## PLANT GROWING, PLANT PROTECTION AND BIOTECHNOLOGY

# Phenotypic Expression of Brown Rust Resistance in Wheat: Element Modeling

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**Abstract**—Surveys have been performed in order to analyze the phenotypic variation in wheat for brown rust resistance, to identify the factors causing the causative agent spread, to adjust the parameter values for assessing the quantitative relationships between the pathogen−host−environment system variables, and to build the imitation model for disease pathogenesis. The highest-level resistance to the disease was typical for the tall wheat plant varieties exhibiting the vertical (less than 15°), deflection (15°−45°), and horizontal (46°−90°) flag-leaf angle patterns; the thick, wax-coating layers (nine scores); the leaf trichome-type indument density of $941.7 \pm 63.8$ per 1 cm$^2$; and the trichome length of $2.2 \pm 0.1$ mm. The proposed system of meteopathology forecast models for the brown rust progression was based on the revealed correlations between the pustule numbers, the agent pustule area, the meteorological factors, and the solar activity. The factor model describing the conjugation of the brown rust progression with the spread and effects of the agents causing the mixed infection of leaves has been built based on phytometrics of crop plants, production capacity, meteorological factors, and solar activities with the use of the Leningradskaya-6 cultivar. It can provide the opportunity to carry out a system analysis of changes in the indicated parameter values relative to the environmental factors. Thus, it was revealed based on the model that the brown rust progression rate is increased with increasing the June precipitation amount relative to the number of temperature degrees above 10°C in May. In addition, the increased rates of wheat flag-leaf damage caused by septoria and powdery mildew tend to limit the progression of brown rust. The imitation model for the wheat brown rust progression is based on the solving system of delay differential equations (DDE) with numerical routines from the DIFSUBDEL software package. The model may be used to create modern expert systems for plant disease forecasting and diagnosing.

**Keywords:** soft wheat (*Triticum aestivum* L.), wheat diseases, disease resistance in wheat, phenotypic variation, modeling for pathogenesis, meteopathology forecasting

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## INTRODUCTION

The common framework policy of the current agricultural development system makes provision for improving its adaptive capacity and involving it in managing the resources in agrobiocenoses with the key levels for undertaking their natural regulatory functions [1, 2]. This approach, along with the digital technologies for monitoring in the phytosanitary aspect and distance sounding of Earth [3, 4], can provide the opportunity both to influence the quantitative interrelations in the pathogen−host−environment system at the population, molecular, and above-individual-organism levels and to develop the science-based systems for plant protection [5].

The data based on the long-term researches of the All-Russia Research Institute of Plant Protection show that the key factors influencing the phytosanitary status of crop agrocenoses may include meteorological conditions, farm-business management, and agricultural technology. In addition, the effective use of the adaptive and environmentally friendly properties of growing plant species and cultivars serves as the most important element of managing the phytosanitary conditions of the wheat crops [6]. All the zonal systems for integrated protection of plants are based on

growing the agricultural varieties resistant to common diseases, pests, and other stress factors [7, 8]. Unfortunately, the proportion of the resistant cultivars in the agrocenoses is no more than 12−15% [9].

Evolution induced various plant defense responses to pathogens, expressed as visible (phenotypic) and invisible alterations in the structures of organs and tissues [10]. The plant selective breeding practice, including artificial selection for economically important traits, is performed based on these knowledge principles and the selection approaches elaborated with screening the varieties of different origin and, therefore, adapted to different environmental conditions, which have certain sets of useful properties for optimum existence in certain conditions. In addition, special attention in different aspects of agricultural science is drawn to the methodology for creating the ideal crop variety model, which can provide the opportunity for a breeder to produce more economically efficient cultivars as much similar as possible to the variety ideal for growing under certain environmental conditions [11].

Climate change influences the distribution of harmful organisms, their bioecological properties, and the interactions in the pathogen-host systems [12]. In addition, the warming trend is evident across recent decades and regions of Russia, and its rates are faster than the average rate of global warming [13].

Various tools of mathematical analysis are used to assess and forecast the impact of nature and climate factors on plant pathogeneses caused by the causative agent spread [14]. Mathematical models for epiphytotics can provide the opportunity to consider the pathogen-host interactions as a complex process depending on a great number of factors [15]. The All-Russia Research Institute of Plant Protection developed the imitation models in two approaches: modeling the systems of crop-and-harmful object type and modeling the processes relative to plant protection measures [9, 16].

Wheat diseases, including brown (leaf) rust *Puccinia triticina* Erikss., greatly limit the productive capacity of a crop. In years of epuphytotics, a decrease in the wheat yield may reach 20−30%. Several successive sporiferous stages are identified in the agent development cycle. The agent uredo stage manifested as brown-rust uredo pustules producing the uredo spores on leaves is of specific threat to the wheat crop. Formation of great numbers of pustules, especially on the flag leaves of wheat, causes their premature death, reducing the rates of photosynthesis and grain mass decrease [17].

In relation to the above mentioned, the objectives of the survey are to reveal the nature-climate factors associated with severity of the brown rust disease and its progression and to develop the meteopathology forecasting system for improving the wheat yields.

## EXPERIMENTAL

The surveys were carried out at the Plant Protection and Quarantine Subdepartment (St. Petersburg State Agricultural University), the Microbiological Plant Protection Laboratory, the All-Russia Research Institute of Plant Protection, and the Department of Mathematics and Mechanics (St. Petersburg State University). The experimental studies were performed at the *Puskinskie and Pavlovskie Laboratorii* Experimental Field, Vavilov All-Russia Institute of Plant Genetic Resources, Federal Research Center. The soft wheat collection served as the plant material for surveys, which was provided for the surveys by the wheat genetic resources unit, Vavilov All-Russia Institute of Plant Genetic Resources.

