Characterization of leaf rust progress in wheat cultivars with different resistance levels and sowing dates

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Abstract A better understanding of leaf rust progress curves is highly desired by wheat breeders and pathologists to achieve more precise and ambitious predictors of disease development. High variations in leaf rust progress across different wheat cropping systems can cause difficulties and uncertainties for study of disease increase rate. A number of standard curves were fitted to a four-season data set on leaf rust severity ratings to find further descriptive disease curve elements for wheat cultivars under different sowing dates. A Gaussian model provided the best fitted parameters to be considered as wheat leaf rust progress curve elements. According to *H*-test results, sowing date and cultivar resistance factors significantly affected the area under disease progress curve (AUDPC), maximum disease severity, and Gaussian parameters *m* and *s*. Multivariate analysis indicated considerable association among AUDPC, leaf rust onset, maximum disease severity, and three Gaussian parameters. With this new proposed approach, a better understanding of the variables to be measured for estimating wheat leaf rust development will be obtained.

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Introduction

Leaf rust caused by *Puccinia recondita* f. sp. *tritici* has been known as a devastating disease in wheat crops grown worldwide. Exposure of crops to conducive agro-ecological conditions can result in the development of severe leaf rust epidemics in susceptible wheat cultivars. For instance, based on the plot-scale research conducted in Kermanshah province, Iran (Naseri and Sasani 2020), the variables of disease onset time, maturity date, mean six-monthly (autumn-winter) temperature, number of days (autumn-winter-spring) with minimum temperatures within the range of 5–25 °C and maximum RH > 60%, resistance index, and sowing time explained 74% of variations in the area under disease progress curve (AUDPC) data of leaf rust in wheat. Although the tools of comparative epidemiology of wheat rusts are a powerful means of improving the accuracy, efficiency and sustainability of disease management programs (Jeger 2004; Kranz and Rotem 2012; Naseri and Marefat 2019; Naseri and Sasani 2020), characterization of leaf rust progress curves in wheat crop needs further consideration.

Most earlier studies focused on comparing the progression of leaf rust epidemics according to final disease severity, apparent infection rate, latent period, and the area under the disease progress curve (AUDPC) for slow-rusting resistance (Jeger and Viljanen-Rollinson 2001). Subba Rao et al. (1990) reported the fitting of a logistic model to the spatiotemporal spread of wheat leaf rust on a susceptible cultivar over two growing seasons in Louisiana. In another study, Franke et al. (2009)

described and quantified spatiotemporal dynamics of leaf rust and powdery mildew in susceptible wheat cultivars at the plot scale. In India, a weather-based prediction model was developed to estimate leaf rust severity in wheat according to the maximum air temperature recorded at four study sites (Kumar 2014). Based on the RUSTDEP model, Rossi et al. (1997) developed a logistic model for the progression of leaf rust epidemics in winter wheat using at least 15 disease variables including leaf area with latent infections, daily increase of rusted leaf area, infection efficiency of uredospores, eruption rate of uredia, and germination of uredospores on leaves. The RUSTDEP model was developed on the basis of a logistic model, which has been reported as the best simulator for the progression of stripe rust in winter wheat (Yang et al. 1991). In the EPIWHEAT model, Savary et al. (2015) considered AUDPC, infection rate, leaf rust severity, latent period, lesion expansion rate and a number of agronomic and environmental indicators to predict occurrence of severe disease epidemics in wheat. However, the involvement of many indicators of leaf rust occurrence and development in the above-mentioned models can lower the wide applicability of disease progress and prediction models because of the difficult and time-consuming assessments. Moreover, an increased number of descriptors in a regression-based prediction model can reduce the predictive ability of the model due to interrelationships among excessive numbers of variables (Pietravalle et al. 2003). It is also believed that the selection of relevant variables from a large set of variables in multiple regression models needs reconsideration. Hence, Luo (2008) advised that the number of predictive variables to be selected for final regression models should be based on principal component analyses (PCA) in order to reduce the number of variables. Kranz (1974) also selected improved disease progress curve elements across 40 different plant-pathogen pathosystems examined over 2 years using PCA tests. However, the significance and strength of associations among common leaf-rust progress curve elements is still little understood. Such information is required to improve the accuracy of disease measurements for wheat breeding, yield-loss estimation, efficient disease control measures, and prediction of leaf rust epidemics. Furthermore, an improved understanding of wheat rust dynamics could be attained by greater attention to disease heterogeneity by involving further effective agro-ecological variables in epidemiological studies (Naseri and Marefat 2019). Kranz

(2003) attributed the strength of association between a curve element and disease progress to the degree of heterogeneity within curve elements. Therefore, attempts were made to explore how accurately leaf rust curve elements described disease dynamics in wheat cultivars differing in disease-resistance levels, and planting and maturity dates.

