

Possible Effect of Abiotic Environmental Factors on Changes in Wheat Resistance to Leaf Rust

M. A. Kolesova¹, V. G. Zakharov², and L. G. Tyryshkin^{1*}

ABSTRACT

Possible influence of 3 abiotic environmental factors (temperature, nitrogen salt, and benzimidazole) on wheat resistance to *Puccinia triticina* was studied. Under the effect of these factors, statistically significant decrease in the rust development was revealed for 6 wheat varieties. Specific changes of virulence in 6 pathogen monopustule isolates under the effect of those factors were revealed with high frequencies. Subjected to a particular factor, we observed an absolute coincidence of the infection types of seedlings infected with rust pathogen clones multiplied in the absence of this factor, and infection types of leaves, incubated in the absence of the factor, but infected with isolates, multiplied in the presence of this factor. Six subpopulations of the pathogen representing mixture of genotypes virulent to 2 wheat varieties under certain conditions were created. We did not find significant differences in two disease development indexes (number of pustules and uredospores' number in pustule) in seedlings affected by a factor and infected with subpopulations multiplied in the absence of the factor, and disease development indexes in leaves not subjected to the factor but in °Culated with subpopulations multiplied in the presence of this factor. According to the results, the influence of studied factors on expression of specific (vertical) and non-specific (horizontal) wheat seedling resistance to rust was not revealed. Obviously, significant decrease in the rust development under the effect of studied environmental factors is primarily (if not only) related to their influence on the pathogen virulence and aggressiveness.

Keywords: Race-specific resistance, Pathogen virulence, Pathogen aggressiveness, Disease development indexes.

INTRODUCTION

Plants resistance to diseases is primarily determined by the allele states of their major and minor resistance genes and the corresponding genes for virulence in pathogens. Vertical (race-specific) resistance is expressed if the pathogen has at least one avirulence allele, and plant has a complementary resistance allele. On the contrary, susceptibility is observed in host plant when pathogen possesses alleles for virulence of all genes corresponding to all

resistance alleles of the host plant (Flor, 1956, 1971).

However, in a disease triangle, the resistance phenotype of plant is greatly influenced by environmental abiotic factors. For example, as earlier as in the 1920s, the differences in wheat and oat seedlings infection with rusts were revealed at different temperatures (Waterhouse, 1929). The changes in infection types for cereals after infection with rusts under the influence of temperature has been confirmed in many experiments. A specific term "temperature-

¹Department of Genetics, N. I. Vavilov All-Russian Institute of Plant Genetic Resources, St. Petersburg, 190000, Russia.

² Department of Breeding, Ulyanovsk Research Institute of Agriculture - Branch of the Samara Scientific Center of the Russian Academy of Sciences, Timiryazevsky, Ulyanovsk District, Ulyanovsk Region, 433315, Russia.

*Corresponding author; e-mail: tyryshkinlev@rambler.ru



sensitive resistance genes” was even proposed to describe this phenomenon (Bromfield, 1961; Martens *et al.*, 1967; Dyck and Johnson, 1983; Browder and Eversmeyer, 1986; Gousseau and Deverall, 1987; McIntosh *et al.*, 1995; Bryant, 2013; Feng *et al.*, 2019).

Information on the effects of the main macro-nutrients on the cereal resistance to biotrophic pathogens is contradictory. According to common viewpoint, nitrogen fertilizers sharply decrease the resistance and phosphorus, especially in combination with potassium, increases it (Peresyphkin, 1989; Dordas, 2008; Shkalikov *et al.*, 2010). This opinion has been proven (Howard *et al.*, 1994; Mascagni *et al.*, 1997; Sweeny *et al.*, 2000; Atiq *et al.*, 2017). Effect of nitrogen fertilizer on resistance of barley (Goncharova *et al.*, 2005) and wheat (Makarova, 2005) to rusts has been studied. In some studies, on the contrary, there was no significant effect of nitrogen on wheat resistance to brown rust (Vavilov, 1918; Stakman and Aamodt, 1924; Wilcoxon, 1980).