The analysis of the element effects of phenotypic variation in wheat varieties on the brown-rust progression rates was conducted for major parameters. They included the angle of flag leaf inclination (468 samples, 2009−2010), the density and length of indumentum filaments, the plant height (701 samples, 2009−2020), the total and production branching ratios, the plant color, and the wax coating layers (1955 samples, 2009−2020). The correlations between the solar activity and the brown rust progression in wheat were studied based on the information on 74 wheat varieties for 1995−2012. The multifactor model for the brown rust progression in single and mixed infections of wheat leaves was built based on the data on the Leningradskaya-6 cultivar, k-64900, for 2009−2020. Disease progression ($d_P$), number of pustules ($N_p$), area of pustules ($A_p$), and type of response ($T_r$) were considered as the main characteristics of wheat pathogenesis relative to the development of the brown rust agent *Puccinia triticina* Erikss. The records of spread and effects of the leaf disease agents following the brown rust disease were performed based on the parameters for the yellow rust, powdery mildew, and septoria infections. The parameters for yellow rust (*Puccinia striiformis* West.) included the disease progression, the number of stripes consisting of pustule and their length, the pustule area, and the type of response. The parameters for powdery mildew (*Blumeria graminis* Speer.) included the disease progression, the number of tan spots and their area, and the response type. With respect to septoria (*Parastagonospora nodorum*, *Zymoseptoria tritici*), the disease progression was observed. The phytopathology parameter values were provided according to the results obtained after the identification and measurements on the wheat flag leaves with the MBC-9 binocular and Mikromed trinocular vision systems [18].

The agrometeorology unit, Vavilov All-Russia Institute of Plant Genetic Resources, and the Royal Observatory of Belgium [19] provided the data on the meteorological conditions and the solar activity characterized by the average total annual number of spots on the sun for 1995−2020. The Far-East Department

of Hydrometeorology and Environmental Monitoring [20] provided the average monthly values for the Wolf's sunspot numbers.

In order to measure the wheat productivity, a complex of parameters, including height in cm, flag-leaf area in cm$^2$, ear length in cm, number of spikelets per ear in units, number of grains per ear in units, 1000-grain weight in g, and grain yield per plant in g, were used [21].

A botanical feature extraction of plants (the angle of inclination between the flag leaf and the stem in scores, waxy coating in scores, leaf color in scale points, and leaf indumentum in scores) was performed based on the methodical recommendations [22]. The quantity assessment of indumentum filaments per 1 cm$^2$ of a flag leaf was performed based on the measurements in no less than 10 fields of vision with 56× magnification. In addition, the indumentum filament length (mm) was measured with the similar magnification of a microscope with the objective and ocular micrometer scales. The classification proposed by N.E. Ionova et al. was used to rank the wheat samples in ascending order of plant height [23].

The electron database containing information on the examined samples has been created with the IBM SPSS statistics for a mathematical treatment of phytopathology and morphometric characteristics of soft wheat and assessment of nature climate factor effects (since 1995) on its varieties. The estimations were performed with the parametric statistics methods based on the standard errors as ±SEM means of 95% confidence intervals and the nonparametric tests for Spearman's rank correlation coefficient.

The correlation matrices were constructed and analyzed with the data on disease progression records for 74 soft wheat varieties during the analysis of the conjugation between the brown rust disease progression rates in wheat, the number of pustules and their area, and the solar activity for 1995–2012. The correlation coefficients were later ranked. Afterwards, the relative index expressed as a proportion of coefficients of Spearman's correlation was estimated as a ratio of a number of negative and positive coefficients measuring the meteodependence of pathogenesis by months between the current (January–August) and previous (September–December) years of phytosanitary monitoring to the number of the analyzed varieties.

The factor analysis method allowing us to analyze the cause–effect relationships between the listed parameters in a simplified form and the factors expressed as hidden (latent) variables hypothetically unmeasurable directly was used to reveal the relationships between the 42 parameters describing the development cycles of leaf disease-causing agents in wheat, its yield components, meteorological conditions, and the solar activity. Constructing the factor model proposed in the study, five statistical factors (F1–F5) describing the linear correlations between the param-
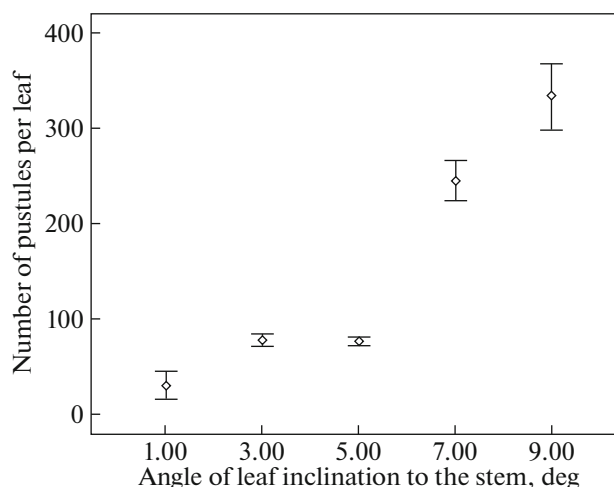


**Fig. 1.** Dependency of the number of flag-leaf brown-rust pustules on the angle of leaf inclination to the stem, degree (2009–2010): 1—vertical (inclination <15°); 3—drooping (15°–45°); 5—horizontal (46°–90°); 7—wilting (91°–135°); and 9—wilted (inclination >135°).

eters indicated above were identified. The revealed factors included the groups of parameters displaying the correlation between each other rather than between them and the parameters of the other factor. The factor analysis algorithm was based on the subsequent identification of factors, including F1 explaining the larger proportion of dispersion of the parameters, F2 explaining the lower share in dispersion, which is second after the first latent factor, etc. The principle component method was used to select the minimum number of factors contributing most to the dispersion model with variable parameters. The Varimax normalized rotation method was used to obtain a simpler structure of factors and their better allocation through reducing the number of parameters related to each factor.

## RESULTS AND DISCUSSION

The analysis of changing the rates of the brown rust disease in wheat relative to the flag-leaf inclination angle can indicate (Fig. 1) that the minimum number of pustules is mostly typical for the varieties exhibiting the vertical distribution of flag leaf (inclination <15°), while the maximum number is usually observed at its wilted distribution (inclination >135°).