Materials and methods

Experimental data collection

During the four growing seasons (2013–2017), leaf rust onset and disease progress in winter wheat were studied in experimental plots at Islamabad Research Station (latitude 34°7′ north, longitude 46°28′ east). The study area has a cool temperate climate with average annual rainfall and temperature of 479.8 mm and 13.7 °C, respectively. The size of experimental plots varied within a 6–24 m^2 range over the study years to deal with difficulties in plot management. The experimental design was a split-plot with three replicates for each of four sowing dates as the main experimental treatments. The treatments consisted of four different sowing dates (early fall, mid-fall, late fall, and early winter) and eight wheat cultivars (Bahar, Baharan, Chamran II, Parsi, Pishgam, Pishtaz, Sirwan, and Sivand). The experimental plots were sown on the following dates: October 10, November 7, December 3 and 31 in 2013; October 12, November 14, and December 19 in 2014; October 27, December 13 and 30 in 2015; and October 11, November 15, December 11, and January 5 in 2016. Cultivars (sub-plot treatment in the experimental design) were representative genotypes currently grown in major wheat-growing regions of Iran. These eight bread wheat cultivars, originating from the breeding program of the Seed and Plant Improvement Institute, Karaj, Iran, were: Bahar (pedigree ICW84–0008-013AP-300 L-3AP-300 L-0AP), Baharan (pedigree KAUZ/PASTOR//PBW343), Chamran II (pedigree Attila50Y//Attila/Bacanora), Parsi (pedigree Dove"s"/Buc"s"//2*Darab), Pishgam (pedigree Bkt/90-Zhong87), Pishtaz (pedigree Alvand//Aldan/Ias58), Sirwan (pedigree PRL/2*PASTOR), and Sivand (pedigree KAUZ"s"/Azadiakd). The experimental design significantly improved the within- and over-season heterogeneity of leaf rust development across the experimental plots. The study field plots were not treated with fungicides so that the

progression of wheat leaf rust could be assessed properly. All agronomic practices (irrigation, fertilizer application, and weed control) were followed as per the standard recommendations for growing irrigated wheat in western Iran. The experimental plots were fertilized with urea 225 kg/ha and superphosphate 50 kg/ha, irrigated by a sprinkler system at 7–10 days intervals, and hand-weeded.

The onset of leaf rust was detected by observing the first appearance of leaf rust pustules in each study plot. The two categories of the early (before mid-spring) and late (after mid-spring) leaf rust onset were defined in this disease descriptor. From an epidemiological viewpoint, early leaf rust onset is one of the prerequisites for the development of severe epidemics in wheat crop under prevailing agro-ecological conditions in Kermanshah (Naseri and Sharifi 2019). The severity of leaf rust was recorded at 7–10 days intervals from the flag leaf stage (early May) to leaf yellowing (mid-June). The disease severity was rated as the percentage of leaf area showing rust pustules on the top three leaves of 3–5 randomly selected plants per plot.

Curve elements & statistical methods

The development of wheat leaf rust across 282 experimental plots (72 in 2014, 63 in 2015, 63 in 2016, and 84 in 2017) was described by six indicators describing the disease progress curves: (1) disease onset defined as the date of the first appearance of brown pustules on the leaf; (2) AUDPC determined using disease severity ratings over time (Jeger and Viljanen-Rollinson 2001; Madden and Nutter 1995); (3) maximum disease severity defined as the highest disease level recorded over the four-years of disease measurement; and the three Gaussian curve parameters b, m, and s. The Gaussian curve and its three parameters were regarded as the rate descriptors for leaf rust progress based on the disease severity ratings. Based on regression analysis, standard curves involving the exponential, line plus exponential, double exponential, critical exponential, logistic, generalized logistic, Gompertz, linear-by-linear, quadratic-by-linear, quadratic-by-quadratic, Fourier, double Fourier, Gaussian, and double Gaussian functions were assessed to characterize the progression of leaf rust on the eight wheat cultivars, differing in resistance level, maturity and sowing time, determined over the four growing seasons. The statistical software GENSTAT (release 12, VSN International, Oxford, UK) was used

