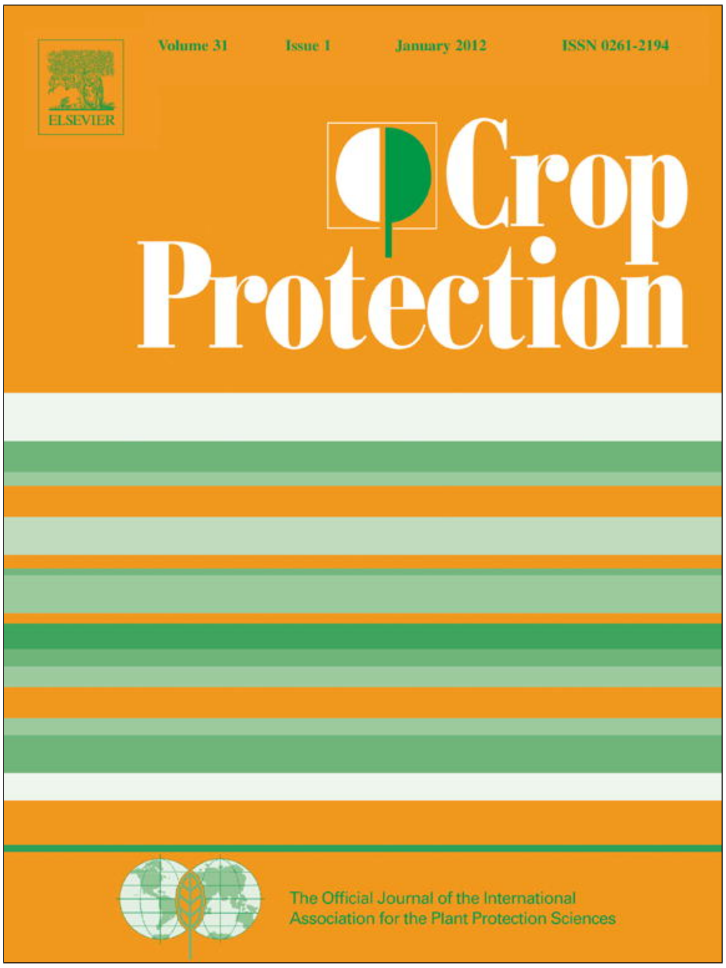
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Spring air temperature accounts for the bimodal temporal distribution of *Septoria tritici* epidemics in the winter wheat stands of Luxembourg

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ABSTRACT

Septoria tritici is the causal agent of leaf blotch in wheat and among the most damaging fungal cereal pathogens in the humid regions of central Europe. The percentage of the leaf area colonized by *S. tritici* was recorded weekly between April and July every season between 2004 and 2010. A total of 11 cultivars with moderate susceptibility [ratings of 4–6 on a 1 (resistant) to 9 (susceptible) scale] were included. The disease level was assessed on the upper three leaf layers at 2 locations between 2004 and 2006 and at 3 locations between 2007 and 2010. The period between sowing and the point of time, when 50% of the leaf area was necrotized due to colonization by *S. tritici* (T_{50}) was estimated for each year, site, cultivar and leaf layer by non-linear regression. T_{50} values followed a bimodal distribution with one maximum at 245 days after sowing (DAS; early epidemics) and one maximum at 270 DAS (late epidemics). Early epidemics were preceded by almost constant daily average temperatures of 13.2 ± 0.8 °C between 181 and 210 DAS. Late epidemics were preceded by an approximately linear increase in temperature from 8.7 ± 0.9 to 12.1 ± 0.9 °C during the same period of time. Based on these differences, it seems possible to predict whether an early or a late epidemic can be expected at least 35 days before the epidemic outbreak. Temperature sums calculated with a base temperature of 6.6 °C starting at sowing and ending when T_{50} was reached were not significantly different between early and late epidemics ($P = 0.73$) and averaged 1721 ± 49°days. Fungicide applications, which resulted into a delay of the epidemic development similar to the difference between early and late epidemics, resulted in a yield increase between 11.7 and 12.6%.

1. Introduction

The fungus *Septoria tritici* Rob. ex Desm. (teleomorph: *Mycosphaerella graminicola* (Fuckel) Schroeter) is a pathogen of cereals and the primary cause of Septoria tritici blotch in wheat (Chungu et al., 2001; Gladders et al., 2001; Magboul et al., 1992; Shaw and Royle, 1989). Leaf blotch was reported to be the most damaging disease in the wheat stands of England and Wales (Cook et al., 1991). Yield losses caused by *S. tritici* in humid regions range from 30 to 50% if left uncontrolled (Ziv and Eyal, 1978; Burke and Dunne, 2006; Royle et al., 1986). The sexual ascospores represent the primary source of inoculum infecting young winter wheat plants in autumn (Gladders et al., 2001; Hunter et al., 1999). The asexual conidiospores are formed in fruiting bodies (pycnidia) and these spores represent the secondary inoculum for the epidemic spread and vertical transfer to the upper leaves in spring and summer (Gladders et al., 2001; Palmer and Skinner, 2002; Royle et al., 1986). After infection, there is a latent period of approximately 20 days (Henze et al., 2007) before necroses with pycnidia appear on newly infected leaves. Infection of the youngest upper three leaf layers is of particular concern, because damage of those leaf layers greatly diminishes yield (Thomas et al., 1989).

