

Assessing plant health in a network of experiments on hardy winter wheat varieties in France: patterns of disease-climate associations

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Abstract A data set generated by a multi-year (2003–2010) and multi-site network of experiments on winter wheat varieties grown at different levels of crop management is analysed in order to assess the importance of climate on the variability of wheat health. Wheat health is represented by the multiple pathosystem involving five components: leaf rust, yellow rust, fusarium head blight, powdery mildew, and septoria tritici blotch. An overall framework of associations between multiple diseases and climate variables is developed. This framework involves disease levels in a binary form (i.e. epidemic vs. non-epidemic) and synthesis variables accounting for climate over spring and early summer. The multiple disease-climate pattern of associations of this framework conforms to disease-specific knowledge of climate effects on the components of the pathosystem. It also concurs with a

(climate-based) risk factor approach to wheat diseases. This report emphasizes the value of large scale data in crop health assessment and the usefulness of a risk factor approach for both tactical and strategic decisions for crop health management.

Keywords *Puccinia triticina* · *Puccinia striiformis* · *Fusarium graminearum* · *F. culmorum* · *F. avenaceum* · *Blumeria graminis* · *Zymoseptoria tritici* · Categorical data · Risk factor · Multiple pathosystem · Correspondence analysis · Logistic regression

Introduction

The variation and variability of importance in wheat diseases has been addressed in a very large number of studies and syntheses. Surveys of wheat diseases for instance have been conducted, especially in the UK (King 1977; Polley and Thomas 1991; Hardwick et al. 2001), the Netherlands (Daamen 1990; Daamen and Stol 1990, 1992, 1994; Daamen et al. 1991, 1992), and Sweden (Wiik and Ewaldz 2009). These studies examine the change in plant disease levels in response to a number of factors, especially to crop management, and notably use of chemicals. Although these surveys provide a wealth of critical information in examining these relations, information of climate effects on plant disease – in particular, on the overall crop health and multiple diseases – appears fragmented. Key references on wheat diseases, such as Roelfs and Bushnell (1985) and Bockus et al. (2010), provide overviews of climate-disease relations in different

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wheat-pathogen systems. These relations however are itemized on a pathosystem basis, and very seldom is an overview presented, where an analysis of the relationships between climatic conditions and crop health, incorporating multiple diseases, would be developed.

An earlier article has presented overall results from the analysis of a large data set generated from a network of experiments on winter wheat where a range of varieties were managed at several levels of crop management (Savary et al. 2016). A main conclusion from this work was that climatic years, wheat varieties, and crop management, in this decreasing order, define the levels of disease epidemic risks in the multiple wheat-disease pathosystem. This conclusion pertained to five winter wheat diseases: brown rust (BR, leaf rust) caused by *Puccinia triticina*, yellow rust (YR, stripe rust) caused by *Puccinia striiformis*, fusarium head blight (FHB, involving a complex of pathogens, including: *Fusarium graminearum*, *F. culmorum*, and *F. avenaceum*; Jennings et al. 2004; Nielsen et al. 2011), powdery mildew (PM) caused by *Blumeria graminis*, and septoria tritici blotch (STB) caused by *Zymoseptoria tritici* (Syn. *Septoria tritici*).

The objective of this report is three-fold: (1) to further assess the importance of climate on disease variability reflected in this data set; (2) to develop and examine an empirical synthesis of climate effects on the multiple pathosystem: [wheat - leaf rust - yellow rust - fusarium head blight - powdery mildew - septoria tritici blotch]; and (3) to assess the prospect of a risk factor approach on wheat health, represented by this multiple pathosystem.

Materials and methods

Network of field experiments

The network of experiments which generated the data analysed here is described in Savary et al. (2016). We summarize the information that especially pertains to the present study. A large network of field experiments has been established and conducted in France over several years, where a range of winter wheat varieties together with up to four levels of crop management were tested. Each experimental plot (15–68 m² in size) represented a given combination of variety by crop management, in various experimental (split-plot, randomized block, or strip-plot) designs with three to four replications.

The winter wheat varieties include cultivars with varying levels of partial resistances to diseases,

especially brown rust. Over the years, the winter wheat varieties involved in the experimental network have varied, some varieties being present over many successive years, others being tested for a limited number of years only. Experimental data pertaining to varieties cultivated for only one year at a limited number of locations were excluded from the data set. As in Savary et al. (2016), the present study involves data generated from experiments involving 45 winter wheat varieties.

The four levels of crop management correspond to four levels of (mostly chemical) extensification. A reference level is Crop Management 2 (CMGT2), which corresponds to conventional, site-specific, recommendations in terms of seeding rate, fertilizer inputs (especially nitrogen), growth regulators, and fungicide. CMGT1 corresponds to an intensified level, where only a technical, not an economic, reasoning is used to increase the fertilizer, crop growth regulators, and fungicide inputs. By contrast, CMGT3 represents an extensified level relative to CMGT2, where chemical inputs, as well as the seeding rate, are reduced according to both economic and technical considerations whereby a reduced wheat yield output is accepted. CMGT4 constitutes a further level of extensification relative to CMGT3, especially with respect to growth regulators, (nitrogen) fertilizer, and fungicides. In the context of the present study, two features of this experimental set-up are particularly important: (1) these levels of management do not correspond to the scaling up of successive levels of chemical protection against diseases, and do not include a ‘no protection’ and a ‘complete, full protection’ levels, and (2) these levels were devised at each site in accordance to local constraints and contexts (e.g., soils, crop rotations), and therefore led to a considerable degree of overlap between the four CMGT levels in terms of levels of inputs actually mobilized.

As in Savary et al. (2016), we report here analyses from 101 experiments conducted during eight successive years (2003–2010), corresponding to a total population of 3525 individual winter wheat plots.

Disease information

Disease data were collected over an extensive period of time (2003 to 2010) by a large community of collaborators. Disease assessments concerned five main winter wheat diseases: brown rust (BR, leaf rust), yellow rust (YR, stripe rust), fusarium head blight (FHB), powdery mildew (PM), and septoria tritici blotch (STB). The

disease data which were retained in this analysis (Savary et al. 2016) were collected from early booting to early grain filling, i.e., from development stage 45 to 85 (Zadoks et al. 1974). Disease assessment pertained to the plot level. In most experiments, foliar diseases (BR, YR, PM, and STB) were assessed as severity (proportion of leaf area infected). When foliar diseases were assessed as incidence (proportion of diseased leaves), disease incidence was converted as severity (I. Félix, unpublished; Savary et al. 2016). FHB was assessed at the plot level as disease incidence. Disease measurements were synthesized as disease intensities (disease severities for the foliage diseases and disease incidence for FHB), and the frequency distribution of disease intensities were analysed (Savary et al. 2016).