The effect of benzimidazole on cereals resistance to rusts was also investigated (Forsyth and Samborski, 1958). Differences in the types of reaction to phytopathogens’ infection of intact plants and leaf segments placed on this chemical solution were studied for many cereal samples (Tyryshkin *et al.*, 2005, 2008). These differences were thought to be associated with the benzimidazole induction of expression of oligogenes for vertical resistance (Tyryshkin *et al.*, 2005, 2008).

Earlier, we showed that changes in the degree of diseases development under the influence of abiotic environmental factors could be largely explained by their effect not on the plant, but on the pathogens’ virulence and aggressiveness (Tyryshkin, 2016).

At the same time, the effect of changes under the influence of the environmental factors in virulence and aggressiveness on the degree of diseases development cannot be considered as the final proof for the

absence of direct influence of the same factors on the change in plant resistance.

The objective of this work was to study the possible effects of three environmental factors including temperature, nitrogen salt, and benzimidazole on specific and non-specific resistance of wheat to leaf rust.

MATERIALS AND METHODS

Three abiotic environmental factors including temperature, benzimidazole, and nitrogen salt were studied for their possible effect on vertical and horizontal resistance to wheat leaf rust of six spring wheat varieties, namely, Zhigulevskaya, Ivolga, Pamiaty Azieva, Novosibirskaya 29, Leningradskaya 6, and Nadejda Kusbassa.

To this end, seeds of wheat varieties were sown on cotton wool rolls in 4 cuvettes. Three cuvettes were placed in light chamber (22°C, 2500 Lux), and one was placed in light chamber at 28°C. Nine days after sowing, seedlings (1-2 leaves stage) growing in one cuvette at 22°C were abundantly poured with ammonium nitrate solution (concentration 1.29 g L⁻¹) (variant N₃). Next day, intact plants of the 3 treatments (22°C – watering (control), 22°C – poured with ammonium nitrate solution, and 28°C – watering) were placed in cuvettes horizontally. From seedlings in the 4th cuvette, leaf segments 5 cm in length were put on cotton wool wetted with benzimidazole solution (concentration 60 mg/L).

Intact plants and leaf segments were sprayed with water suspensions of the rust causal agent uredospores (3×10³ spores mL⁻¹) using hand atomizer. Complex population of *Puccinia triticina* Erikss, sampled on susceptible wheat varieties in 2020 in North-West Region of Russia, was used for inoculation.

Cuvettes were covered with polyethylene film and glasses and placed in chamber at 22°C in darkness. The cuvette, in which seedlings were grown at 28°C was placed in a chamber at the same temperature. After a

day, the polyethylene and glass were removed, the intact plants being returned to a vertical position and put under light. The cuvette with leaf segments on the benzimidazole was covered with glass. Ten days later, the number of rust pustules in the middle part of 10 leaves of intact plants 5 cm long, as well as on the leaf segments on the benzimidazole solution, was counted.

To study the influence of the factors on race-specific resistance, 6 monopustule isolates (= Clones= Single spore cultures) of *P. triticina* were sampled from Nadejda Kusbassa plants in control variant (pouring plants with water, 22°C) of the first experiment. These isolates were maintained on leaf segments of the variety placed on Water-Wetted Cotton Wool (WWCW). The seedlings of 6 wheat varieties were grown in cuvettes on a WWCW at 22 and 28°C.

To study the effect of benzimidazole, each pathogen' isolate was used to infect 10 leaf segments of Nadejda Kusbassa variety placed on a WWCW at 22°C. Four days later, 5 segments were transferred onto cotton wool wetted with benzimidazole solution (60 mg L⁻¹). Clones multiplied in the presence of benzimidazole were used to in°Culate leaf segments of experimental wheat varieties, placed on WWCW. For in°Culation, leaf with several well-formed pustules was tightly attached to leaf segments, and then these leaf segments were pulverized with water. The same clones, multiplied on the leaf segments on WWCW, were used to infect wheat varieties leaf segments on water and on benzimidazole.

To study the effect of the nitrogen salt, each isolate of the pathogen was used to infect leaf segments of Nadejda Kusbassa placed on WWCW at 22°C. Four days later, 5 segments were transferred onto cotton wool wetted with ammonium nitrate solution (1.29 g L⁻¹). Clones multiplied under the presence of the salt were used to in°Culate the varieties leaf segments placed on a WWCW. Clones multiplied on water-placed leaf segments were used to infect leaf segments of experimental wheat varieties on water and on ammonium nitrate solution.