The point of time when an epidemic occurs is of practical importance because early epidemics increase the likelihood of more severe damage than if an epidemic occurs later in the growing season. Due to a lack of cultivars with good agronomic performance and high level of plant resistance towards the pathogen, the control of *S. tritici* largely depends on fungicides, resulting in the development of a high level of resistance of the pathogen towards strobilurins and in a minor shifting of resistance levels towards azoles (Beyer et al., 2011). To achieve the best control with the

Abbreviation: DAS, days after sowing.

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remaining effective fungicides with a minimum number of sprays (to delay further development of fungicide resistance), it is crucial that these are applied during the period of infection. If an application is too early, it will be ineffective given that the pathogen is not present and too late the application will also be ineffective because infection has already occurred.

S. tritici epidemics vary greatly among years and locations, suggesting a strong influence of the environment (Wiik and Ewaldz, 2009). Crucial steps of the pathogen's life cycle, such as spore transfer and germination, depend upon the availability of water and therefore rain in May favours *S. tritici* epidemics (Wiik and Ewaldz, 2009) in particular at temperatures about 17 °C (Shaw, 1990). If leaf wetness durations exceeded 48 h, fungicide applications were carried out resulting in approximately the same level of yield in four out of five seasons compared with a standard spraying regime but in a reduction of fungicide applications by 20% (Burke and Dunne, 2008). Several studies were carried out to elucidate relationships between meteorological variables and disease severity at critical periods and often resulted in models that performed well in the region where they were developed or neighbouring countries (Coakley et al., 1985; Pietravalle et al., 2003; El Jarroudi et al., 2009). Weather conditions in Luxembourg during the growing season are rather favourable for infection by *S. tritici*, with an average air temperature and annual precipitation of 8.3 °C and 875 mm (data obtained from station Findel, WMO ID 06590, period 1971–2000), respectively.

Since *S. tritici* epidemics were reported to depend on high humidity and moderate temperatures (Eyal et al., 1987), we hypothesize that temperature and relative humidity should differ between years and locations with an epidemic compared to non-epidemic situations, especially during periods critical for infection by *S. tritici*. This information should be useful for improving the predictive ability to forecast for *S. tritici* epidemics each year. Therefore, the objective of this study was to figure out the differences in the meteorological conditions that led to either early or late *S. tritici* epidemics in the winter wheat stands of Luxembourg.

2. Materials and methods

2.1. Acquisition of disease data

S. tritici epidemics were monitored every year between 2004 and 2006 at two locations (Everlange: 49° 46′ N/5° 57′ E, 309 m above sea level; Reuler: 50° 03′ N/6° 01′ E, 452 m above sea level) and between 2007 and 2010 at three locations (additional site: Burmerange: 49° 29′ N/6° 19′ E, 248 m above sea level) in Luxembourg (Table 1). Unless stated otherwise, disease assessment data used in the present study originated from plots that did not receive a fungicide spray. The plot size was 1.25 m × 8 m. Ten plants were marked in each plot and the percentage of leaf area colonized by *S. tritici* was estimated on the main shoot of the same ten plants at weekly intervals. Plants from four replication plots were assessed for each location, observation date, year and cultivar (Table 1). Personnel were trained prior to disease assessments using an online software package for identification and quantification of cereal leaf pathogens (http://prozentualer-befall.jki.bund.de/schadbilder.php?show=5). Disease assessments were carried out between the end of April and the end of June, which corresponds to approximately 180–270 DAS in Luxembourg. Disease severity on the top three leaf layers (flag leaf (F) and the two leaves below designated F-1 and F-2) was considered, because those are the leaf layers that largely determine the final yield (Thomas et al., 1989).

2.2. Acquisition of meteorological data

At each of the three test sites meteorological data were measured by standard automatic weather stations, operated by the official agricultural meteorological service of Luxembourg. Air temperature and relative humidity were measured 2 m above ground and total precipitation at 1 m above ground. The uncorrected data were subsequently pre-processed using an automatic data processing chain including error detection and correction as well as linear gap interpolation procedures according to the

Table 1
Growing periods (year of harvest), growing locations, cultivar names, cultivar susceptibility towards *Septoria tritici* (scale 1 (=low susceptibility) to 9 (=high susceptibility)), previous crops, sowing dates and days after sowing, when leaves were necrotized by 50% due to *S. tritici* colonization and classification of the epidemic as either early or late.