The very strongly asymmetric distribution frequencies of disease intensities (with a very large number of individual plots with no disease, some plots with low disease, and very few plots with high disease intensity) led to considering disease intensities in a binary form, i.e., above or below a given threshold (Savary et al. 2016). This threshold must be defined on the basis of actual distribution frequencies of disease intensity, in order to enable categorical data analyses (Savary et al. 1995). Categorization of disease information also allowed reducing data noise due to the long duration of the network of experiments, and to the different investigation groups involved in data collection (Savary et al. 2016). The disease intensity threshold t was defined as: $t = \text{mean} - 0.05 (s/\text{mean})$, where ‘mean’ is the arithmetic mean of disease intensity, and s is its standard deviation. The respective t values were: 0.102, 0.076, 0.663, 0.233, and 12.91 % for BR, YR, FHB, PM, and STB, respectively (Savary et al. 2016). Each disease may thus be considered in two classes (diseaseBIN = 0 or 1) each: BR0 and BR1, YR0 and YR1, FHB0 and FHB1, PM0 and PM1, and STB0 and STB1 for brown rust, yellow rust, fusarium head blight, powdery mildew, and septoria tritici blotch, respectively. These two classes are referred to as ‘non-epidemic’ and ‘epidemic’, respectively, in the following analyses.

Weather data

Owing to the very large number of experiments conducted at many different locations (some in research stations, but many in farmers’ fields), weather data for each experimental site - year were not recorded. We used the spatialized climatological database of Météo-France,

SAFRAN, which covers the 1970–2011 period and the entire French territory. Surface hourly weather variables available in SAFRAN are interpolated on an $8 \times 8 \text{ km}^2$ grid covering France with a mesoscale atmospheric analysis system (Durand et al. 2009). In their assessment of the reliability of this interpolated climatological data base, Quintana-Seguí et al. (2008) concluded that this interpolation system was robust. The trials were not georeferenced. The trials were located at most 50 km away from the nearest administrative centre. We therefore chose to represent the climatic conditions at each experimental site - year by daily climatic weather conditions at the nearest department administrative centre.

Disease assessments considered in the analysis were made in the late development of the crop, from early booting to early grain filling (Zadoks et al. 1974; Savary et al. 2016). Disease measurements at such late development stages presumably account well for the development of disease in the spring, but probably poorly account for disease development in the early phase of plant disease epidemics when primary inoculum comes into play, is mobilized, and initiates early disease levels. We developed synthesis climatic variables accounting for the latter part of the growing season, i.e. from March till the end of June. Each experimental site - year was represented by climatic summaries over these four months: Tn (mean of the daily minimum temperatures), Tx (mean of the daily maximum temperatures), RR (mean of daily rainfall), FRD (fraction of rainy days over the four-month period), RH (mean of the average daily relative humidity), and GR (mean daily radiation).

Analytical strategy and statistical methods

An initial stage in the analysis of the data consisted in characterizing the climatic environment of the network of experiments. This was achieved first through the graphical examination of variability of synthesis climatic variables over years. Second, a principal component analysis was conducted on the (standardized to unit variance) mean of the daily minimum and maximum temperatures (Tn and Tx), mean of daily rainfall (RR), and fraction of rainy days over the four-month period (FRD), considering each experimental site - year as one possible realization of the combination of these variables. These four synthesis climate variables (Tx, Tn, RR, FRD) pertaining to temperature and rainfall were chosen as they are the most commonly measured in weather stations and discussed in the literature in their

relations with wheat diseases. Outputs of the analysis were examined according to the successive years and French regions where experiments had been conducted.

Relationships between disease data in a binary form (non-epidemic vs. epidemic: diseaseBIN =0 or 1; BR0-BR1, YR0-YR1, FHB0-FHB1, PM0-PM1, and STB0-STB1) and the synthesis climatic variables were then examined. In a first stage, the synthesis climatic variables were converted in their quartiles (TxQUART, TnQUART, RRQUART, GRQUART, RHQUART, and FRDQUART). Contingency tables were then built, representing the joint frequency distributions between each (binary) disease variable and each synthesis climatic variable represented by its quartiles. The level of association between disease and climate variables was then assessed by the chi-square values associated with each of these (5 disease \times 6 climate variables =30) contingency tables.

Multiple correspondence analysis (Benzécri 1973; Greenacre 1984; Savary et al. 1995) was then used to synthesize and graphically display the multiple associations between the five diseases and climate variables, using a chi-square metric. Several multiple correspondence analyses were conducted. Strong associations among climate variables (e.g., between RR and FRD, represented here by their quartile conversions, RRQUART and FRDQUART) led many of the analyses performed to yield similar patterns of associations. Multiple correspondence analysis outputs were compared with respect to fraction inertia accounted for by axes and squared-cosines associated with variables (Benzécri 1973; Greenacre 1984; Savary et al. 1995). The multiple correspondence analysis which synthesized best the overall associations among climate variables, and which involved TxQuart, TnQUART, and RRQUART, was retained. This analysis is also in line with the former principal component analysis, which involves temperature and rainfall information.

In a last stage, binary logistic regression (Harrell 2001; Steinberg and Colla 2007; Savary et al. 2011) was used to analyse relationships between disease occurrence and synthesis climate variables. For each disease, the following model was used:

$$\ln \left[\frac{P(\text{diseaseBIN} = 1)}{1 - P(\text{diseaseBIN} = 1)} \right] = \alpha + \sum \beta_i \text{CLIM}_i$$

where diseaseBIN is a binarized disease intensity, with diseaseBIN =0 representing a non-epidemic and

diseaseBIN =1 representing an epidemic, CLIM_{*i*} is a vector (Tn, Tx, RR, GR, RH, and FRD) of continuous climate variables, α is a constant and β_i is a vector of parameters. In this phase of the analyses, each disease was considered separately, and the likelihood of occurrence of epidemic of a given disease was considered the outcome of the combination of the synthesis climate variables pertaining to each plot in each site-year, so that climate variables were considered as predictors of epidemic occurrence.

Results

Variation in climate over years and regions

An overview of the contrasts in climatic conditions among years is provided by Fig. 1. Figure 1 indicates large variation over years of the mean daily minimum (Tn) and maximum (Tx) temperatures over the period March–June. One may distinguish warm years such as years 2003 and 2007, which are associated with the highest median values of Tn; and years 2003, 2007, and 2009, which are associated with the highest median values of Tx. Cold years are 2004 and 2010, corresponding to the lowest Tn values; and years 2004, 2006, and 2008, when the lowest median values of Tx were observed. Large differences between years in average daily rainfall (RR) and frequency of rainy days (FRD) for the period March–June are also indicated: years 2007 and 2008 correspond to both the highest rainfall amounts and the highest frequencies of rainy days; and years 2003 and 2010 have the lowest frequency of rainy days.

