniospores over-summering during crop-free periods by using a "green bridge" during this time (ROELFS and BUSHNELL, 1985).

Wind speed is often used to explain how exogenous inoculum is transported to regions, thus strengthening leaf rust epidemics or making them possible (HIRST and STEDMAN, 1967; SACHE, 2000). Contrary to the findings in literature, our correlogram for wind speed shows mainly negative correlations. This suggests that wind speed can be too high for urediniospores to adhere to leaf surfaces before appressorium development, but it is unlikely that this effect could hinder the development of leaf rust for a long period of time. Thus, the strongest effect of wind speed on leaf rust severity might be accelerated drying of leaf surfaces at higher wind speeds. This might lower leaf wetness below the levels required for infection and germination of urediniospores (STUCKEY and ZADOKS, 1989). Especially in late summer, early autumn, at the time of winter wheat sowing, and in spring, leaf wetness accelerates the development of leaf rust. Therefore, long periods of leaf dryness can result in massive obstruction or even long-term interruption of the developmental cycle of P. triticina (DE VALLAVIEILLE-POPE et al., 1995).

Powdery mildew

Like leaf rust, powdery mildew is one of the most important fungal diseases in winter wheat in Germany. Apart from weather conditions, wheat variety also affects the infestation level in the field, whereby the wheat varieties used today are increasingly resistant to *B. graminis*. Our own analyses based on descriptive lists of varieties (Federal Plant Variety Office 1990 to 2010, Federal Office for Varieties of the German Democratic Republic 1976 to 1989) used during the years 1976 to 2010 also showed these tendencies.

Powdery mildew is likely to capitalize from warmer temperatures in winter. Mild winters allow more conidia to survive the winter, resulting in more initial inoculum at the beginning of spring (BOLAND et al., 2004). Our findings support this theory as they show significant positive relationships between minimum temperatures and powdery mildew severity at the beginning of February until early December. Minimum temperatures seemed to be around the lower limit for powdery mildew development from March to December because minimum temperatures during this time frame were positively correlated with disease severity.

The negative correlations between mid-October and late November found in this study are not discussed in literature, and no biological process explaining this phenomenon can be found (temperatures in late autumn are usually at the lower limit for disease development, so higher temperatures cannot impede the development of powdery mildew). The same pattern can also be seen as positive correlations in the correlogram for freezing days and disease severity.

Temperature sensitivity of powdery mildew was observed during the three months before the monitoring date and in late August of the preceding year. This effect was also documented by AUST (1981a) and STEPHAN (1957). It seems that before anthesis and during late summer, when powdery mildew conidia are struggling to survive and capitalize on the "green bridge", temperatures can be too high for optimal development.

An interesting difference in patterns was seen in March and April between correlograms for minimum temperatures and disease severity and maximum temperatures and disease severity. In the correlograms for these months, minimum temperatures seemed to be around the lower limit, as indicated by the positive correlations, and maximum temperatures seemed to be around the upper limit, as indicated by negative correlations. This suggests that the optimal temperature range for powdery mildew on winter wheat is extremely small. Moreover, this contradicts the findings of TE BEEST et al. (2008), who did not find maximum temperatures in spring and early summer approaching the upper temperature limit for powdery mildew. According to their data, the warmer temperatures are from spring onward, the better for powdery mildew development. STEPHAN (1957) showed that powdery mildews do in fact have a rather small window of optimal temperature for overall development. However, our data suggest that temperatures in March and April are critical for powdery mildew infection, penetration, germination and sporulation. This was also emphasized by MORGOUNOV et al. (2011). It seems to be analog to Chester's findings on the "critical month" of leaf rust development (CHESTER, 1946). Warmer conditions during this period can give powdery mildew a good start into the new vegetation season by shortening latency and infection periods and by amplifying the number of generations until anthesis. This was observed in the analysis of correlations between minimum temperatures and disease severity and of correlations between disease severity and the number of days with temperatures between 17 and 23°C, which are approximately the optimal temperatures for powdery mildew development (PRIGGE et al., 2005; YARWOOD et al., 1954).

The negative influence of very high temperatures on powdery mildew severity in the weeks before the monitoring date and in late summer goes hand in hand with high radiation periods with a significantly negative impact on disease severity. This corresponds to the findings of SPENCER (1978) and MARTIN (1975), who found that high insolation conditions and therefore higher leaf surface temperatures (TE BEEST et al., 2008) can hamper germination of powdery mildew conidia.

The correlogram for precipitation sums and powdery mildew severity displays two patterns. Firstly, precipitation averaged over periods of at least one month during the whole time frame considered had a significantly negative effect on disease severity, especially in autumn. Secondly, precipitation sums averaged over the first 20 days before monitoring showed significant positive correlations with disease severity.

The first pattern is in agreement with the findings of SPENCER (1978) and BOUGHEY (1949), who found that powdery mildew is more dangerous under drier conditions. Laboratory experiments have shown that the conidia of powdery mildew have a higher moisture content than, for example, urediniospores of leaf rust, and that they do not have to rely on precipitation events for moisture (YARWOOD et al., 1954). The second pattern shows that the additional moisture content is not sufficient at higher temperatures in summer. Then, precipitation events must provide the moisture needed, in particular, for infection and germination of conidia. High relative humidity is a well known prerequisite for those developmental processes (HASSEBRAUK, 1959; PRIGGE et al., 2005; FRIEDRICH, 1994; MERCHÁN VARGAS, 1984).

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