Year	Location	Cultivar(s)	*Septoria* susceptibility[a]	Previous crop	Sowing date	T_{50} (DAS)			E = early L = late
						F	F-1	F-2	
2004	Everlange	Achat	5	Oilseed rape	14.10.2003	286	276	255	L
	Reuler	Bussard	6	Oilseed rape	16.10.2003	282	275	271	L
2005	Everlange	Achat	5	Wheat	22.10.2004	260	256	253	E
		Parador	n.d.a.	Oilseed rape	22.10.2004	265	250	236	E
	Reuler	Flair	4	Oilseed rape	05.10.2004	292	280	276	L
2006	Everlange	Akteur	6	Fallow	10.10.2005	266	253	246	E
		Flair	4	Fallow	10.10.2005	267	258	249	E
	Reuler	Dekan	4	Maize	13.10.2005	288	284	280	L
2007	Burmerange	Cubus	6	Oilseed rape	11.10.2006	250	247	242	E
	Everlange	Achat	5	Pea	10.10.2006	255	251	248	E
		Akteur	6	Pea	10.10.2006	249	249	253	E
	Reuler	Akteur	6	Maize	07.10.2006	261	257	251	E
2008	Burmerange	Cubus	6	Oilseed rape	06.10.2007	288	273	272	L
	Everlange	Rosario	5	Fallow	09.10.2007	293	271	255	L
	Reuler	Schamane	4	Oilseed rape	10.10.2007	302	286	283	L
2009	Burmerange	Cubus	6	Oilseed rape	06.10.2008	270	267	261	E
	Everlange	Achat	5	Oilseed rape	13.10.2008	265	259	248	E
		Privileg	4	Oilseed rape	13.10.2008	265	261	256	E
	Reuler	Schamane	4	Oilseed rape	10.10.2008	286	279	288	L
2010	Burmerange	Cubus	6	Oilseed rape	01.10.2009	287	275	271	L
	Everlange	Achat	5	Oilseed rape	15.10.2009	280	267	259	L
		Privileg	4	Oilseed rape	10.10.2009	286	273	263	L
	Reuler	Manager	4	Oilseed rape	28.10.2009	331	412	327	L

n.d.a. = no data available.
[a] According to BSA (2010).

method described in WMO (1995). Air temperature values were stored as 10 min mean values, precipitation data as 10 min totals, respectively.

2.3. Data analyses

The day of sowing was chosen as starting point for time (i.e., time = 0) measurements in this study to standardize all time courses for plant age. For practical purposes, developmental stages of cereal crops are often characterized using the growth stage scale by Zadoks et al. (1974). Since one unit on the growth stage scale may correspond to different durations in the studied years and locations due to different growth conditions, we preferred to use the number of days after sowing. The relationship between the number of days after sowing and the growth stages for all data used in the present study is shown in Fig. 1.

The percentage of leaf area necrotized due to *S. tritici* was plotted against time for each year, location, cultivar and leaf layer. For an example see Fig. 2. The period of time, until 50% of the leaf area was necrotic (T_{50}) was estimated using a sigmoid regression model of SigmaPlot version 10 (Systat Software GmbH, Erkrath, Germany; https://www.systat.com/). The regression model was:

$$y = \frac{100}{1 + e^{-\left(\frac{x - T_{50}}{b}\right)}},$$

where y = colonized leaf area (%) and b = slope parameter.

A frequency distribution of the T_{50} values was plotted for each of the upper three leaf layers (Fig. 3). Means and standard errors of the daily averages of temperature and relative humidity were calculated (1) from the pooled meteorological data preceding early epidemics and (2) from the pooled meteorological data preceding late epidemics (Fig. 4) for the time frame 2004–2010. Means and standard errors of the daily precipitation were also calculated (Fig. 4). The largest differences in the temperature time courses were observed between 181 and 210 DAS and were tested for their predictive value by leave-out-one cross validation. For each day of this period, the sum of squares (SSQs) of the difference between the temperature of the case that was left out and the average temperature of the remaining cases that were followed by an early and a late epidemic were calculated separately. We expected that the left out case will be followed by a late epidemic, if the SSQ difference towards the average temperatures of late epidemics is smaller as compared to early epidemics an *vice versa*. The expectation was compared with the observations and classified as either true or false. Since different cultivars grown at the same location in the same year always fell into the same class (early or late epidemic, Table 1), we considered cultivars grown at the same location and the same year as only one case study by calculating the averages of both for the calculation of the sum of squares. Effects of year, location, previous crop and cultivar on T_{50} values were tested by subjecting data to analyses of variance (SPSS version 16, IBM Corporation Armonk, New York, USA; http://www-01.ibm.com/software/analytics/spss/). Total daily precipitation data, the daily average relative humidity and the daily average air temperature measured between 160 and 270 days after sowing of winter wheat were subjected to a factor analysis (SPSS). Factor scores were extracted using the regression method. Measurements of each day