The research into the effects of the wheat flag-leaf indumentum on the specificity of the brown rust disease progression has shown that the proportion of sampled plants having no indumentum in the group of varieties unaffected by the disease comprises 37.3%, while the sample proportion in the group of varieties showing signs of a disease comprises 22.7%. The tendency for increasing rates of wheat disease progression along with increasing the flag-leaf indumentum den-
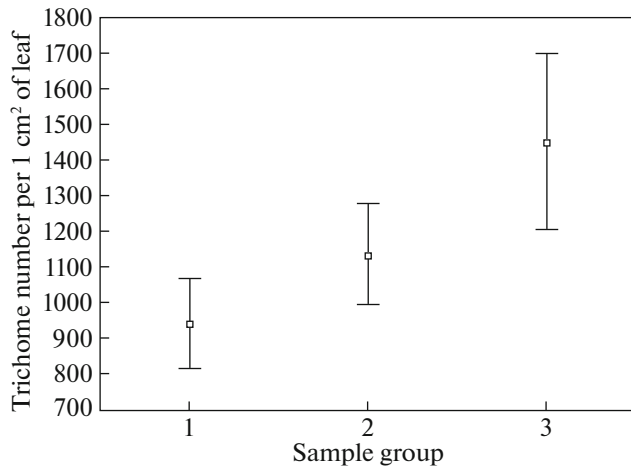
**Fig. 2.** Dependency of brown-rust progression on density of indumentum covering the wheat flag leaf (2009–2020). Group 1: $d_P = 1.7G \pm 0.1$; $N_p = 11.7\,G \pm 19.0$; $A_p = 0.03833 \pm 0.00718$ mm$^2$; $T_r = 1.2 \pm 0.8$; group 2: $d_P = 12.3 \pm 0.3$; $N_p = 121.8 \pm 11.3$; $A_p = 0.07688 \pm 0.01396$ mm$^2$; $T_r = 2.3 \pm 1.1$; group 3: $d_P = 39.3 \pm 1.5$; $N_p = 406.3 \pm 34.8$; $A_p = 0.08376 \pm 0.00689$ mm$^2$; $T_r = 3.3 \pm 0.9$.
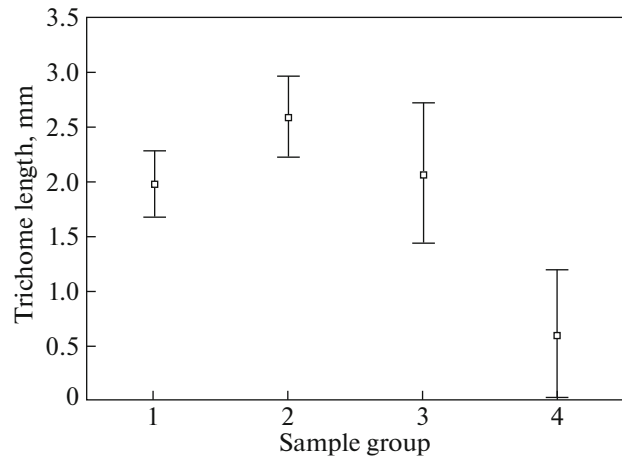


**Fig. 3.** Dependency of brown-rust progression on length of trichomes forming wheat flag-leaf indumentum (2009–2020). Group 1: $d_P = 4.7 \pm 0.2$; $N_p = 43.5 \pm 5.1$; $A_p = 0.04807 \pm 0.00497$ mm$^2$; $T_r = 1.6 \pm 0.1$; group 2: $d_P = 19.3 \pm 0.3$; $N_p = 188.9 \pm 23.7$; $A_p = 0.11055 \pm 0.04442$ mm$^2$; $T_r = 2.6 \pm 0.1$; group 3: $d_P = 33.4 \pm 0.7$; $N_p = 327.1 \pm 29.2$; $A_p = 0.08246 \pm 0.00801$ mm$^2$; $T_r = 3.2 \pm 0.1$; group 4: $d_P = 64.8 \pm 3.1$; $N_p = 753.6 \pm 105.0$; $A_p = 0.08942 \pm 0.01210$ mm$^2$; $T_r = 3.9 \pm 0.1$.

sity was revealed. The indumentum may contribute to better retaining the spores on the leaf surface and creating the specific conditions for their subsequent spreading and penetrating (Fig. 2). Minimal damage by a disease was found in the samples of wheat with a number of indumentum filaments (of trichomes) comprising $941.7 \pm 63.8$ units per 1 cm$^2$, while the maximal damage was recorded at $1451.4 \pm 124.7$ units per 1 cm$^2$ of leaf. A tendency for reducing the brown rust progression in wheat, along with increasing the indumentum filaments, was identified (Fig. 3). It may be associated with an access difficult for spores to the leaf tissues. The highest rate of the brown rust progression ($d_P = 64.8 \pm 3.1$) was recorded in the group of samples with the minimal indumentum filament length of $0.6 \pm 0.3$ mm. The genotypes characterized by the maximum indumentum filament length of $2.2 \pm 0.1$ mm tended to demonstrate the strong disease resistance. The lower number of brown rust pustules ($N_p = 149.2 \pm 10.0$; $d_P = 17.1 \pm 1.8\%$) was recorded in the samples of wheat with a strong wax layer on the flag leaf surface when compared with genotypes having a thin layer of wax ($N_p = 248.9 \pm 26.2$; $d_P = 23.4 \pm 1.7\%$).

A significant decrease in the number of brown rust pustules in the tall wheat samples ($N_p = 127.7 \pm 26.2$ units) compared to the plants with the low ($N_p = 265.1 \pm 45.6$ units) and medium ($N_p = 265.0 \pm 43.6$ units) heights was revealed for 2009–2020. In addition, the degree of disease damage in wheat tended to increase along with the total branching ratio. The highest number of pustules ($N_p = 206.9 \pm$

39.6 units), the disease progression ($d_P = 14.4 \pm 1.6\%$), and the area of one pustule ($A_p = 0.06120 \pm 0.00290$; the response type: $3.4 \pm 3.7$) were revealed at the total branching ratio for eight and nine branches per plant. The lowest number of the agent pustules on the leaf surface of the unbranched plants (one stem) was recorded as $N_p = 52.0 \pm 3.7$ units, corresponding to $d_P = 8.4 \pm 0.4\%$.