to perform all statistical tests and fit nonlinear models by maximum likelihood method/tests. To test goodness of fit to standard curves, the co-efficient of determination (R^2) and Fisher's (F) tests were used. Estimations of leaf rust progress over time using the standard curves were evaluated by regressing fitted values against observed values. According to the above-mentioned tests used to fit model, Gaussian function provided the best fit to wheat-leaf-rust-severity data compared to other standard models. The graph of a Gaussian function presents a symmetric bell curve (Fig. 1) which illustrates the probability density function of a normally distributed indicator with expected value m and variance s. The Gaussian model is of the form:

$$Y = a + b \times Gauss((x{-}m)/s)$$

In the Gaussian model, a is the constant term, b is the height of the curve's peak, m is the position of the center of the peak, s (the standard deviation) is the width of Gaussian bell, and x is the time intervals (in days) between disease measurements. To determine the effects of sowing date and wheat cultivar factors on leaf rust progress curves, the factor levels were ranked by performing the Kruskal-Wallis one-way ANOVA test. This test demonstrated the significant differences in leaf rust progression levels between rankings based on the H-test results. Based on the maximum leaf rust severity during the four study years, the categorization of leaf rust resistance for the eight commercial wheat cultivars was made as follows: resistant for cvs Parsi, Pishtaz, Sirwan (< 40%), partially resistant for cvs Bahar, Baharan, Pishgam (< 50%), and susceptible (> 70%) for cvs Chamran II and Sivand.

According to the correlation analysis, simple relationships among the descriptors of leaf rust progress curve elements were examined. Then, to improve the accuracy of estimating leaf rust progress, a principal component analysis (PCA) using correlation matrix was applied to disease progress curve elements. The eigenvalues (the proportion of total variance explained by each principal component) greater than 1.0 were considered as interpretable (Sharma 1996). A loading value (defining the correlation between the variable and principal component) above 0.35 was considered significant (Kranz 1974). Contributions of leaf rust descriptors in principal components based on the eigenvalues and loading values reflected the importance of the

Fig. 1 Schematic Gaussian curve and parameters (b = height of curve peak, m = center of peak, s = standard deviation or curve width); x refers to time intervals between measurements

$$Y = a + b * \text{Gauss}((x - m)/s)$$
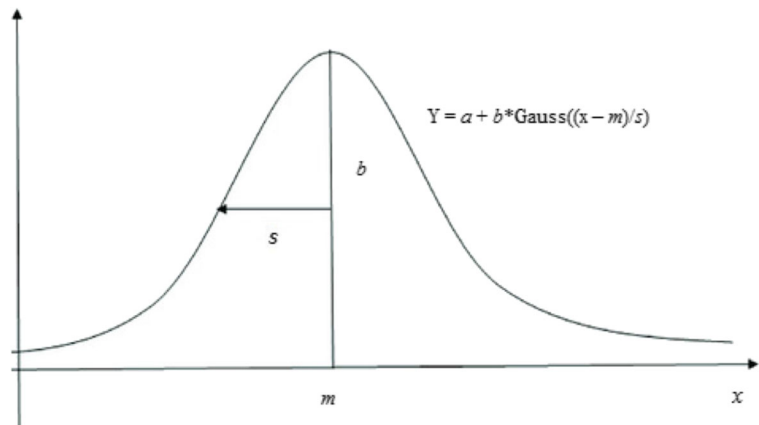
disease progress curve element for describing disease development in the wheat crop.

Results

The progression of leaf rust on winter wheat planted at various dates was recorded in an experiment conducted over four growing seasons in Kermanshah province. Fourteen standard curves were fitted to the disease severity data collected from the experimental plots to determine the best curve for characterizing the progression of wheat leaf rust over the four seasons. The Gaussian model provided the best description of the four-season-severity dataset obtained from a significantly wide range of leaf rust levels on the wheat cultivars (Table 1). The Gaussian parameters, b, m and s, were estimated for each experimental plot and study year. The examination of a Gaussian function provided a significant fit ($P < 0.001$) for the 2013–2014 and 2015–2016 growing seasons. The other two study years, 2014–2015 and 2016–2017, were excluded from this part of statistical analysis due to the lack or low levels of leaf rust development. The proportions of variation explained by Gaussian functions for the study years were 0.94% for 2013–2014 and 0.99% for 2015–2016. The estimated parameters of the Gaussian model fitted to leaf rust severity were regarded as indicators of disease progression in wheat cultivars with different resistance levels and sowing dates. The three Gaussian parameters in addition to the three indicators of leaf rust severity, AUDPC, disease onset time, and maximum disease severity, were considered to be the disease progress curve elements. The mean, standard deviation, and range values were obtained for the continuous variables

regarded as leaf rust progress curve elements (Table 2). Larger standard deviations than average values demonstrated a wide range of heterogeneity in the AUDPC, Gaussian parameters, and maximum disease severity data.