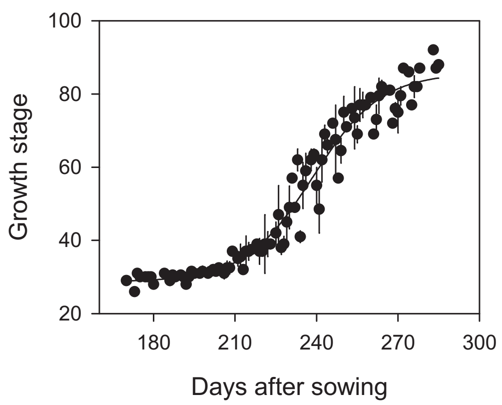

Fig. 1. Relationship between the number of days after sowing and the winter wheat growth stages according to Zadoks et al. (1974). Plot symbols represent medians of the data from the years and locations listed in Table 1. Error bars represent standard errors.

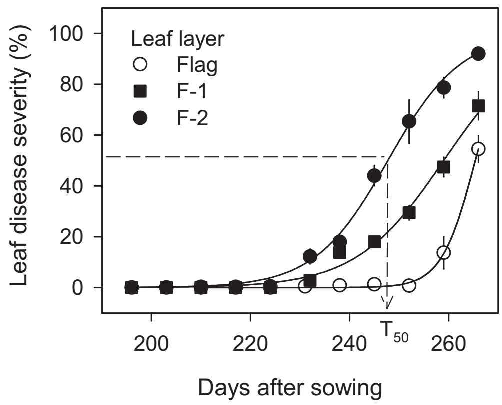

Fig. 2. Disease progress of leaf colonization of *Septoria tritici* in wheat. Location Everlange, season 2009, cultivar Achat. The period of time, until 50% of the leaf area was necrotized due to *S. tritici* colonization (T_{50}), was estimated for the upper three leaf layers by non-linear regression. Plot symbols represent means of 40 plants; error bars represent standard errors of the mean.

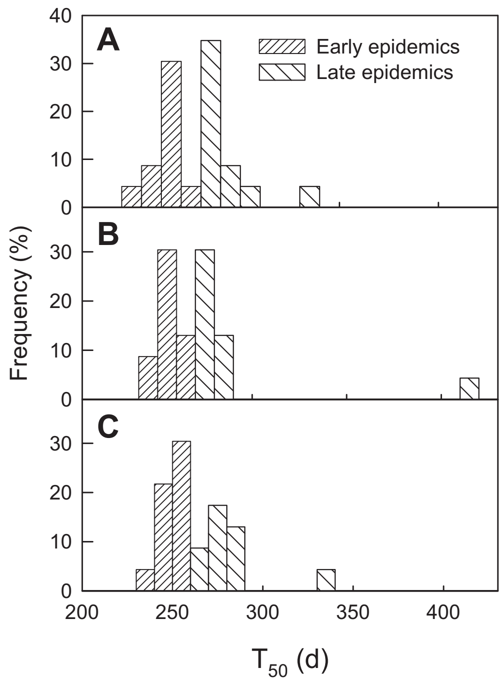

Fig. 3. Frequency distribution of the number of days since sowing, until 50% of the leaf area was necrotized due to *Septoria tritici* infection (T_{50}) for (A) flag leaves, (B) Leaf layer (F-1), (C) Leaf layer (F-2). Data originated from 7 years, 3 locations and 11 cultivars (Table 1).