The poor progression of a disease (relative to the number and the area of brown rust pustules) was recorded in the samples with light-green leaves ($d_P = 5.7 \pm 1.0$; $N_p = 28.1 \pm 5.4$; $A_p = 0.03402 \pm 0.00283$ mm$^2$; $T_r = 1.6 \pm 0.1$). It was recorded as highest in the samples with grey-green leaves ($d_P = 16.6 \pm 0.9$; $N_p = 130.3 \pm 1.0$; $A_p = 0.05273 \pm 0.00220$ mm$^2$; $T_r = 2.4 \pm 0.1$).

The long-tern surveys (1995–2012) revealed the most important factors contributing to increasing or decreasing the rates of disease progression to build the relative statistical models. Thus, the increased temperature and relative humidity in May had profound effects on increasing severity of moderate brown rust disease in wheat in July–August, which was characterized by a number of pustules on the flag-leaf surface. It was recorded in 81.1 and 66.2% of wheat samples, respectively (Table 1). In addition, an increase in the area of a micromycete pustule, along with an increase in the temperature in May, was recorded in 67.6% of samples. This pattern may be explained by the fact that the potential for infection of the brown rust agents at

**Table 1.** Correlations between the meteorological conditions throughout the periods of phytosanitary monitoring and the brown rust progression in 74 soft wheat varieties (1995−2012)

| Share of correlation coefficients, % | Data for the current period of keeping records | | | | | | | | Data for retention periods of keeping records | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
| Temperature (0°C) | | | | | | | | | | | | |
| Number of pustules per leaf, units | | | | | | | | | | | | |
| Positive | 56.8 | 70.3 | 54.1 | 70.3 | 81.1 | 29.7 | 43.2 | 41.9 | 78.4 | 66.2 | 75.7 | 83.8 |
| Negative | 39.2 | 28.4 | 43.2 | 27.0 | 18.9 | 70.3 | 55.4 | 56.8 | 21.6 | 33.8 | 23.0 | 12.2 |
| Area of a pustule, mm$^2$ | | | | | | | | | | | | |
| Positive | 45.9 | 48.6 | 50.0 | 41.9 | 67.6 | 52.7 | 43.2 | 58.1 | 50.0 | 48.6 | 36.5 | 28.4 |
| Negative | 47.3 | 43.2 | 41.9 | 50.0 | 27.0 | 43.2 | 50.0 | 36.5 | 41.9 | 39.2 | 59.5 | 66.2 |
| Amount of precipitation (mm) | | | | | | | | | | | | |
| Number of pustules per leaf, units | | | | | | | | | | | | |
| Positive | 27.0 | 79.7 | 86.5 | 67.6 | 16.2 | 90.5 | 75.7 | 58.1 | 45.9 | 12.2 | 98.6 | 39.2 |
| Negative | 70.3 | 20.3 | 12.2 | 29.7 | 81.1 | 6.8 | 21.6 | 41.9 | 52.7 | 86.5 | 1.4 | 58.1 |
| Area of a pustule, mm$^2$ | | | | | | | | | | | | |
| Positive | 51.4 | 41.9 | 31.1 | 44.6 | 45.9 | 27.0 | 27.0 | 39.2 | 52.7 | 36.5 | 51.4 | 45.9 |
| Negative | 43.2 | 51.4 | 56.8 | 48.6 | 47.3 | 66.2 | 64.9 | 56.8 | 39.2 | 56.8 | 37.8 | 45.9 |
| Relative humidity (%) | | | | | | | | | | | | |
| Number of pustules per leaf, units | | | | | | | | | | | | |
| Positive | 70.3 | 20.3 | 77.0 | 14.9 | 66.2 | 32.4 | 31.1 | 9.5 | 10.8 | 9.5 | 14.9 | 58.1 |
| Negative | 25.7 | 78.4 | 21.6 | 82.4 | 32.4 | 63.5 | 66.2 | 89.2 | 87.8 | 90.5 | 85.1 | 39.2 |
| Area of a pustule, mm$^2$ | | | | | | | | | | | | |
| Positive | 37.8 | 52.7 | 37.8 | 45.9 | 47.3 | 52.7 | 32.4 | 37.8 | 31.1 | 64.9 | 55.4 | 44.6 |
| Negative | 54.1 | 40.5 | 55.4 | 48.6 | 43.2 | 41.9 | 56.8 | 55.4 | 60.8 | 27.0 | 37.8 | 48.6 |

the uredo stage in the winter wheat and wild cereal plants as the hosts of uredo mycelia preserved in them tends to increase from the second ten-day period in May. Warm and humid weather contributes to more rapid production of aggregate generations of uredo spores, which increases the natural background infection and, subsequently, contributes to a more severe disease progression in the soft wheat. An increase in temperature and a decrease in precipitation amount in June, on the contrary, limited the disease progression, which was reflected in the inverse and direct correlations revealed between the meteorological parameters indicated above and the disease progression characterized by the number of pustules.

A higher proportion of positive coefficients of correlation between the number of the brown rust pustules on the flag-leaf surface in most varieties in July-August and the average month temperature of a previous period, i.e., September−December of the past year and January−May of the last year, was revealed. Warm weather in the autumn, winter, and spring seasons tends to increase the spread and the accumulation potential for infection of a fungal population in the winter cereal crops and the wild cereal plants. Low temperatures in winter, on the contrary, may be followed by the overall death rate in infectious agents overcoming the winter.

Humid conditions, including increases in the amount of precipitation (November, February−April, and June) and relative humidity (January, March, and May), served as the key parameters determining preservation and enhancing potential for brown rust infection in winter wheat and wild cereal plants, which contributed, afterwards, to increasing the damage caused by the disease in soft wheat.

The average temperature of a summer season did not have any significant effects on the area of an agent pustule. In addition, a decrease in amount of precipitation in June−August contributed to increasing the susceptibility of plants to a disease, which was characterized by increasing the area of a micromycete pustule.