Moderate and severe epidemics of leaf rust occurred on commercial wheat cultivars during 2013–2014 and 2015–2016 growing seasons, respectively. The lack of leaf rust development in 2014–2015 and mild disease development in 2016–2017 were recorded. From the analysis of correlation between different leaf rust curve elements (continuous variables), significant ($P \leq 0.05$) associations of the variable AUDPC with maximum disease severity and the Gaussian parameters m and s were observed (Table 3). The maximum disease severity responded significantly ($P \leq 0.05$) to the Gaussian parameters m and s. The Gaussian parameter m was found to be correlated significantly with the parameters b and s.

To ease the interpretation of the Kruskal-Wallis one-way ANOVA results, eight wheat cultivars were classified into three groups, resistant (Parsi, Pishtaz, Sirwan), partially resistant (Bahar, Baharan, Pishgam), and susceptible (Chamran II, Sivand) cultivars. Based on the H-test results, the greatest and lowest mean values for leaf rust AUDPC were obtained in the late/very late sowing dates of susceptible cultivars (mean = 61.06; rank = 1) and early/optimum sowing dates of resistant cultivars (mean = 38.11; rank = 6), respectively (Table 4). However, the mean AUDPC value for the early/optimum sowings was greater on susceptible cultivars (mean adjusted $H = 7.83$; $P = 0.046$) compared to the resistant and partially resistant cultivars. In case of maximum leaf rust severity, the H-test (mean adjusted $H = 8.31$; $P = 0.040$) indicated the greatest mean value for the late/very late sowings of the susceptible cultvars (mean = 60.32; rank = 1). In early/optimum

Table 1 Standard models examined for characterization of leaf rust progress curves in wheat cultivars with different resistance levels under different sowing dates

Models	2013-2014[a]		2015–2016	
	R^2	F prob.	R^2	F prob.
Exponential	0.58	0.077	0.87	< 0.001
Line + Exponential	0.79	0.007	0.91	0.012
Double exponential	0.79	0.813	0.98	nd[b]
Critical exponential	0.79	0.009	0.98	< 0.001
Logistic	0.62	0.784	0.91	0.010
Generalized logistic	0.61	1.000	0.86	nd
Gompertz	0.61	0.846	0.96	< 0.001
Linear-by-linear	0.58	0.084	0.87	< 0.001
Linear-by-quadratic	0.81	0.003	0.97	< 0.001
Quadratic-by-quadratic	0.97	< 0.001	0.99	nd
Fourier	0.92	< 0.001	0.97	< 0.001
Double fourier	0.99	nd	nd	nd
Gaussian	0.94	< 0.001	0.99	< 0.001
Double Gaussian	0.96	nd	nd	nd

[a] The 2 years, 2014–2015 and 2016–2017, were excluded from this analysis due to the lack of or mild development of leaf rust on wheat cultivars

[b] nd = Not detected by statistical procedure

sowings, the mean maximum disease severity for the susceptible cultivars (mean = 49.92; rank = 3) was greater compared with both the resistant cultivars (mean = 37.96; rank = 6) and partially resistant cultivars (mean = 39.30; rank = 5). There was a lack of significant difference between the rankings determined for the Gaussian parameter b (mean adjusted $H = 7.27$; $P = 0.101$) of leaf rust progress on the eight commercial wheat cultivars. For the Gaussian parameters m (mean adjusted $H = 8.38$; $P = 0.037$) and s (mean adjusted $H = 8.17$; $P = 0.047$), the lowest and greatest mean values were detected for the early/optimum sowings of resistant cultivars and late/very

Table 3 Correlation coefficients for continuous variables of leaf rust progress curve

Variables	AUDPC	MDS	b	m	s
Area under disease progress curve (AUDPC)	1.00				
Maximum disease severity (MDS)	**0.90**[a]	1.00			
Gaussian parameter b	−0.01	0.02	1.00		
Gaussian parameter m	**0.43**	**0.55**	**0.21**	1.00	
Gaussian parameter s	**0.48**	**0.56**	0.06	**0.77**	1.00

[a] Bold numbers refer to significance at 0.05 probability level

late sowings of susceptible cultivars, respectively (Table 4).