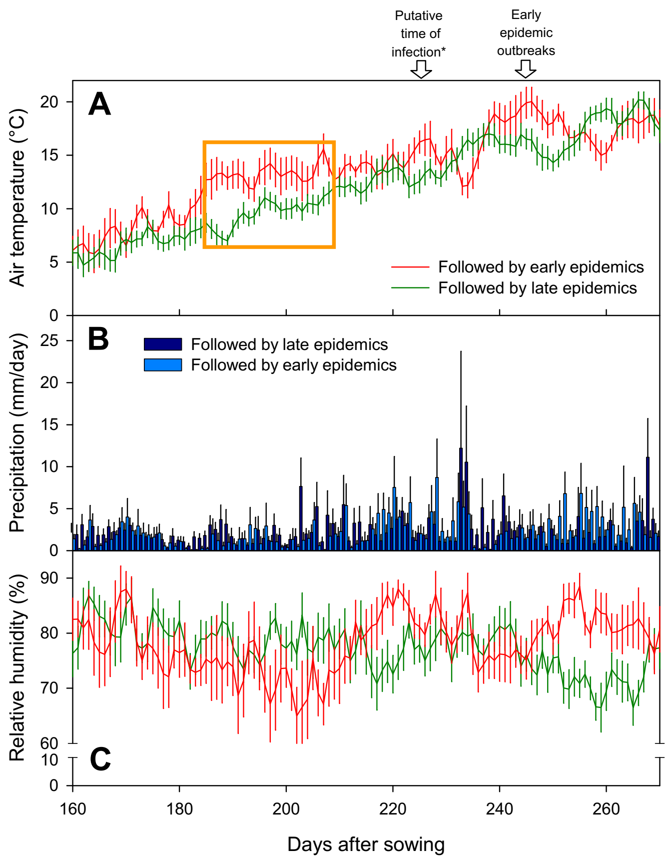

Fig. 4. Differences between average daily air temperatures (A), average daily precipitation (B) and average daily relative humidity (C) measured before early (on average 245 days after sowing (DAS), see Fig. 3) and late *Septoria tritici* epidemics (on average 270 DAS). Vertical lines represent standard deviations. Averages and standard deviations were calculated from all early and all late epidemics for the period between 2004 and 2010. *The putative time of infection was estimated by subtracting the latent period (20 d, Henze et al., 2007) from the point of time when early epidemics were observed (245 DAS).

were treated as individual variables, such that factor scores were extracted from 111 measurements for each year and location. The first two factors explaining most of the variance within the respective data set were plotted against each other and different plot symbols were used to indicate whether an early or a late S. *tritici* epidemic was observed after the respective meteorological conditions (Fig. 5).

3. Results

The period of time, until 50% of the leaf area of the upper three leaves were necrotized due to *S. tritici* infection ranged from 230 to 410 DAS (Fig. 3). T_{50} values for very late epidemics had to be extrapolated, because 50% of necrotized leaf tissue due to *S. tritici* colonization was not reached until natural senescence of the wheat stands in these cases. The effects of year, location, and leaf layer on T_{50} values were significant at $P < 0.001$ while the effects of wheat cultivar and previous crop on T_{50} values were non-significant at $P = 0.72$ and $P = 0.45$, respectively. The effect of the sowing date on T_{50} values was non-significant for leaf layers F ($P = 0.38$) and F-2 ($P = 0.32$). The effect of the sowing date on the T_{50} values of leaf layer F-1 was significant at $P = 0.03$, but depended solely on an outlier. After elimination of the outlier, the effect of sowing date on T_{50} values of F-1 was also non significant ($P = 0.19$). Even though the effect of the leaf layers on T_{50} values was significant, only minor differences could be observed between the leaf layers concerning their frequency distribution of T_{50} values (Fig. 3). Frequency distributions of T_{50} values of the upper three leaf layers had two maxima, one at approximately 245 DAS and the second at 270 DAS (Fig. 3). The cases belonging to the group with the maximum at 245 DAS are subsequently referred to as "early epidemics", the case studies belonging to the group with the maximum at 270 days as "late epidemics".

Average daily air temperatures preceding early epidemics were higher compared to late epidemics except for the short periods between 233 and 235 DAS and 257 and 261 DAS, where temperatures preceding late epidemics were significantly higher (Fig. 4A). Average daily air temperatures preceding early epidemics were almost constant at 13.2 ± 0.8 °C between 181 and 210 DAS, whereas average air temperatures preceding late epidemics slowly increased from about 8.7 ± 0.9 to 12.1 ± 0.9 °C in the same period of time (Fig. 4A).

The average time course of precipitation was similar for early and late epidemics (Fig. 4B). Within the period of observation (160–270 DAS), 258 mm of precipitation were recorded on average for early epidemics and 275 mm for late epidemics (Fig. 4B).

Relative humidities were higher between 197 and 198 DAS, between 201 and 203 DAS and 206 and 207 DAS prior to late epidemics compared to early epidemics (Fig. 4C). Relative humidities were higher between 217 and 222 DAS and between 252 and 267 DAS prior to early epidemics compared to late epidemics (Fig. 4C). Relative humidities preceding early and late epidemics did not differ significantly for all other periods between 160 and 270 DAS (Fig. 4C).

Leave-out-one cross validation revealed that temperatures observed between 181 and 210 DAS allowed a correct prediction of whether the left out case was followed by an early or a late epidemic in 16 out of 18 available year–location combinations (Table 2). Based on the cumulative daily precipitation data or the average relative humidity recorded between 160 and 270 DAS, factor analysis was unable to unambiguously predict whether an early or a late epidemic followed (Fig. 5A,B), as indicated by the overlap of the events preceding early and late epidemics. In contrast, the first two factors extracted from the average daily temperature data measured between 160 and 270 DAS were suitable to predict, if an early or a late epidemic followed (Fig. 5C).