**Table 2.** Correlations between the solar activity (by sunspots) and the brown rust progression in 74 soft wheat varieties (1995−2012)

| Share of correlation coefficients, % | Month | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. |
| Number of pustules per leaf | | | | | | | | |
| Positive | 37.8 | 41.9 | 40.5 | 23.0 | 36.5 | 40.5 | 35.1 | 36.5 |
| Negative | 60.8 | 54.1 | 55.4 | 74.3 | 59.5 | 58.1 | 62.2 | 60.8 |
| Area of a pustule, mm$^2$ | | | | | | | | |
| Positive | 51.4 | 41.9 | 37.8 | 48.6 | 50.0 | 39.2 | 50.0 | 47.3 |
| Negative | 43.2 | 50.0 | 54.1 | 45.9 | 43.2 | 52.7 | 44.6 | 47.3 |

The model reflecting the dependence of variation in the number of brown rust pustules in wheat ($N_p$) on the temperature ($T_{May}$), the relative humidity ($H_{May}$), and the amount of precipitation ($P_{May}$) recorded in May with the Frassineto variety, k-40269, was built, which is expressed as

$$N_p = -5594.45 + 193.03 T_{May} + 47.15 H_{May} - 0.99 P_{May}$$

($R^2 = 0.74$ denotes a coefficient of determination).

The prevalence of inverse correlations between the number of brown rust agent pustules in wheat and the average monthly number of the solar spots was found, which could indicate a probable increase in the disease progression rates along with a decrease in the number of the solar spots (Table 2). With respect to the area of a pustule, the trends were alternative.

The factor model explaining 81.2% of total dispersion measuring the variation of items was built with the method for the principle components of a factor analysis with the varimax rotation process rotating the axis. It was based on the assessment of relationships between the parameters for the brown rust progression with the other agent-induced leaf diseases and the parameters for the yield components of the Leningradskaya-6 wheat variety, k-64900, with the meteorological condition for 2009−2020 (Table 3). The first, second, third, fourth, and fifth factors (F1, F2, F3, F4, and F5, respectively) explain 33.3, 17.3, 13.5, 9.7, and 7.4% of the total dispersion of variables, respectively.

Dependencies between the certain parameters for the brown-rust disease progression in wheat and the factors influencing pathogenesis are described in F3. The disease progression and the pustule number and area tended to decrease along with the increased rates of wheat leaf damage caused by powdery mildew and septoria. The disease progression tended to increase along with an increase in the number of temperature degrees above 10°C in May and the amount of precipitation in June.

In F1, the increased rates of the yellow-rust disease progression, along with decreasing the number of temperature degrees in August and reducing the solar activity (by the number of sunspots and the Wolf's index), was recorded. In F5, an increase in the wheat yield, along with a decrease in the area of powdery mildew spots and increases for precipitation in May and the number of temperature degrees in June, were shown.

Based on the open data on the patterns of the brown-rust agent spread in wheat [26], a mechanistic mathematical model describing the dynamics of variables for phytopathogen status in the spring−summer season was built. In order to build a model, it was presupposed that there was the presence of some amount of infection in the air at the start of a growing season. This situation is typical for many grain-sowing regions, where the uredo spores are annually dispersed by wind. The formulated model represents a system of five first-order nonlinear delay differential equations (DDE). The certain rate of change in a corresponding variable for the brown rust agent status is set for each of them:

$$\frac{dx_{ss}}{dt} = k_{s,ss}x_s(t) - d_{ss}x_{ss}(t) - k_{ss,se}x_{ss}(t), \quad (1)$$

$$\frac{dx_{bs}}{dt} = k_{ss,se}x_{ss}(t) - d_{se}x_{se}(t) - k_{se,p}x_{se}(t - \tau_L), \quad (2)$$

$$\frac{dx_p}{dt} = k_{se,p}x_{se}(t - \tau_L) - (d_p^e + d_p^i)x_p(t), \quad (3)$$

$$\frac{dx_s}{dt} = k_{p,s}x_p(t) - d_s x_s(t) - k_{s,ss}x_s(t), \quad (4)$$

and

$$\frac{dx_n}{dt} = k_p(t - \tau_i) + (d_p^e + d_p^i)x_p(t), \quad (5)$$

where $x_s$ denotes the number of spores in the air above a unit of leaf surface, $x_{ss}$ is the number of spores settled on a leaf, $x_{se}$ are spores embedded within the leaf, $x_p$ is the number of pustules, and $x_n$ denotes the number of necroses. The parameters indicated above (so-called variables for status of a pathogen at the uredo stage) characterize pathogenesis at the present moment, while their aggregation ($x_s$, $x_{ss}$, $x_{se}$, $x_p$, and $x_n$) may be considered as a vector of status of a pathogen at the uredo stage in the dimension of variables for status.

Equations (1)−(5) have the coefficients of spore settling ($k_{s, ss}$), embedding the spores settled ($k_{ss, se}$), pustule spore production rates ($k_{p, s}$), nonviability of spores settled at risk of death ($d_{ss}$), pustule death induced by external factor effects ($d_p^e$), pustule death caused by pustule natural death ($d_p^i$), and spore death in the air ($d_s$).