Principal component analysis of climate variables at the locations and years corresponding to the network of experiments indicates correlations between temperature variables (Tx, Tn) and rainfall variables (RR, FRD). The latter are collinear to the first principal component, while the former are collinear to the second principal component, indicating independence of these two groups (Fig. 2a). The contrasting climatic conditions across growing seasons of the successive years are shown in Fig. 2b, where experimental sites - years are plotted and grouped by years. Figure 2b indicates that warm-rainy growing seasons (2007) are contrasted against dry-cold ones (2004, 2010). Some years (especially 2003, also 2009) show wide temperature variation (along the second, temperature-correlated, axis) and narrow

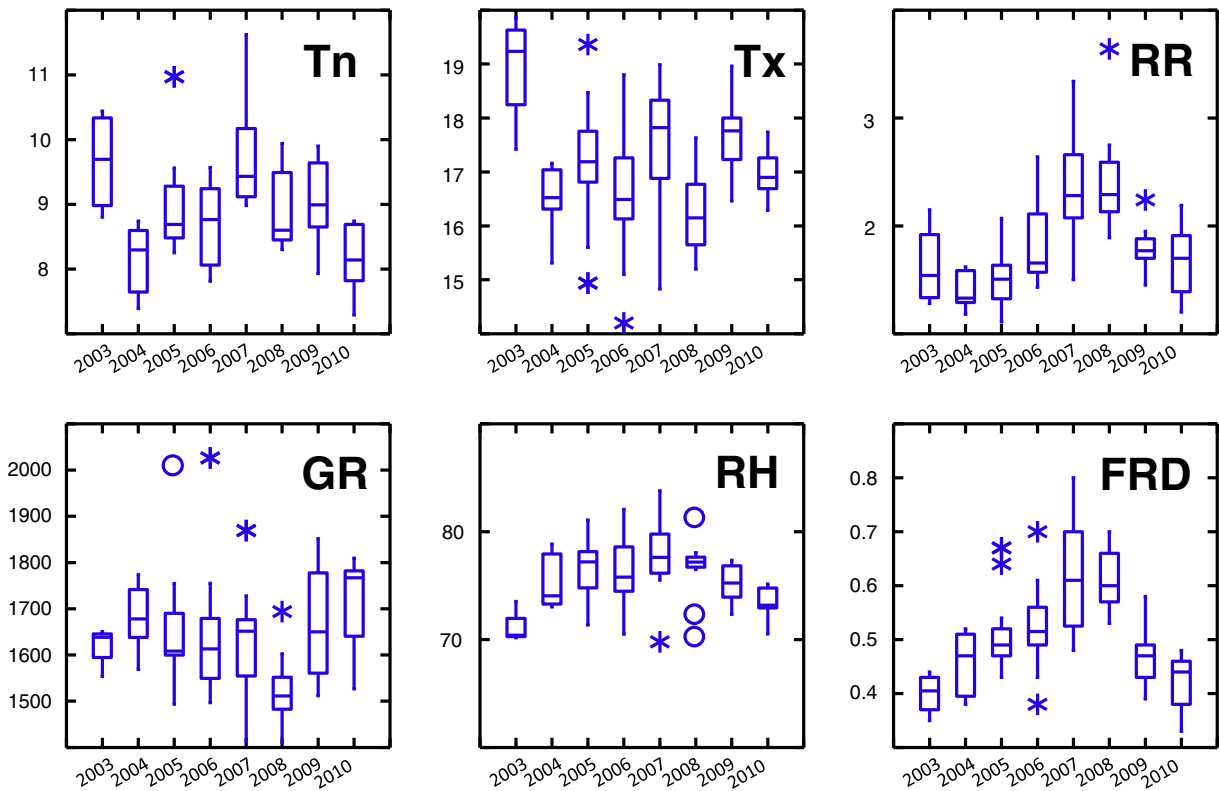


Fig. 1 Boxplots of the variations in daily minimum and maximum temperature, average daily rainfall, and proportion of rainy days over wheat growing seasons Tn: Mean daily minimum air temperature (°C); Tx: Mean daily maximum air temperature (°C); RR: Mean daily rainfall (mm); GR: Global radiation (kJ.m⁻²); RH: Relative humidity; FRD: Mean fraction of rainy days (no unit). The

period considered is March to June in each year from 2003 to 2010. Median values are shown as horizontal marks across boxes. Stars represent outside values, i.e., values within a 1.5 to 3.0 interquartile range from the box edge; open circles represent far-outside values, i.e., values beyond a 3.0 interquartile range from the box edge

rainfall levels (along the first, rainfall-correlated, axis). Experimental sites - years are shown again, but grouped by French regions, in Fig. 2c, where the overall contrasts are shown among growing regions, from rainy and cool regions (Bretagne) to colder (Normandie), to dryer and warmer (SudBP: South of Paris basin), and rainy and warm (Sud-Ouest).

Climate - multiple disease linkages: Chi-squares and multiple correspondence analysis

The levels of associations of climate variables with binary disease levels are shown in Table 1. All the chi-square values (with three degrees of freedom each) associated with paired climate and disease variables are significant ($P < 0.001$). Chi square values provide measures of the level of linkage between binary disease variables and climate variables represented by the quartiles of their distributions. Chi-square values involving

temperatures (TxQUART and TnQUART) are especially high with brown rust (BR: $\chi^2 = 1345.48$ and 599.56 , respectively), and also fusarium head blight (FHB: $\chi^2 = 117.75$ and 122.84). TnQUART is also strongly associated with PMBIN and STBIN. Mean daily rainfall (RRquart) is especially strongly associated with FHB ($\chi^2 = 1245.95$), and also with the binary levels of brown rust ($\chi^2 = 182.78$) and septoria tritici blotch (STB: $\chi^2 = 170.24$). Chi-square values involving daily global radiation (GR) broadly follow the combined patterns of associations that involve temperatures (Tx, Tn) and rainfall (RR), with strong associations of GR with BR, FHB, and STB; conversely, chi square values involving relative humidity (RH) are especially high in the case of BR ($\chi^2 = 239.53$) and FHB ($\chi^2 = 250.94$); and the chi-square values involving the fraction of rainy days (FRD; χ^2 especially high for BR, FHB, and also STB) match those associated with daily rainfall (RR) and temperatures (Tx and Tn).