Growth stage 65 (anthesis, Zadoks et al., 1974) was reached between 209 (which was an outlier) and 258 DAS (Fig. 1).

4. Discussion

Early epidemics were preceded by almost constant daily average temperatures of 13.2 ± 0.8 °C between 181 and 210 DAS. Late epidemics were preceded by an approximately linear increase in temperature from 8.7 ± 0.9 to 12.1 ± 0.9 °C during the same period of time. Given the fact that early epidemic outbreaks were observed at about 245 DAS and considering recent reports that length of the latent period of *S. tritici* is approximately 20 days (Henze et al., 2007), the difference in air temperature between 181 and 210 DAS probably affects events before infection, such as the establishment and propagation of fungal structures on the lower leaf layers. Average daily temperatures of 10-day time slots between 160 and 250 DAS did not contain enough information to distinguish early and late epidemics based on factor analysis (data not shown). Leave-out-one cross validation based on the shorter time frame between 181 and 210 DAS allowed a separation of early from late epidemics with an accuracy of 89%. Hence, temperatures within this time frame might be suitable to predict whether an early or a late epidemic can be expected at least 35 days in advance.

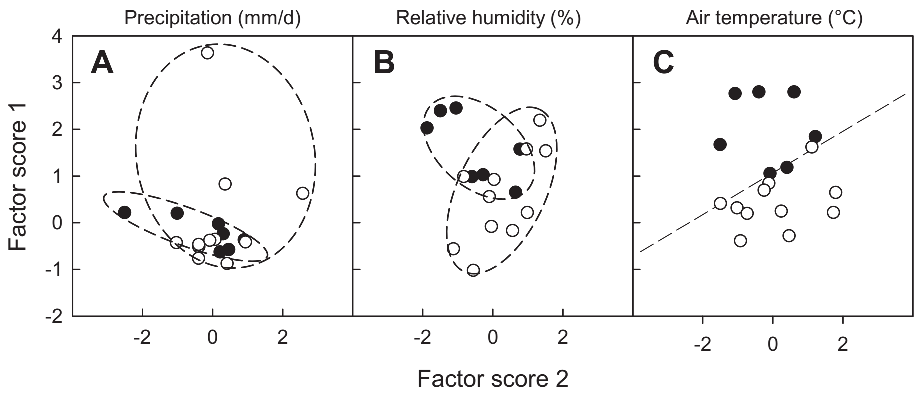

Fig. 5. Factor scores extracted from the daily precipitation (A), daily average relative humidity (B), or daily average air temperatures (C) measured between 160 and 270 days after sowing of winter wheat for the period between 2004 and 2010. Measurements of each day were treated as variables, such that factor scores were extracted from 111 measurements. The first two factors explaining most of the variance within the respective data set were plotted against each other and data from weather stations being located at a place and time where early (●) and late (○) *Septoria tritici* epidemics followed were labelled using different plot symbols.

Since very close correlations between the leaf area colonized by leaf diseases and yield were observed by Seck et al. (1991), it seems reasonable to assume that early epidemics result in higher yield losses than late epidemics. In some years and locations, the temporal distance between the epidemic outbreaks in the untreated control plots and in neighbouring plots where a fungicide application was carried out in the same location and in the same cultivar corresponded approximately to the temporal difference between early and late epidemics. In 2009, the T_{50}s for the untreated controls were 252 and 259 DAS for cultivars Boomer (location Christnach) and Achat (location Everlange), respectively. Due to fungicide applications, T_{50}s were delayed to 268 and 275 DAS, respectively. Yields were 12.16 and 11.73% higher for the late epidemics induced by fungicide use, as compared to the early epidemics observed in the untreated control plots. Even though the fungicides also suppressed other pathogens (which were observed at much lower levels than *S. tritici*) these numbers may serve as a first rough estimate of the difference in damage caused by an early epidemic as compared to a late epidemic.

Table 2
Leave-out-one cross validation. The year–location combination indicated in the first two columns was not included in the calculation of the average daily temperatures between 181 and 210 days after sowing (DAS). For each day of this period, the difference between the temperature of the case that was left out and the average temperature of the remaining cases that were followed by an early and a late epidemic was calculated separately and squared. The smaller the sum of square (SSQ) difference, the more similar was the left out case with temperature time courses preceeding either early or late epidemics (epi). We expected that the left out case will be followed by a late epidemic, if the SSQ difference towards the average temperatures of late epidemics is smaller as compared to early epidemics and *vice versa*. The expectation was compared with the observations and classified as either true or false.