Equation (1) describes the changes in the number of spores settled per unit of leaf surface area. The first

**Table 3.** Factor analysis of wheat yield, disease progression, meteorological conditions, and solar activity

| Item | Load factors | | | | |
|---|---|---|---|---|---|
| | F1 | F2 | F3 | F4 | F5 |
| Height, cm | −0.16 | **0.89** | 0.05 | 0.28 | 0.13 |
| Flag leaf area, cm$^2$ | 0.39 | 0.40 | 0.13 | 0.67 | −0.01 |
| Ear length, cm | 0.07 | 0.00 | 0.14 | 0.65 | 0.55 |
| Number of spikelets per ear, units | 0.07 | 0.11 | −0.04 | 0.39 | 0.48 |
| Number of grains per ear, units | 0.08 | −0.41 | −0.10 | 0.00 | **0.81** |
| Grain weight per ear, g | −0.42 | −0.59 | −0.14 | 0.11 | 0.57 |
| 1000-grain weight, g | −0.41 | −0.64 | −0.25 | 0.07 | 0.20 |
| Grain yield per plant, g | 0.07 | −0.05 | 0.38 | −0.06 | **0.84** |
| Number of temperature degrees above a threshold at 10°C (May, from day 11) | **0.70** | 0.15 | **0.58** | 0.05 | −0.07 |
| Amount of precipitation (May, from day 11), mm | 0.02 | −0.24 | 0.22 | 0.09 | **0.86** |
| Number of temperature degrees (June), °C | 0.31 | 0.13 | −0.12 | 0.06 | **0.74** |
| Amount of precipitation (June), mm | −0.06 | 0.29 | **0.73** | −0.53 | −0.05 |
| Number of temperature degrees (July), °C | 0.68 | 0.24 | 0.26 | 0.44 | −0.24 |
| Amount of precipitation (July), mm | −0.08 | 0.09 | 0.17 | **−0.92** | −0.06 |
| Number of temperature degrees (Aug.), °C | **0.84** | 0.20 | 0.03 | −0.14 | 0.08 |
| Amount of precipitation (Aug.), mm | 0.10 | 0.24 | 0.15 | **−0.90** | −0.10 |
| Relative humidity (May), % | 0.56 | 0.48 | 0.21 | 0.33 | −0.25 |
| Relative humidity (June), % | 0.31 | **0.71** | −0.06 | 0.29 | −0.36 |
| Relative humidity (July), % | 0.21 | 0.68 | −0.42 | −0.19 | −0.15 |
| Relative humidity (Aug.), % | 0.13 | **0.90** | −0.08 | 0.07 | −0.05 |
| Hydrothermal coefficient (July) | −0.23 | **0.79** | 0.01 | −0.46 | −0.08 |
| Hydrothermal coefficient (Aug.) | 0.11 | **0.79** | 0.17 | −0.44 | 0.09 |
| Brown rust progression, % | −0.11 | −0.05 | **0.84** | 0.08 | −0.04 |
| Number of brown-rust pustules, units | 0.10 | −0.06 | **0.82** | −0.05 | 0.30 |
| Area of a brown-rust pustule, mm$^2$ | −0.03 | 0.14 | **0.85** | 0.00 | 0.06 |
| Yellow-rust progression, % | **−0.92** | 0.21 | −0.06 | 0.14 | 0.04 |
| Number of yellow-rust pustules, units | **−0.95** | 0.08 | −0.01 | 0.11 | 0.11 |
| Area of a yellow-rust pustule, mm$^2$ | **−0.80** | −0.22 | 0.31 | 0.28 | −0.08 |
| Number of yellow-rust pustules per stripe, units | **−0.98** | −0.03 | −0.04 | −0.06 | 0.04 |
| Number of yellow-rust stripes, units | **−0.97** | 0.10 | −0.05 | −0.05 | 0.07 |
| Yellow-rust stripe length, mm | **−0.96** | 0.09 | −0.03 | −0.17 | −0.09 |
| Progression of septoria, % | 0.16 | 0.16 | **−0.51** | 0.36 | −0.23 |
| Progression of powdery mildew, % | −0.50 | −0.12 | **−0.70** | 0.21 | −0.13 |
| Number of powdery mildew spots | −0.30 | 0.08 | **−0.72** | 0.20 | −0.17 |
| Area of powdery mildew spots, mm$^2$ | −0.36 | 0.03 | −0.49 | 0.35 | **−0.72** |
| Number of sunspots (average number per year), units | **0.86** | 0.20 | 0.04 | 0.25 | 0.37 |
| Number of sunspots (in July), units | **0.82** | 0.23 | 0.01 | 0.28 | 0.37 |
| Number of sunspots (in Aug.), units | **0.88** | 0.23 | 0.09 | 0.14 | 0.33 |
| Wolf's sunspot number (July), scores | **0.81** | 0.22 | 0.03 | 0.29 | 0.38 |
| Wolf's sunspot number (Aug.), scores | **0.88** | 0.23 | 0.10 | 0.16 | 0.35 |

summand in its right part characterizes the process of spore settling on leaf surface from the air. The rate of this process may be experimentally estimated in practice with $k_{s,\,ss}$ coefficient of spore settling. In order to do this, it is accepted that the $\Delta N_{ss}^0$ spores can settle per unit of a leaf surface area for the $\Delta t$ time. $N$ is used to denote the number of spores in the air column above the leaf-surface area unit. Therefore, the coefficient of spore settling ($k_{s,\,ss}$) may be calculated with the following formula:

$$k_{s,ss} = \frac{\Delta N_{ss}^0}{\Delta t N}. \quad (6)$$

It can be assumed that the rate of altitudinal concentration, $n(h)$, of uredo spores in the air above the analyzed part of the leaf surface has an exponential pattern; i.e.,

$$n(h) = n^0 \exp\left\{-\frac{h}{H}\right\}, \quad (7)$$

where $n^0$ denotes the concentration of uredospores in the air column close to the leaf surface.

It is easy to show with the use of equation (7) that the values for $N$, $n^0$, and $H$ are associated with the following relationship:

$$N = n^0 H. \quad (8)$$

When conducting the field surveys, the values for $n^0$, $H$, and, respectively, $N$ may be estimated based on the measurement results for the number of uredo spores that settled on the surface of detectors of different heights. In addition, the value for $n^0$ close to the surface of the lower detector may be estimated with the following formula:

$$n^0 = \frac{\Delta N_{ss}^0}{\bar{V} \Delta t}, \quad (9)$$

where $\bar{V}$ denotes the average rates of uredo spore settling (for the brown rust spores, it comprises 1.26 m/s (24)).

The value for $H$ may be calculated based on the measurement results for a number of spores, $\Delta N_{ss}^0$ and $\Delta N_{ss}^d$, settling, relatively, on the surfaces of a detectors installed at the lower and upper levels for $\Delta t$.