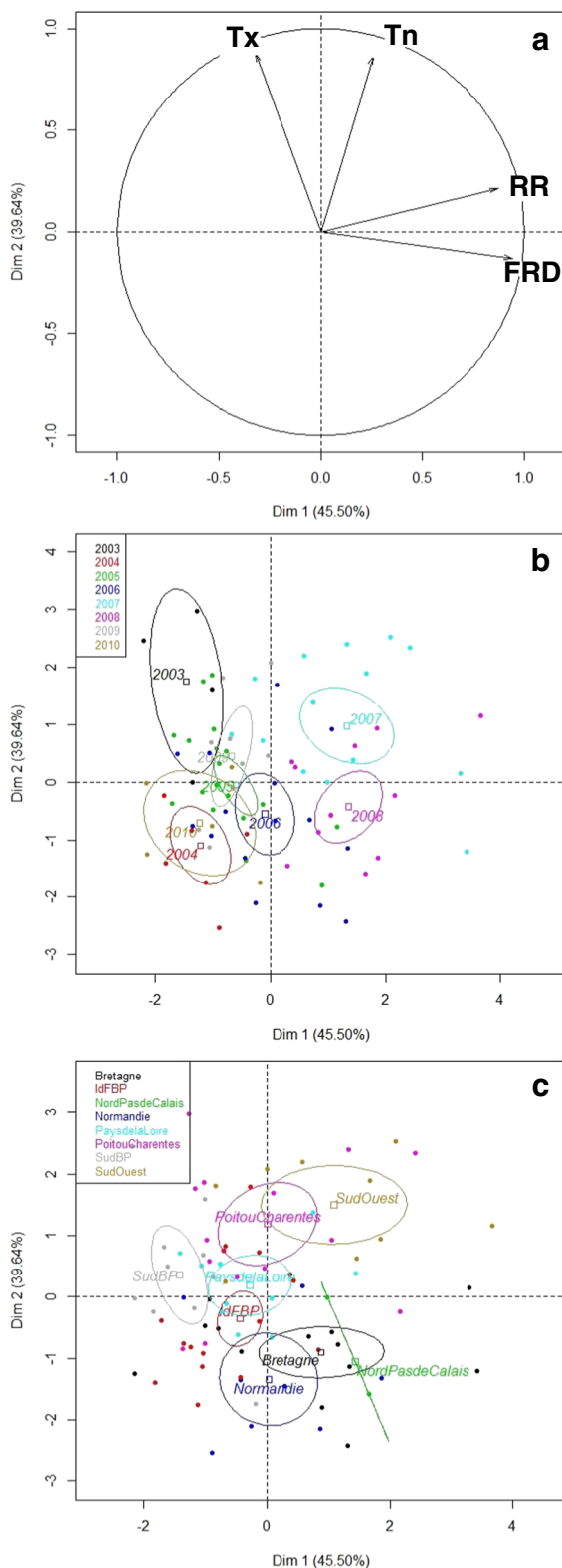


Fig. 2 Principal component analysis of weather data over the successive experimental years, 2003–2010, in a network of winter wheat experiments in France. Statistical units are individual location-years. **a** factor map of weather variables of the analysis. Tn, Tx, RR, and FRD are average daily minimum temperature, average daily maximum temperature, average daily rainfall, and average fraction of rainy days over the period March–June of each growing season, respectively. **b** Distribution of climatic years at the different locations-years (confidence ellipses around years, 95 %). **c** Distribution of regional weather patterns at the different location-years (confidence ellipses around French regions, 95 %)

Pair-wise distributional associations (i.e. contingency tables) provide the basis of correspondence analysis between climate and disease variables. Correspondence analysis generates a numerical and graphical synthesis of associations described in multiple contingency tables (Greenacre 1984). We report here outputs of only one of the correspondence analyses conducted since climate variables are strongly correlated; this analysis provides a summary of the patterns of associations found.

The graphical output of this analysis is shown in Fig. 3, where patterns of climatic conditions during a growing season are apparent. First, seasons with high rainfall (RR4) are opposed to growing seasons with low rainfall (RR1 and RR2) along the first diagonal of the graph; second, warm growing seasons (Tx4, Tn3, Tn4) are contrasted against cold ones (Tx1, Tn2) along the second diagonal. As a result, four quadrants, ‘rainy’, ‘cold’, ‘dry’, and ‘warm’ may be identified on the graph. Non-epidemics (BR0, YR0, FHB0, PM0, and STB0) are clustered at the origin of axes, indicating their predominant occurrence under average, neutral climatic conditions. By contrast, occurrence of brown rust (BR1) is strongly associated with warm temperatures (Tx4, Tn3); fusarium head blight (FHB1) is strongly associated with rainy (RR4) conditions; and yellow rust YR1 appears to correspond to colder (Tx1, Tn2) growing seasons. Occurrence of powdery mildew (PM1) appears associated with intermediate climate conditions, involving both rainy conditions, but not in the extreme, along the first diagonal (RR4 and RR3 vs. RR1 and RR2), and moderately warm conditions along the second diagonal (Tx4, Tn3, Tn4 vs. Tn2, Tx1). Occurrence of septoria tritici blotch (STB1) appears mostly associated with rainy conditions, irrespective of temperatures.

Table 2 provides the numerical background of the correspondence graph of Fig. 3. Interpretation of a correspondence analysis is based on the inertia of variable-

Table 1 Chi-square values of associations between climate variables and binarized disease levels

| Weather variable quartiles | BRBIN | YRBIN | FHBBIN | PMBIN | STBBIN |
|----------------------------|---------|-------|---------|--------|--------|
| TxQUART | 1345.48 | 38.13 | 117.75 | 47.16 | 99.65 |
| TnQUART | 599.56 | 56.05 | 122.84 | 161.60 | 171.67 |
| RRQUART | 182.78 | 64.78 | 1245.95 | 66.70 | 170.24 |
| GRQUART | 501.98 | 56.62 | 133.23 | 7.58 | 304.56 |
| RHQUART | 239.53 | 44.95 | 250.94 | 37.36 | 30.48 |
| FRDQUART | 300.61 | 42.21 | 456.43 | 85.60 | 165.82 |

Entries are values of chi-squares with: (2 disease levels – 1) x (4 weather variable quartiles – 1) = 3 degrees of freedom. All chi-squares are significant at $P < 0.001$

BRBIN, YRBIN, FHBBIN, PMBIN, STBBIN: Binarized levels (non-epidemic vs. epidemic) of brown rust (BR), yellow rust (YR), fusarium head blight (FHB), powdery mildew (PM), and septoria tritici blotch (STB), respectively

TxQUART, TnQUART, RRQUART, GRQUART, RHQUART, NBRQUART: quartiles of mean daily maximum temperature (Tx) over four months (March–June), of mean minimum daily temperature (Tn), of daily rainfall (RR), of daily global radiation (GR), of mean daily relative humidity (RH), and of average frequency of rainy days (FRD)

classes (i.e., their frequency), their coordinates along each generated axis, their contributions to axes (the fraction of axis inertia accounted for by each variable-class), and their reciprocal contributions to axes (or ‘squared cosines’, the fraction of inertia of each variable-class which is accounted by each of the generated axes). Only the two first axes of the analysis (which are used to plot the graph of Fig. 3) are discussed here, which represent 16.15 and 13.35 %, thus an accumulated 29.50 %, of the total inertia of the analysed data. Table 2 shows an even distribution of inertias among the successive classes of each climate variable, i.e., Tx1...Tx4, Tn1...Tn4, and RR1...RR4, reflecting the use of quartiles to represent their variation. This is not the case for disease variables in their binary form (disease-0 and disease-1) since these classes are defined on the frequency distributions of the intensity of each disease (Savary et al. 2016).