Left out case		SSQ difference towards…		Expected	Observed	Classification
Location	Year	…Early epi	…Late epi			
Everlange	2004	503.1	**184.4**	L	L	True
Reuler	2004	494.2	**225.3**	L	L	True
Everlange	2005	587.0	**320.2**	L	E	False
Reuler	2005	818.5	**386.8**	L	L	True
Everlange	2006	564.9	**358.6**	L	E	False
Reuler	2006	686.2	**486.9**	L	L	True
Burmerange	2007	**443.8**	1185.4	E	E	True
Everlange	2007	**381.3**	987.2	E	E	True
Reuler	2007	**631.7**	834.3	E	E	True
Burmerange	2008	996.6	**305.9**	L	L	True
Everlange	2008	669.3	**203.2**	L	L	True
Reuler	2008	1030.1	**352.6**	L	L	True
Burmerange	2009	**307.4**	525.5	E	E	True
Everlange	2009	**293.8**	755.4	E	E	True
Reuler	2009	441.2	**433.0**	L	L	True
Burmerange	2010	581.9	**279.4**	L	L	True
Everlange	2010	462.5	**276.3**	L	L	True
Reuler	2010	972.6	**661.3**	L	L	True

For each case study, the smaller SSQ is highlighted in bold.

Assuming a latent period of approximately 20 days (Henze et al., 2007), fungicide applications targeting the period of infection should be applied around 225 DAS for the control of early epidemics and around 245 DAS for control of late epidemics. Usually, fungicide application is not recommended or allowed after growth stage 65 (anthesis), because (1) the damage caused by late epidemics is lower, and (2) there is not necessarily a sufficient pre-harvest interval. Growth stage 65 was observed between 209 and 258 DAS. In wheat stands where Fusarium head blight needs to be controlled, triazole application is often recommended between growth stages 61 and 65 and this application would also control late *S. tritici* epidemics.

Some standard spraying schedules recommend a spray at growth stage 39 (http://www.hgca.com/hgca/wdmg/Framesets/when2spray.htm), which corresponds to a range from 185 to 234 DAS in our study and falls partly into the time frame when the largest differences in air temperatures before early and late epidemics were observed (Fig. 4A). In the situations where a late epidemic occurs, a spray against *S. tritici* might not be necessary at growth stage 39, but might be applied later to match conditions favourable for disease development.

Even though differences between winter wheat genotypes concerning their leaf blotch susceptibility were shown and proposed for use in breeding programs (Czembor et al., 2011), we did not find a significant effect of the cultivar on T_{50} values. It should be noted, that the differences in susceptibility towards *S. tritici* were rather small (ranking of 4–6 on a 1–9 scale, Table 1) among the cultivars used here, probably too small to result in a significant difference.

Wiik and Ewaldz (2009) reported that precipitation in May was the factor most consistently related to leaf blotch disease intensity in Southern Sweden. The current work (Fig. 5A) did not allow an unambiguous separation of early and late epidemics based on precipitation data. Given previous reports on the importance of water for *S. tritici* infections (Mahtour et al., 2011), the point that a factor analysis was unable to separate early from late epidemics based on precipitation (Fig. 5A) or relative humidity (Fig. 5B) measurements recorded before epidemic outbreaks was surprising and deserves further analysis. Maybe a temporal resolution of one day is not sufficient to detect crucial effects of humidity.

Renfro and Young (1956) reported that infection failed when temperature was 7 °C or lower during a 2-day period post inoculation. More recently, Henze et al. (2007) observed no epidemic outbreaks at temperatures <6.6 °C around the time of infection. Cumulative temperature calculated with a base temperature of 6.6 °C starting at sowing and ending when T_{50} was reached were not significantly different between early and late epidemics ($P = 0.727$) and averaged 1721 ± 49 °days. Hence, approximately equal temperature sums were required for early and late epidemics in our study. The separation of early and late epidemics based on the factor scores extracted from average daily temperatures measured between 160 and 270 DAS (Fig. 5C) illustrates that spring temperatures contain enough information to account for the difference between early and late *S. tritici* epidemics in the wheat stands of Luxembourg.

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References

Beyer, M., Kiesner, F., Verreet, J.-A., Klink, H., 2011. Fungicide sensitivity of *Septoria tritici* field isolates is affected by an interaction between fungicidal mode of action and time. J. Plant Pathol. 93, S1.7–S1.13.

Burke, J., Dunne, B., April 2006. *Septoria tritici* in winter wheat – to spray or not to spray? Irish Farmers J., 14–18.

Burke, J., Dunne, B., 2008. Investigating the effectiveness of the Thies Clima "Septoria Timer" to schedule fungicide applications to control *Mycosphaerella graminicola* on winter wheat in Ireland. Crop Prot. 27, 710–718.

BSA, 2010. Beschreibende Sortenliste Getreide, Mais, Öl- und Faserpflanzen, Leguminosen, Rüben, Zwischenfrüchte. http://www.bundessortenamt.de/internet30/fileadmin/Files/PDF/bsl_getreide_2010.pdf (accessed 06.04.11.).