According to the PCA test, the two principal components accounted for 75% of the variation in leaf rust progress curve elements determined over the four growing seasons for the eight commercial wheat cultivars with different levels of disease resistance and sowing dates (Table 5). The first principal component explained 57% of the total data variance. This factor showed the greatest loading value (−0.49) for the negative contribution ($P \leq 0.05$) of maximum leaf rust severity. The disease onset time was found to be the only variable with a significantly positive contribution for this factor. Furthermore, the AUDPC and Gaussian parameters m and s contributed negatively ($P \leq 0.05$) to the first principal component. The first principal component also showed indirect association of disease onset with other variables significantly linked to this factor. This revealed that an earlier disease onset corresponded with greater AUDPC, maximum severity rating, Gaussian bell width or standard deviation (parameter s), and a higher Gaussian peak center (parameter m) for leaf rust progress in the wheat crop. Moreover, similar significant contributions of AUDPC, disease onset, Gaussian parameters m and s, and maximum disease severity to the first principal component demonstrated similar importance of these

Table 2 Average, standard deviation, and range values determined for continuous descriptors of leaf rust development in wheat cultivars with different resistance levels and sowing dates

Descriptors	Average	Standard deviation	Range
Area under disease progress curve	128.40	240.10	0.00 to 1482.60
Maximum disease severity	18.21%	27.68%	0.00% to 100.00%
Gaussian parameter b	2,448,774.00	20,803,186.00	0.00 to 199,707,682.00
Gaussian parameter m	2.72	4.61	0.00 to 33.70
Gaussian parameter s	0.46	1.15	0.00 to 6.22

Table 4 Analysis of leaf rust descriptors using Kruskal-Wallis one-way ANOVA for wheat cultivars planted at different dates

Resistance levels[a]	Planting date categories	Area under disease progress curve	Maximum disease severity	Gaussian parameters		
				b	m	s
Resistant	Early-Optimum	38.11 (6)[b]	37.96 (6)	36.86	38.07 (6)	38.57 (6)
	Late-Very late	44.89 (4)	44.11 (4)	48.39	55.61 (2)	51.96 (2)
Semi-resistant	Early-Optimum	41.03 (5)	39.30 (5)	39.27	39.87 (5)	38.80 (5)
	Late-Very late	47.59 (3)	50.16 (2)	50.06	51.81 (3)	47.97 (3)
Susceptible	Early-Optimum	49.33 (2)	49.92 (3)	50.67	42.28 (4)	46.64 (4)
	Late-Very late	61.06 (1)	60.32 (1)	57.03	56.79 (1)	59.32 (1)
Mean adjusted H		7.83	8.31	7.27	8.38	8.17
Ranking $Chi\ P$		0.046	0.040	0.101	0.037	0.047

[a] Resistant cultivars: Pishtaz and Sirwan; semi-resistant cultivars: Baharan, Parsi and Pishgam; susceptible cultivars: Bahar, Chamran II and Sivand

[b] Values inside parentheses refer to the significant ranking ($P \le 0.05$)

various disease descriptors to characterize the progression of wheat leaf rust.

The second principal component, accounting for 18% of total variance in the data, showed a highly significant contribution from the height of the Gaussian curve peak (parameter b) to characterize the diverse range of wheat leaf rust progress curves over the growing seasons. The PCA results on the significant relationships among the AUDPC, disease onset, maximum disease severity, and three Gaussian parameters were in agreement with the results of the correlation analysis. In brief, the H-test, correlation, and PCA analyses confirmed the significant dependence of occurrence and

Table 5 Principal component analysis of leaf rust curve elements characterized for wheat cultivars with different resistance levels under different sowing dates

Variables	Principal components	
	1	2
Area under disease progress curve	**−0.45**[a]	0.32
Disease onset time	**0.43**	0.04
Maximum disease severity	**−0.49**	0.24
Gaussian parameter b	−0.07	**−0.86**
Gaussian parameter m	**−0.45**	−0.30
Gaussian parameter s	**−0.42**	−0.11
Eignvalues	3.39	1.09
Percentage variation explained	56.51	18.08
Cumulative variation	56.51	74.59

[a] A bold number refers to significant loading when Chi-squared $P \le 0.05$

progression of leaf rust in wheat on the six disease progress curve elements examined during the four growing seasons across the experimental plots.