Direct contributions to axes indicate that, among the disease variables, brown rust (BR1) and to a lesser extent FHB (FHB1) and PM (PM1) contribute to defining axis 1 (horizontal), while FHB (FHB1) and STB (STB0 and STB1), and to a lesser extent BR (BR1), contribute to defining axis 2. Disease variables such as brown rust (BR0 and BR1) and fusarium head blight (FHB0 and FHB1) are associated with high reciprocal contributions of axes to the inertia of individual variable-classes (the accumulated reciprocal contributions over the two first axes are in the range of 0.50 to 0.60). This correspondence analysis thus accounts well for these binary variables (as 50 to 60 % of the inertia of each variable class is accounted for by the two first

axes). On the other hand, reciprocal contributions for STB0 and STB1 by the two first axes are moderate (0.166, or 16.6 % of the inertia accounted for), small for powdery mildew (PM0 and PM1), and the smallest for YR0 and YR1. Powdery mildew and yellow rust are

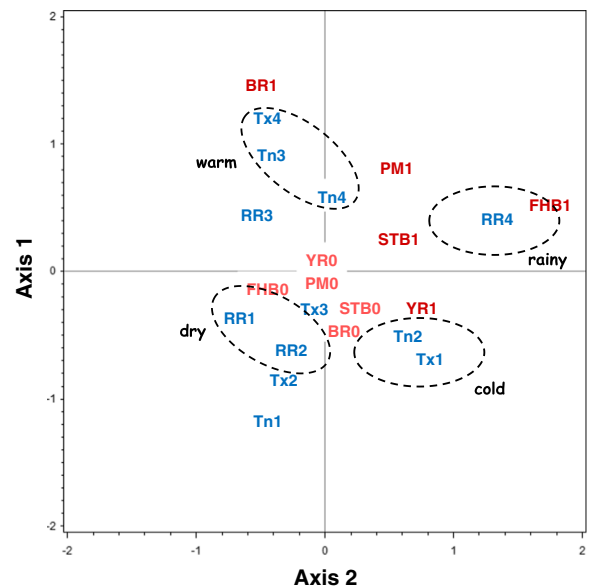


Fig. 3 Multiple correspondence analysis of binarized disease levels and quartiles of climate variables distributions. Binarized disease levels: non-epidemics (0) and epidemics (1) of brown rust (BR), yellow rust (YR), fusarium head blight (FHB), powdery mildew (PM) and septoria tritici blotch (STB). Successive quartiles of mean daily maximum (Tx) and minimum (Tn) temperature, and daily rainfall (RR) are indexed from 1 to 4. Axes 1 and 2 account for 16.15 and 13.35 % of total inertia, respectively. Dashed ellipses and comments (‘dry’, ‘rainy’, ‘warm’, ‘cold’) are the authors’ interpretations (see text)

Table 2 Multiple correspondence analysis of weather variables and binarized levels of diseases

| Variables (classes) | Inertia | Axis 1 (inertia: 16.15 %) | | | | Axis 2 (inertia: 13.35 %) | | |
|---------------------|---------|---------------------------|--------------|------------|------------|---------------------------|------------|--|
| | | Coordinate | Contribution | | Coordinate | Contribution | | |
| | | | To axis | Reciprocal | | To axis | Reciprocal | |
| Tx1 | 0.0536 | -0.61 | 0.041 | 0.122 | 0.81 | 0.086 | 0.215 | |
| Tx2 | 0.0562 | -0.77 | 0.056 | 0.160 | -0.31 | 0.011 | 0.026 | |
| Tx3 | 0.0525 | -0.14 | 0.002 | 0.007 | -0.06 | 0.001 | 0.002 | |
| Tx4 | 0.0519 | 1.28 | 0.199 | 0.620 | -0.43 | 0.027 | 0.070 | |
| Tn1 | 0.0542 | -1.17 | 0.145 | 0.432 | -0.42 | 0.023 | 0.056 | |
| Tn2 | 0.0534 | -0.42 | 0.020 | 0.059 | 0.70 | 0.067 | 0.166 | |
| Tn3 | 0.0539 | 0.93 | 0.094 | 0.282 | -0.37 | 0.019 | 0.046 | |
| Tn4 | 0.0528 | 0.61 | 0.043 | 0.130 | 0.06 | 0.001 | 0.001 | |
| RR1 | 0.0538 | -0.29 | 0.009 | 0.028 | -0.64 | 0.054 | 0.134 | |
| RR2 | 0.0536 | -0.65 | 0.046 | 0.140 | -0.25 | 0.008 | 0.021 | |
| RR3 | 0.0538 | 0.49 | 0.027 | 0.080 | -0.50 | 0.033 | 0.081 | |
| RR4 | 0.0532 | 0.44 | 0.022 | 0.066 | 1.34 | 0.247 | 0.619 | |
| BR0 | 0.0142 | -0.37 | 0.049 | 0.552 | 0.12 | 0.006 | 0.057 | |
| BR1 | 0.0572 | 1.49 | 0.196 | 0.552 | -0.48 | 0.024 | 0.057 | |
| YR0 | 0.0011 | 0.01 | 0.000 | 0.002 | -0.01 | 0.000 | 0.008 | |
| YR1 | 0.0703 | -0.34 | 0.001 | 0.002 | 0.73 | 0.004 | 0.008 | |
| FHB0 | 0.0102 | -0.09 | 0.003 | 0.049 | -0.30 | 0.043 | 0.560 | |
| FHB1 | 0.0613 | 0.54 | 0.018 | 0.049 | 1.84 | 0.257 | 0.560 | |
| PM0 | 0.0042 | -0.05 | 0.001 | 0.047 | -0.04 | 0.001 | 0.026 | |
| PM1 | 0.0672 | 0.87 | 0.020 | 0.047 | 0.64 | 0.013 | 0.026 | |
| STB0 | 0.0207 | -0.10 | 0.003 | 0.023 | -0.24 | 0.022 | 0.143 | |
| STB1 | 0.0507 | 0.23 | 0.007 | 0.023 | 0.59 | 0.054 | 0.143 | |

Variables are categories (classes) of the original quantitative variables. Disease variables are binarized disease levels, i.e., non-epidemics (0) vs. epidemic

Tx1–4, Tn1–4, RR1–4: quartiles of mean daily maximum temperature (Tx), of mean daily minimum temperature (Tn), and of daily rainfall (RR) over four months (March–June)

Contributions to axes are fractions of axis inertia (sum over contributions of variables to each axis = 1) that are accounted for by each individual variable (class)

Reciprocal contributions are fractions of variable (class) inertia that are accounted for by successive axes (sum over axes of successive relative contributions for each variable = 1)

actually better accounted for on axes other than axes 1 and 2, which are not shown in this analysis.