Chungu, C., Gilbert, J., Townley-Smith, F., 2001. *Septoria tritici* blotch development as affected by temperature, duration of leaf wetness, inoculum concentration, and host. Plant Dis. 85, 430–435.

Coakley, S.M., McDaniel, L.R., Shaner, G., 1985. Model for predicting severity of *Septoria tritici* blotch on winter wheat. Phytopathology 75, 1245–1251.

Cook, R.J., Polley, R.W., Thomas, M.R., 1991. Disease-induced losses in winter wheat in England and Wales 1985–1989. Crop Prot. 10, 504–508.

Czembor, P.C., Radecka-Janusik, M., Mańkowski, D., 2011. Virulence spectrum of *Mycosphaerella graminicola* isolates on wheat genotypes carrying known resistance genes to *Septoria tritici* blotch. J. Phytopathol. 159, 146–154.

El Jarroudi, M., Delfosse, P., Maraite, H., Hoffmann, L., Tychon, B., 2009. Assessing the accuracy of simulation model for Septoria leaf blotch disease progress on winter wheat. Plant Dis. 93, 983–992.

Eyal, Z., Scharen, A.L., Prescott, J.M., van Ginkel, M., 1987. The Septoria Diseases of Wheat: Concepts and Methods of Disease Management. CIMMYT, Mexico, D.F.

Gladders, P., Paveley, N., Barrie, I., Hardwick, N., Hims, M., Langton, S., Taylor, M., 2001. Agronomic and meteorologic factors affecting the severity of leaf blotch caused by *Mycosphaerella graminicola* in commercial wheat crops in England. Ann. App. Biol. 138, 301–311.

Henze, M., Beyer, M., Klink, H., Verreet, J.-A., 2007. Characterizing meteorological scenarios favorable for *Septoria tritici* infections in wheat and estimation of latent periods. Plant Dis. 91, 1445–1449.

Hunter, T., Coker, R.R., Royle, D.J., 1999. The teleomorph stage, *Mycosphaerella graminicola*, in epidemics of *Septoria tritici* blotch on winter wheat in the UK. Plant Pathol. 48, 51–57.

Magboul, A., Geng, S., Gilchrist, D., Jackson, L., 1992. Environmental influence on the infection of wheat by *Mycosphaerella graminicola*. Phytopathology 82, 1407–1413.

Mahtour, A., El Jarroudi, M., Delobbe, L., Hoffmann, L., Maraite, H., Tychon, B., 2011. Site-specific Septoria leaf blotch risk assessment in winter wheat using weather-radar rainfall estimates. Plant Dis. 95, 384–393.

Palmer, C.-L., Skinner, W., 2002. *Mycosphaerella graminicola*: latent infection, crop devastation and genomics. Mol. Plant Pathol. 3, 63–70.

Pietravalle, S., Shaw, M.W., Parker, S.R., van den Bosch, F., 2003. Modeling of relationships between weather and *Septoria tritici* epidemics on winter wheat: a critical approach. Phytopathology 93, 1329–1339.

Renfro, B.L., Young, H.C., 1956. Techniques for studying varietal response to Septoria leaf blotch of wheat. Phytopathology 46, 23–24.

Royle, D.J., Shaw, M.W., Cook, R.J., 1986. Patterns of development of *Septoria nodorum* and *S. tritici* in some winter wheat crops in western Europe, 1981–83. Plant Pathol. 35, 466–476.

Seck, M., Roelfs, A.P., Teng, P.S., 1991. Influence of leaf position on yield loss caused by wheat leaf rust in single tillers. Crop Prot. 10, 222–228.

Shaw, M.W., 1990. Effects of temperature, leaf wetness and cultivar on the latent period of *Mycosphaerella graminicola* on winter wheat. Plant Pathol. 39, 255–268.

Shaw, M.W., Royle, D.J., 1989. Airborne inoculum as a major source of *Septoria tritici* (*Mycosphaerella graminicola*) infections in winter wheat crops in the UK. Plant Pathol. 38, 35–43.

Thomas, M.R., Cook, R.J., King, J.E., 1989. Factors affecting development of *Septoria tritici* in winter wheat and its effect on yield. Plant Pathol. 38, 246–257.

Wiik, L., Ewaldz, T., 2009. Impact of temperature and precipitation on yield and plant diseases of winter wheat in southern Sweden 1983–2007. Crop Prot. 28, 952–962.

WMO, 1995. Publication No 3006. In: Manual on Codes, vol. I. International Codes, Secretariat of the World Meteorological Organization, Geneva Switzerland.

Zadoks, C., Chang, T.T., Konzak, C.F., 1974. A decimal code for the growth stages of cereals. Weed Res. 14, 415–421.

Ziv, O., Eyal, Z., 1978. Assessments of yield component losses caused in plants of spring wheat cultivars by selected isolates of *Septoria tritici*. Phytopathology 68, 791–796.