In this case, it may be estimated with the following equation:

$$H = \frac{\Delta h_d}{\ln \dfrac{\Delta N_{ss}^0}{\Delta N_{ss}^d}}, \quad (10)$$

where $\Delta h_d$ denotes the difference between the detectors installed at the lower and upper levels.

Substituting the $H$ value produced in equation (8) and the subsequent $N$ value obtained in equation (6),

the actual unknown value for the spore settling coefficient denoted by $k_{s,\,ss}$ can be found.

The second summand (1) describes the process ending in settled spore death, which is characterized by the coefficient of their nonviability, $d_{ss}$.

The $d_{ss}$ coefficient is regarded as constant. It is not difficult to make sure that the inverse of $d_{ss}$:

$$T_{ss}^d = (d_{ss})^{-1}, \quad (11)$$

has the dimension of time, representing the certain time of settled spore death.

Indeed, it is assumed, for instance, that $k_{ss,\,se} = 0$ and $d_{ss} \neq 0$ in equation (1). Equation (1) is solved subject to the initial conditions as $t = 0$ and $x_{ss} = x_{ss}^0$. Therefore, the appropriate law of changing the number of settling spores can be found with the following formula:

$$x_{ss} = x_{ss}^0 \exp\left(-\frac{t}{T_{ss}^d}\right). \quad (12)$$

Equation (12) shows that $T_{ss}^d$ is equal to the time interval. After the end of it, the number of the settling spores is reduced to $e$ times because of death.

Finally, the third summand in equation (1) characterizes the settling spore reduction caused by their transition to the status of "embedding spores."

Equation (2) describes the subsequent stage of pathogen spreading, which represents penetrating the host plant tissues by the settled spores developing the germ tubes, which enter more frequently through the stomata. The summands of the right part of this equation describe three processes in the life cycles of a fungus. The first of them describes a transition of the settled spores into the status of embedded spores, which is characterized by $k_{ss,\,se}$ coefficient of their embedding and penetrating the host plant tissues with the germ tubes.

A coefficient of penetration the tissues with the germ tubes of the settled spores, $k_{ss,\,se}$, may be used in the following form:

$$k_{ss,se} = k_{ss,se}^0 \tilde{P}(x_n), \quad (13)$$

where $k_{ss,se}^0$ denotes a coefficient of settled spore embedding on the clean leaf surface and $\tilde{P}$ denotes a probability of an impact of the spores settled on the nondamage area.

The $k_{ss,se}^0$ coefficient depends on the air temperature, $T_a$, and humidity $q_a$ [25]. The optimum temperature for the brown rust infection in plants is 15−20°C. Under these conditions, the moisture is required to remain on plants for no less than 4−5 h. The infection spread rates tend to be slower at lower and, likewise, higher temperatures. The infection begins at +5−6°C in case of plant retaining moisture for 10−12 h. In

addition, infection does not occur at the temperature lower than +5°C.

The probability, $\tilde{P}$, in equation (11) depends on a necrosis number, $x_n$. In order to estimate it, the area of one necrosis, $s_0^n$, is introduced to consider the issue. In case of one necrosis, the probability of occurrence of a settled spore on the nondamage surface comprises $p_0 = 1 - s_0^n$ (for a single area of the analyzed part). With respect to the necroses relative to the law of uniform dispersal, $x_n$, the probability of occurrence on the nondamage part is calculated with the following formula:

$$\tilde{P} = (1 - s_0^n)^{x_n}. \tag{14}$$

Taking into consideration equation (14), it is expressed as:

$$k_{ss,se} = k_{ss,se}^0 (1 - s_0^n)^{x_n}. \tag{15}$$

The second summand in the right part (2) describes the process of death of uredo-spore germ tubes, which is characterized by the coefficient of death, $d_{se}$. The third summand describes transformation of the embedded spores with germ tubes into the pustules over the time interval, $\tau_L$, known as the latent period.

It is well known that the length of a latent period, $\tau_L$, is described as a function of air temperature. According to the surveys performed by S.S. Sanin [26], the new uredo pustules tend to occur in 4–5 days, 8–9 days, and 15–16 days at the average daily temperatures of +20°C, +15°C, and +10°C, respectively.

Equation (3) describes the formation of pustule on the leaf surface. The formation rate value for the pustules embedded from the spores is set by the first summand in the equation's right part, representing the rate value set to the time range interval similar to the latent period, $\tau_L$.

The second summand in the right part of equation (3) characterizes the rate of death of pustules, which is determined by the coefficient of death, $d_p$:

$$d_p = d_p^e + d_p^i, \tag{16}$$

where $d_p^e$ denotes a coefficient of pustule death induced by external factor effects and $d_p^i$ denotes a coefficient of pustule death induced by pustule natural death.

Equation (4) describes the variation in the number of spores in the air above a unit of the leaf surface ($x_s$). The first summand in the right part characterizes the rate of increase in the number of spores above the leaf surface, which is caused by the process called sporula-tion resulting in the formation of spores. It is determined by a coefficient of pustule spore production rates: $k_{p,s}$. Coefficient $k_{p,s}$ is associated with the coefficient of pustule death induced by pustule natural death, $d_p^i$, as a ratio:

$$k_{p,s} = N_s d_p^i, \tag{17}$$

where $N_s$ denotes a total number of spores produced by one pustule.

The value of $N_s$ (17) may be determined following the considerations as indicated below. The area of the nondamage leaf surface per pustule is taken into consideration:

$$s' = \frac{(1 - s_0^n)^{x_n}}{x_n}. \tag{18}$$

The maximum area of a pustule formed on the leaf surface is denoted as $s_0^p$. The pustules tend to reach the maximum area relative to the maximum number of produced spores, $N_0$, at $s' > s_0^p$. Herewith, the average pustule size at $s' < s_0^p$ is $s_0^p/s'$ times lower than the maximum number, while the number of spores produced by them can, respectively, comprise:

$$N_s = N_0 \frac{s'}{s_0^p} = \frac{N_0(1 - s_0^n)^{x_n}}{s_0^p x_n}. \tag{19}$$

Therefore, the expression of $k_{p,s}$ coefficient in equation (4) has the following form:

$$k_{p,s}(x_p, x_n) \begin{cases} d_p^i N_0, & \dfrac{(1 - s_0^p)^{x_n}}{s_0^p x_p} > 1, \\[3mm] d_p^i \dfrac{N_0(1 - s_0^p)^{x_n}}{s_0^p x_p}, & \dfrac{(1 - s_0^p)^{x_n}}{s_0^p x_p} \le 1. \end{cases}$$

The second summand in the right part of equation (4) describes the reduction in spores above the leaf surface, which is caused by their death and their settling on the leaf surface, expressed by the third summand.