Risk analyses and logistic regressions

A logistic regression model was tested for each disease variable in turn, represented by their binary form: BRBIN, YRBIN, FHBBIN, PMBIN, and STBBIN. The analyses are synthesized in Table 3. All models are associated with significant ($P < 0.001$) likelihood ratios. The area under the Receiver Operating

Characteristic (ROC) curve was computed for each model and used to assess their predictive ability (Harrell 2001). Areas under the ROC values were close to 1 in the case of brown rust, fusarium head blight, and powdery mildew, but smaller in the case of yellow rust and septoria tritici blotch.

One important outcome of logistic regression is the derivation of estimates of risk factors (Harrell 2001; Savary et al. 2011), which correspond to the β_i coefficients of the tested logistic model. Furthermore, the odds ratio, computed as $\exp(\beta_i)$, corresponds to the change in

Table 3 Logistic regressions of the likelihood of epidemic occurrences with weather variables as predictors

| Variable | Number of cases with BIN = 1 | Likelihood Ratio | | Area under ROC Curve | Parameter Statistics by Weather Variable | | | | |
|----------|------------------------------|------------------|--------|----------------------|--|----------|-------|--------|-------------------|
| | | LR | P | | Parameter | Estimate | SE | P | Odds ratio |
| BRBIN | 719 | -1075 | <0.001 | 0.909 | Constant | -58.757 | 2.824 | <0.001 | 10 ⁻²⁶ |
| | | | | | Tn | -0.024 | 0.993 | 0.08 | 0.98 |
| | | | | | Tx | 2.567 | 0.116 | <0.001 | 13.03 |
| | | | | | RR | -1.275 | 0.199 | <0.001 | 0.28 |
| | | | | | GR | -0.002 | 0.001 | 0.001 | 1.00 |
| | | | | | RH | 0.183 | 0.027 | <0.001 | 1.20 |
| | | | | | FRD | 0.084 | 0.012 | <0.001 | 1.09 |
| YRBIN | 55 | -256 | <0.001 | 0.787 | Constant | 18.754 | 6.106 | 0.002 | 10 ⁸ |
| | | | | | Tn | 0.057 | 0.279 | 0.837 | 1.06 |
| | | | | | Tx | -0.427 | 0.279 | 0.125 | 0.65 |
| | | | | | RR | 0.686 | 0.468 | 0.143 | 1.99 |
| | | | | | GR | -0.004 | 0.002 | 0.029 | 1.00 |
| | | | | | RH | -0.186 | 0.073 | 0.011 | 0.83 |
| | | | | | FRD | 0.042 | 0.034 | 0.218 | 1.04 |
| FHBBIN | 515 | -1191 | <0.001 | 0.849 | Constant | -0.45 | 2.319 | 0.846 | 0.64 |
| | | | | | Tn | -0.86 | 0.121 | <0.001 | 0.42 |
| | | | | | Tx | 0.812 | 0.111 | <0.001 | 2.25 |
| | | | | | RR | 2.223 | 0.196 | <0.001 | 9.23 |
| | | | | | GR | -0.002 | 0.001 | 0.008 | 1.00 |
| | | | | | RH | -0.178 | 0.029 | <0.001 | 0.84 |
| | | | | | FRD | 0.067 | 0.012 | <0.001 | 1.07 |
| PMBIN | 215 | -618 | <0.001 | 0.836 | Constant | -52.194 | 3.899 | <0.001 | 10 ⁻²³ |
| | | | | | Tn | 0.854 | 0.12 | <0.001 | 2.35 |
| | | | | | Tx | 0.178 | 0.14 | 0.204 | 1.19 |
| | | | | | RR | -1.206 | 0.271 | <0.001 | 0.30 |
| | | | | | GR | 0.008 | 0.001 | <0.001 | 1.01 |
| | | | | | RH | 0.35 | 0.04 | <0.001 | 1.42 |
| | | | | | FRD | 0.021 | 0.015 | 0.158 | 1.02 |
| STBBIN | 1052 | -2058 | <0.001 | 0.659 | Constant | 8.919 | 1.625 | <0.001 | 7472 |
| | | | | | Tn | -0.101 | 0.07 | 0.151 | 0.90 |
| | | | | | Tx | -0.035 | 0.072 | 0.625 | 0.97 |
| | | | | | RR | 0.454 | 0.136 | 0.001 | 1.57 |
| | | | | | GR | -0.001 | 0 | 0.031 | 1.00 |
| | | | | | RH | -0.142 | 0.019 | <0.001 | 0.87 |
| | | | | | FRD | 0.051 | 0.008 | <0.001 | 1.05 |

Variables: BRBIN, YRBIN, FHBBIN, PMBIN, STBBIN: Binarized levels (non-epidemic vs. epidemic) of brown rust (BR), yellow rust (YR), fusarium head blight (FHB), powdery mildew (PM), and septoria tritici blotch (STB), respectively

Parameters: mean over four months (March–June) of daily minimum temperature (Tn), of mean maximum daily temperature (Tx), of daily rainfall (RR), of daily global radiation (GR), of mean daily relative humidity (RH), and of average frequency of rainy days (FRD)

the odds of an epidemic occurring per unit change in X_i , the corresponding predictor (Harrell 2001). Large positive values of β_i and of the associated odds ratio

correspond to a strong, positive relationship between the predictor and the occurrence of an epidemic, while large negative values of β_i and odds ratio close to 0

correspond to a strong, negative relationship between the predictor and the occurrence of an epidemic.

In the case of brown rust, Table 3 indicates that all the predictors considered have significant ($P < 0.01$) contributions to the odds of an epidemic occurring, except the mean daily minimum temperature (Tn): Tx (mean daily maximum temperature), RH (mean relative humidity), and FRD (fraction of rainy days) are positively associated with increased odds, whereas RR (mean daily rainfall) and GR (global radiation) are negatively associated with increased odds of epidemic occurrence. By contrast, only two significant ($P < 0.05$) predictors, GR and RH, were identified in the case of yellow rust, both with negative association with the odds of epidemic occurrence. In the case of fusarium head blight a number of significant ($P < 0.01$) predictors were found, Tx, RR, and FRD having positive, and Tn, GR, and RH having negative associations with increased odds of FHB epidemics. Four predictors were identified in the case of powdery mildew: Tn, GR, and RH, with positive associations, and RR with a negative association with the occurrence of PM epidemics. In the case of septoria tritici blotch, four predictors ($P < 0.05$) were found, RR and FRD with positive, and GR and RH with negative contributions to the odds of STB epidemics occurrence.