To study the effect of temperature, each pathogen isolate was used to infect leaf segments of the susceptible variety placed on WWCW at 22°C and, after four days, 5 segments were transferred to WWCW at 28°C. Clones of the pathogen multiplied at 28°C were used to in°Culate incubated at 22°C leaf segments of the varieties' plants grown at 22°C too. Clones multiplied at 22°C were used to in°Culate leaf segments of seedlings grown at 22°C and incubated at the same temperature (control). The same clones were used to in°Culate leaf segments of seedlings grown at 28°C and incubated at 22°C, as well as leaf segments of seedlings grown at 22°C, but incubated at 28°C.

Infection types were scored 8 days after in°Culation according to Mains and Jackson (1926), where 0 is host resistance, pathogen avirulence and 3 – plant susceptibility, pathogen virulence.

To study the effect of environmental factors on nonspecific resistance, seedlings of wheat varieties Zhigulevskaya and Leningradskaya 6 were grown in the light chamber at 22°C. Leaf segments were placed in 3 cuvettes: on WWCW, benzimidazole solution (60 mg L⁻¹), and NH₄NO₃ (1.29 g L⁻¹). The segments in each cuvette were in°Culated with complex population of *P. triticina* and incubated at 22°C, except the cuvette with leaf segments on WWCW were placed in light chamber at 28°C. As a result, 6 subpopulations were developed, and they were maintained on water-placed leaf segments of Zhigulevskaya and Leningradskaya 6 varieties.

To study the effect of benzimidazole on nonspecific resistance, a subpopulation sampled from a variety leaf segments, placed on the chemical solution, was multiplied in 2 cuvettes on leaf segments of the same variety placed on WWCW or benzimidazole. Suspensions of uredospores of the same concentration were prepared from these two formed in°Culums. The spores' concentration was determined after their count in 5 µL suspension drops under light microscope (×56) and was equaled by



adding water. Leaf segments of each variety seedlings were placed in 3 cuvettes: Two on WWCW, one on cotton wool wetted with benzimidazole solution. Leaf segments on water were infected with subpopulations of the pathogen multiplied on water and benzimidazole, and leaf segments on benzimidazole were infected with a subpopulation multiplied on leaf segments in water.

Analogical experiment was done with solution of NH_4NO_3 to reveal the effect of nitrogen salt on horizontal resistance. Subpopulation from a variety leaf segments, placed on ammonium nitrate, was multiplied in 2 cuvettes on leaf segments of the same variety placed on water-wetted or salt solution wetted cotton wool. After 10 days suspensions of uredospores of the same concentration were prepared from these 2 cuvettes. Leaf segments of each variety seedlings were placed in 3 cuvettes: two on WWCW, one on cotton wool wetted with ammonium nitrate solution. Leaf segments on water were infected with subpopulations of the pathogen multiplied on water and NH_4NO_3 , and leaf segments on the salt solution were infected with an in°Culum multiplied on leaf segments in water.

To study the effect of temperature, subpopulation sampled from a certain variety at 28°C was reproduced on leaf segments of the same variety incubated at 22 and 28°C. Spores' suspensions from these 2 in°Culum were created and uredospores concentrations in them were equaled. Segments of the experimental varieties leaves infected with subpopulation and multiplied at 22°C were incubated at 22 and 28°C, and those infected with in°Culum and multiplied at 28°C were incubated at 22°C.

Eight days after the infection, the number of pustules on leaf segments and average number of spores in pustules were calculated. To determine uredospores' amount, suspension of spores from 25 pustules was prepared in 2 mL of water, and spores' number was determined in 3 drops of 2 μL volume under light microscope.

Statistical data analysis was carried out using single-factor ANOVA test (Dospekhov, 1979). For statistically significant differences, criterion of Least Significant Difference (LSD) was used.

RESULTS AND DISCUSSION

For seedlings of all 6 experimental varieties of wheat, significant decreases in the development of leaf rust was observed under the influence of 3 abiotic environmental factors – two chemical (solution of benzimidazole and of ammonium nitrate) and one physical factor (temperature) (Table 1).