Equation (5) characterizes the process of necrosis formation on the leaf surface. The first summand in its right part describes the process of necrosis formation because of the pustule natural death after the end of the infection period, $\tau_i$.

The second summand in the right part of equation (5) characterizes the necrosis formation during the infection period because of the pustule death induced by external factor effects with the use of the coefficients of $d_p^e$ for pustule death caused by external factors and $d_p^i$ for pustule natural death.

The task formulated in the aspect of mathematics represents the Cauchy problem for the delay differential equation (DDE) system in the following form:

$$y'(t) = f(t, y(t), y(t - \tau)), \quad t \geq t_0,$$
$$y(t) = \psi(t), \quad t \in [t_0 - \tau, t_0]. \tag{20}$$

In order to find the solution for $y(t)$ at $t \geq t_0$, it is necessary to set the initial values, $\psi(t)$, in the following interval: $t \in [t_0 - \tau, t_0]$. The most rational approach to a numerical solution of a system (20) is a step method, i.e., substituting the values into the system of ordinary differential equations (ODEs) for each time interval:

$$t \in [t_0 + p\tau, t_0 + (p + 1)\tau]:$$
$$y'(t) = f(t, y(t), \tilde{y}(t - \tau)),$$
$$t \in [t_0 + p\tau, t_0 + (p + 1)\tau], \tag{21}$$

where $p = 0, 1, ..., [T/\tau] + 1$, where $T$ denotes the modeling time. In addition, it is supposed that $\tilde{y}(t - \tau)$ is known since this value is calculated in the interval $[t_0 + (p - 1)\tau, t_0 + p\tau$ with interpolating the solution obtained previously in this interval of solution or the initial values, $\psi(t)$, set in the interval, $t \in [t_0 - \tau, t_0]$.

It should be noted that different algorithms for numerical solutions of a differential equation system are used [27]. In addition, the DIFSUBDEL software package described previously in detail [28] was used in this survey for numerical solution of a system of delay differential equations (1)−(5).

The imitation model for brown-rust spread in wheat, which is present in the survey, may be used to create the modern expert systems for forecasting and plant disease diagnostics.

Various levels of intensity of damage to the wheat varieties, caused by a disease associated with their morphometrical properties included can both indicate the necessity to use the adaptive approach to the agricultural technology choice and require the adjustment of a system of protection measures [29]. Special attention should be drawn to breeding the disease-resistant varieties and, particularly, creating the genotypes displaying a wider range of adaptive properties [12].

The most important factors having an impact on exhibiting the phenotypic variation in disease resistance of wheat usually represent the complex of meteorological factors (temperature, amount of precipitation, humidity) and the solar activity [30]. In addition, the data on the solar activity effect on the arable-crop disease spread are quite inconsistent in various open sources. The current survey-derived data on increased rates of the brown-rust infection, along with decreasing the number of sunspots, quite reconcile the data found in the survey indicated below [31], which prove that the brown-rust epiphytotics mostly occurred in the years of weak and, less frequently, medium solar activity.

Therefore, it was indicated based on the pathogenesis-related factor model built with the 2009−2020 datasets that the brown-rust spread mostly tends to increase along with a rise in temperatures higher than 10°C in May and the amount of precipitation in June. It quite coincides with the data obtained in surveys of 1995−2012. The dependence revealed in the survey coincides with the data presented in the paper of V.V. Chekmarev (2016) [30].

Wide-scale crop monitoring is of great importance for forecasting the disease spread in the arable crops including wheat [3]. It is recommended that monitoring should involve the parameters for the pustule number and area calculated with an ellipse formula as specific damage-response framework of pathogenesis of brown-rust in wheat in addition to the conventional parameters relevant to the spread of a disease. It should be noted that wheat variety differentiation by disease resistance is based on identifying the type of response, while measuring the size of a pustule is an important criterion for this scale.

## CONCLUSIONS

Therefore, the survey results showed that the highest-level resistance to the brown rust disease was typical for the tall wheat plant varieties (over 98 cm). They exhibited the vertical (less than 15°), deflection (15°−45°), and horizontal (46°−90°) flag-leaf angle patterns. The thick wax coating layers (nine scores), the leaf trichome-type indument density of 941.7 ± 63.8 per 1 cm$^2$, and the trichome length of more than 1.5 mm were typical for them. The negative correlations between the disease progression, the total and productive branching ratios, and the wheat flag-leaf color were revealed. In addition, the lowest disease progression rate was recorded in the samples with light-green leaves.

The system of meteopathology forecast models for brown rust progression, based on both revealing a multitude of correlations between the disease-damage parameter values, the meteorological factors, and the solar activity and further revealing the dominance trends on their changing has been developed. Thus, based on the model used in the 2009−2020 experiments, it was revealed that the brown rust progression rate is mostly increased with the increases in the number of temperature degrees above 10°C in May and the precipitation amount in June. In addition, the rates of the wheat brown rust progression tended to decrease with the increased rates of damage caused by septoria and powdery mildew.

The survey results may be of certain interest for grain production industries, including agricultural enterprises specializing in growing wheat as food, forages, and seeds. They should be useful for seed breeding and farming and developing the mechanisms for organic agriculture. The mathematical models pro-

duced and described above may be used to develop the information systems for expert monitoring the agrocenoses in the phytosanitary context, forecasting, and supporting the decision-making in plant protection.

## COMPLIANCE WITH ETHICAL STANDARDS

This article does not contain any studies involving animals or human participants performed by any of the authors.

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