Table 3 provides parameters for logistic models of the relative odds of epidemic occurrence for five wheat diseases. Comparison of the absolute value of parameters within a logistic model, and between models, in

Table 3 is however rendered difficult by the differences in dimensions among the predictor variables (Tn, Tx, RR, GR, RH, and FRD). To facilitate comparison of the effects of different predictors on the same disease, and compare the effects of the same predictor across different diseases, Fig. 4 provides corrected odds ratios (corOR), which were first computed according to the range of the variables (Harrell 2001), and which, when smaller than 1, were transformed as $1/\text{corOR}$ to represent odds of non-epidemics. In Fig. 4, factors positively associated with epidemics are shown in red (dark red when $P < 0.01$), and factors negatively associated with epidemics (positively associated with non-epidemics) are shown in blue (dark blue when $P < 0.01$). Figure 4 points at the strong effect of high maximum temperature (Tx), associated with high relative humidity (RH) and high fraction of rainy days (FRD), on the likelihood of BR epidemics; high rainfall (RR), and to some extent, high global radiation (GR), are by contrast associated with non-epidemics. Only two risk factors emerge in the case of YR, both in a negative association with the odds of yellow rust epidemics: high global radiation (GR) and high relative humidity (RH) are associated with non-epidemics; among the other climate variables one notes the negative effect of high maximum temperatures (Tx), and the positive effects of high rainfall (RR) and frequent rainy days (FRD) on the odds of yellow rust epidemics, but in this case $P > 0.01$. Three risk factors are positively associated with the odds of FHB: Tx, RR, and FRD, and three risk factors are negatively

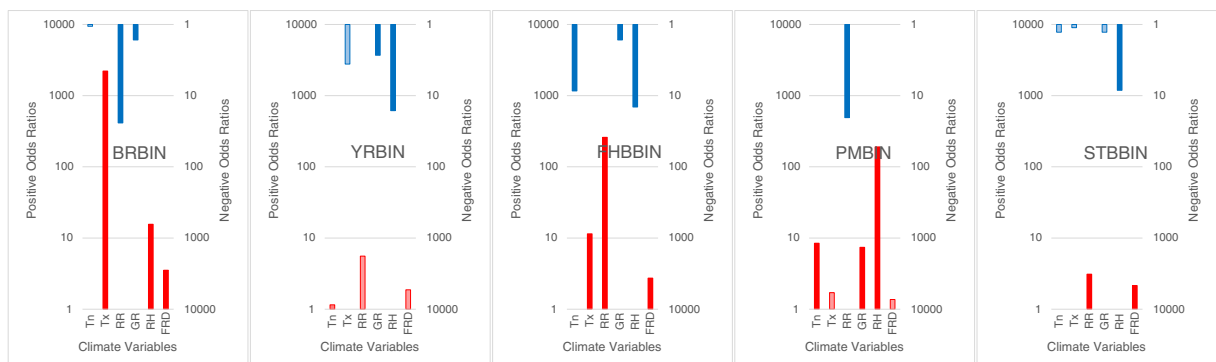


Fig. 4 Bar chart of odds ratios of climate risk factors of wheat diseases corrected for their distributional ranges. Disease risks are binarized (epidemic vs. non-epidemic) levels of brown rust (BRBIN), yellow rust (YRBIN), fusarium head blight (FHB), powdery mildew (PMBIN), and septoria tritici blotch (STB). Parameters for predictors in logistic regressions are plotted as vertical bars on logarithmic scales. Parameters with positive effects are plotted from bottom to top (*left axis*); Parameters with negative

effects are plotted from top to bottom (*right axis*). To facilitate comparison of the effects of different predictors, corrected odds ratios (corOR) were first computed according to the range of the variables (Harrell 2001). Second, corrected odds ratios were transformed as $1/\text{corOR}_i$ when they were below 1, to represent odds of non-epidemics. Dark bars indicate probability of a predictor being significant $P < 0.01$; Hued bars indicate $P > 0.01$

associated with these odds: Tn and RH, and to some extent GR. Three risk factors are associated with the odds of powdery mildew epidemics: Tn, GR, and RH, and RR is one factor opposed to these odds. Lastly, high rainfall (RR) and high fraction of rainy days (FRD) are risk factors positively and significantly associated with STB epidemics, whereas high RH is opposed to this association.

Discussion

Overall climate - multiple disease patterns

Correspondence analysis generates a very general image of the relationships of wheat diseases with climate. According to Fig. 3, brown rust is associated with warm, fairly rainy growing seasons; Yellow rust corresponds to cool seasons and very variable rainfall patterns; Fusarium head blight is associated with rainy growing seasons and variable temperatures; Powdery mildew corresponds to fairly warm and rainy conditions; and septoria tritici blotch is associated to rainy rather than dry conditions.

Such a picture broadly conforms with the large body of literature on the topic. Brown rust is well-adapted to warm conditions, with, for instance, (1) a high (26 °C) optimum temperature for its latency period duration (Eversmeyer et al. 1980), and (2) a very broad temperature range for spore germination (0 to 32 °C; Tollenaar 1985) as well as for infection (5 to 25 °C; Tomerlin et al. 1983; de Vallavieille-Pope et al. 1995). Brown rust also requires moisture to accomplish its cycle (e.g., 4–6 h of moisture for infection to take place), a requirement which is shared by yellow rust (de Vallavieille-Pope et al. 1995). Yellow rust has been widely reported as a pathogen of cool environments (Rapilly 1979). Threshold (minimal and maximal) temperatures for spore germination of *P. striiformis* have been reported to be 5 and 20 °C (optimum 15 °C; Clifford and Harris 1981); infection has been associated with a narrow (5 to 12 °C) temperature range (de Vallavieille-Pope et al. 1995); and a wide range of temperatures where the latency period duration is moderately affected has been reported (latency period of 10–14 days between 13 and 23 °C; Tollenaar and Houston 1967). By contrast, Fusarium head blight has been widely associated with humid conditions (Kriss et al. 2010; Shah et al. 2013, 2014), with markers such as relative humidity and

various measures of moisture or wetness clearly associated with increased disease. Sudden daily variation in relative humidity (sharp increases at the end of the day) has been reported to trigger ascospore liberation in FHB (Paulitz 1996). Consideration of relative humidity brings about temperature variation, in addition to rainfall, among the main climatic factors of this disease (Parry et al. 1995). Figure 3 indicates that occurrence of FHB is at the same (chi-square) distance from Tx1 and Tn2, on the one hand, and Tn4, on the other, and therefore this output does not specifically point at high temperatures associated with FHB. The factorial map of Fig. 3, which only accounts for $16.15 + 13.35 = 29.50\%$ of total inertia, is necessarily incomplete. The climatic factors associated with powdery mildew in wheat have comparatively been less studied in detailed experiments. The analysis by Te Beest et al. (2008) points at humid, rainy, and fairly warm conditions in spring and early summer favouring powdery mildew, in agreement with Fig. 3. By contrast, Daamen et al. (1992) emphasise the erratic behaviour of powdery mildew in the growing season, much in contrast with its predictability from the preceding autumn and winter temperatures. The critical role of moisture and rain in the spore wash-off from the canopy, spore survival prior to liberation, and infection efficiency is quantitatively documented in the detailed simulation model by Rossi and Giosuè (2003). Regarding septoria tritici blotch, Fig. 3 is suggestive only on the non-association of STB with dry conditions. There are many references in the literature on the linkages of STB with rainfall (e.g., Holmes and Colhoun 1974; Shaner and Finney 1976). By contrast with yellow rust, the response of STB appears less sensitive to temperature in its monocycle (Wainshilbaum and Lipps 1991).