Discussion

The research included the most commonly used descriptors of occurrence and progression of leaf rust in wheat to improve the accuracy and applicability of future models for predicting severe epidemics, estimating yield losses, screening cultivars for resistance, and to reduce the time taken for disease measurements. Because the estimated value of a regression-based model may decrease due to increasing collinearity of an excessive number of disease variables (Pietravalle et al. 2003), attempts were made to identify appropriate wheat leaf rust progress curve elements. The evaluation of six disease curve elements obtained from a four-year study of leaf rust progression in eight wheat cultivars with diverse levels of resistance and sowing dates was performed using the PCA based on approaches adopted by Luo (2008) and Kranz (1974). In agreement with Kranz (2003), the experimental design increased not only leaf rust variability across the 282 plots studied over a four-year period (Naseri and Sasani 2020), but also the variation in the disease progress curve elements.

Vanderplank (1963) and Kranz (1974) introduced a number of influential curve elements including the AUDPC, disease onset time, the rate of disease progress, apparent infection rate, and final disease intensity to be

used in comparative epidemiology. Earlier studies developed logistic models to characterize spatiotemporal dynamics of leaf rust on susceptible wheat genotypes at the field plot and regional scales (Subba Rao et al. 1990; Franke et al. 2009). Rossi et al. (1997) and Savary et al. (2015) reported the logistic basis od the prediction models RUSTDEP and EPIWHEAT, respectively, for wheat leaf rust pathosystems. They fitted more than 15 disease curve elements involving hourly and daily disease measurements in the field and laboratory. However, it was impossible to characterize the progress of leaf rust in wheat cultivars with different resistance levels and sowing dates over four growing seasons according to the logistic model in this research. The findings of this study showed the best fit of the Gaussian model in characterizing disease progress in the wheat crop. Therefore, the three Gaussian parameters were considered as leaf rust progress curve elements. To the best of our knowledge, this is the first record of the fitted Gaussian curve parameters for wheat leaf rust. All the above-mentioned logistic models were developed based on a lower variance disease data obtained from more homogenous wheat genotypes, mostly susceptible to leaf rust. Thus, variations in disease curves determined for cultivars with different levels of disease resistance and growth stages (due to various sowing dates) could not be explained by the logistic models. Pennypacker et al. (1980) recommended the Weibull function as a general model to characterize plant disease progress curves. This study showed the greater efficiency of the Gaussian function to model the heterogeneous progression of wheat leaf rust when compared to the other standard models. In fact, this advantage of fitted Gaussian parameters is achieved through larger variation in leaf rust progress curves. Such wide range heterogeneity in the disease data improves the strength of linkage between curve elements to disease progress according to Kranz (2003). The confirmation of such comparison of the logistic and Gaussian models deserves further experimentation of rust-wheat pathosystems in the future.

Although previous epidemiological studies on wheat leaf rust examined one or more disease curves (Subba Rao et al. 1990; Rossi et al. 1997; Franke et al. 2009; Savary et al. 2015), the significant associations of the AUDPC, disease-onset time, and maximum disease severity with the three Gaussian parameters have been considered for the first time as leaf rust progress curve elements. In accordance with Kranz (2003), the high variation in disease data improved the strength of associations between the curve variables and wheat leaf rust progress. Furthermore, the maximum leaf rust severity rating, based on the present PCA results, showed the highest relevance to the disease progress trend. Moreover, such notable contributions of the disease onset time and maximum disease severity in assessing the progress of leaf rust in the wheat crop may help in accelerating future research to predict leaf rust epidemics, screen cultivars for the efficiency and durability of disease resistance, assess efficiency of control procedures, and estimate yield losses. Thus, the detection of disease onset and maximum severity could be much easier than fitting disease progress curve parameters. In comparison to the cumbersome task of assessing excessive disease curves required by earlier leaf rust progress models (Rossi et al. 1997; Savary et al. 2015), the present influential and easy-to-measure curve elements may improve the applicability of future simulating models. In conclusion, these findings have advanced the current knowledge of wheat leaf rust progress curves and provided new clues on the considerable value of estimates of AUDPC, disease onset time, and maximum disease severity, in combination with the Gaussian parameters, to characterize wheat leaf rust progress at the field scale.

Compliance with ethical standards

Conflict of interests The authors declare that they have no conflict of interests.

Ethical statement The research presented in this manuscript did not involve any animal or human participants.

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