Logistic regression and risk factors for individual wheat diseases

Logistic regressions (Table 3, Fig. 4) further document climate associations with wheat diseases. These results broadly concur with the many reports on the effects of climate variables during the growing season on wheat diseases, which were briefly summarized above. These results may also suggest in some cases specific characteristics of the considered disease cycles. For instance, the contrasting associations of Tx (positive) and Tn (negative) with the odds ratios of an FHB epidemic occurrence, together with the associations of moisture

variables (RR, RH, FRD), may reflect daily characteristics favouring disease development. Similarly, STB epidemics are associated with increased (RR), and more frequent (FRD) rainfall, but not with increased (mean) relative humidity (RH). Mean daily relative humidity cannot account for the effects of daily variation (minimum or maximum) in relative humidity on STB. However, a high mean daily relative humidity does account for both high maximum and high minimum relative humidity in a day. This analysis thus does not lead to associating humid days (minimum and maximum) with STB. Only two risk factors are found for yellow rust, possibly reflecting: (1) the existence of far more important determinants of disease than climate in the case of yellow rust – the data set incorporates observations on a range of different varieties, (2) the importance of climate factors affecting yellow rust epidemics in the preceding autumn and winter, and (3) the fact that very few (55) cases of epidemics were considered in a population of 3525 observations.

Shifts in population structures

The data analysed in this work were collected in the last years preceding important transitions in population structures of *Puccinia striiformis* in many parts of the world, including Europe (Milus et al. 2009; Hovmøller et al. 2011; Ali et al. 2014) and France (Sørensen et al. 2014). New strains of the pathogen present striking differences with the previously existing ones, including an adaptation to warmer conditions (Hovmøller et al. 2011). Had this analysis been conducted on more recent data, the positioning of yellow rust in Fig. 3, as well as the risk factors associated with the disease, might have been different.

Better addressing the early stages of plant disease epidemics

The core of the disease information available in the analysed data set is constituted by assessments at the late stages of crop development. This information is necessary to inform on the status of disease, but the absence of disease information at an early stage of crop development (e.g., tillering) precludes the incorporation of factors which might have played an important role in the early stage of disease epidemics. Much of the epidemiological literature emphasises this early stage, since the survival, mobilization, and early multiplication of

the primary inoculum may have strong bearings on the ensuing dynamics (Savary 2014). This has been particularly documented in the case of yellow rust epidemics (Coakley and Line 1981), which are favoured by mild winters, enabling the primary inoculum to survive (Hovmøller 2001; Gladders et al. 2007). Winter conditions appear to also affect the survival of the primary inoculum of brown rust (Eversmeyer and Kramer 1998) and septoria tritici blotch (Suffert et al. 2011). Further, Daamen et al. (1992) also identified a series of climate factors (warm autumns and winter enabling inoculum survival; warm spring allowing its mobilisation) that influence powdery mildew epidemics.

Categorical information, synthesis climate variables, and binarized disease data

In these analyses, we: (1) chose to use synthesis climatic variables, (2) pertaining only to spring and summer (March–June), in line with the late development stages when disease data were available, and (3) opted to compact the available disease intensity information in a binary form. Each disease epidemic in an individual plot was thus represented by a single binary disease measure, and a vector of simplified climate variables. In the process, many potentially important elements of the relationships between climatic conditions and disease development were excluded from the study, such as the effects of climate on the early stage of disease development, and also the accumulated effects of climate on disease epidemics, in interaction with crop growth.

The categorization of disease data made use of distribution-dependent, and therefore disease-dependent, thresholds. As a result, these thresholds distinguished near-absence from any level of disease (in the case of yellow rust and powdery mildew), very low levels of disease from any higher disease level (in the case of brown rust and fusarium head blight), and low disease levels from higher levels (in the case of septoria tritici blotch). For convenience, these levels have been referred to in binary form as ‘non-epidemic’ and ‘epidemic’, despite the fact that they may represent quite different stages in the course of an epidemic: STB0 includes some plots where the early stages of a septoria tritici blotch epidemic had taken place, while this is not the case for yellow rust in plots categorized as YR0. Caution therefore is necessary in interpreting results across diseases.

Despite this simplified approach, correspondence analysis leads to fairly interpretable results that are broadly in accordance with the known behaviour of the considered diseases with varying climatic conditions. The logistic models of Table 3 agree with the correspondence analysis and its supporting chi-squares (Table 1). These models actually involve many climate variables in four cases (brown rust, fusarium head blight, powdery mildew, and septoria tritici blotch); only in the case of yellow rust are only two climatic variables identified significantly.

These results indicate the value of such large scale data. They are encouraging in indicating that the approach used here might generate far more applicable results, should more precise disease data be available. Disease progress may be represented through several attributes (Kranz 1988; Campbell and Madden 1990; Madden et al. 2007): date of onset, maximum intensity, successive disease levels at pre-set development stages, and area under progress curve, for example. The availability of measurement of disease intensity at multiple stages in the crop development would certainly improve the quality of analyses, and enable distinguishing factors that are associated: first, with disease establishment, and then, with disease intensification, which are essential to understand disease dynamics and their management.

Plant health and risk factors

Plant health is a fuzzy term (Döring et al. 2012), which we operationalized here, perhaps in a narrow, but tractable, manner, as the collection of main diseases occurring on a crop in a given geographical and temporal space. We believe that a risk factor approach is especially suited to address crop health.

Risk factor approaches have been followed to address individual wheat diseases, such as yellow rust and powdery mildew (Te Beest et al. 2008), or septoria tritici blotch (Te Beest et al. 2009). These studies address individual diseases with fairly detailed climatic variables. A hierarchical risk factor approach that addresses crop health as a whole, involving multiple diseases, has seldom been used in plant pathology (e.g., Savary et al. 2011). Yet, risk factor analysis is a key instrument, for instance in public health (Lim et al. 2012): (1) to address multiple environmental factors influencing diseases, (2) which may be infectious or non-infectious, and (3) to generate hierarchies on the respective influences of these factors. This can have

applications to tactical (within season) disease management, but also strategic management through control instruments that require careful deployment over space (regions, landscapes) and time (successive seasons) such as host plant resistances, and also implications for the definition of crop health policies. Addressing simultaneously the entire set of plant diseases in a risk factor approach carries great promises in quantifying risk hierarchies and priorities for crop health management.

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