On average, ammonia nitrate solution, high temperature, and benzimidazole decreased the number of rust pustules in wheat varieties by 62.7, 59.1, and 64.0%, respectively. These changes in rust development were previously regarded as evidence for the effect of environmental factor directly on the expression of plant resistance genes (Martens *et al.*, 1967; Dyck and Johnson, 1983; Gousseau and Deverall, 1987; Ramage and Sutherland, 1995; Goncharova *et al.*, 2005; Makarova, 2005; Dordas, 2008; Tyryshkin *et al.*, 2005, 2008).

At the same time, they can be the result of not only changes in resistance, but also of changes in the pathogenic properties of the parasite (virulence and aggressiveness). Earlier, it has been shown that, under the influence of several physical and chemical factors, modification and variability of virulence and aggressiveness of phytopathogens is very common. To prove this variability, an original experimental approach was proposed. Environmental factors influenced the pathogens when they were multiplied on susceptible host genotypes, and the experimental plant genotypes that were used to study virulence and aggressiveness, were not exposed to these factors (Tyryshkin, 2016).

Theoretically, the third possible explanation of the drastic changes in leaf rust development under abiotic factors could

Table 1. Number of pustules per unit leaf surface area on wheat seedlings under different abiotic environmental conditions.

Variety	Variants				LSD
	Intact plants, pouring, temperature		Leaf segments on, temperature		
	Water (22°C)	Solution N ₃ (22°C)	Water, (28°C)	Benzimidazole (22°C)	
Zhigulevskaya	45.3	12.1	24.3	13.3	3.2
Ivolga	38.1	14.6	8.4	5.2	5.0
Pamiaty Azieva	38.3	11.0	15.2	19.2	4.7
Novosibirskaya 29	41.2	19.1	16.1	17.1	6.0
Leningradskaya 6	42.0	18.9	19.2	12.2	3.3
Nadejda Kusbassa	50.8	19.6	21.3	25.1	6.3

be their influence on decrease of uredospores germination. However, in this experiment, evidently, no chemical compound could influence the germination rate because this process is on leaf surface, and benzimidazole and nitrogen salt are in plant tissues. Moreover, in our previous work, we did not find significant changes of *P. triticina* spores germination rate under the effect of benzimidazole, nitrogen salt, and elevated temperature (Tyryshkin, 2016).

To identify possible changes in wheat race-specific resistance, we used an approach of comparisons of infection types (phenotypic result of interaction of major genes for resistance in plant and for virulence in parasite) of wheat genotypes to infection with monopustule *P. triticina* isolates in 3 variants of the treatment. First, neither the plant nor the pathogen was subjected to certain abiotic factor. Second, host leaves not subjected to the factor were infected with the pathogen isolates multiplied under the factor influence. Third, host leaves were subjected to the factor and infected with isolates multiplied in the absence of this factor. The differences in reaction types between first and second treatments would indicate changes of the pathogen virulence under the effect of a certain factor. Reduction in infection types in treatment 3 compared to treatment 2 should clearly indicate the direct effect of a factor on host vertical resistance.

Changes in infection types from 3 (susceptibility/virulence) on leaves placed

on water and infected with *P. triticina* isolates and multiplied on leaves on water, up to 0 on leaf segments on water, after infection with the isolates and multiplied in the presence of benzimidazole, were observed in 14 cases out of 36 pairs of interaction (Table 2). Evidently, these changes indicate high frequency of variability in phenotypical expression of virulence under the chemical effect. In this treatment, leaves of wheat varieties did not have contact with benzimidazole.

In all the studied combinations, the infection types of leaves on benzimidazole infected with the fungus clones and multiplied in the absence of the factor, coincided with those leaf segments in water that were infected with pathogen isolates and multiplied in the presence of benzimidazole (Table 2). In our viewpoint, this indicates that the chemical does not directly affect the resistance of wheat varieties to the leaf rust pathogen genotypes under study. If it were not so, in some cases, we should have observed lower infection types in the first case.

At incubation of leaf segments on ammonium nitrate solution, a decrease in infection types compared to the incubation of leaves in water was found in 19 out of 36 pairs of interaction (Table 3). This could be the result of changes in the virulence of some pathogen clones under the influence of this chemical factor, and/or change in race-specific resistance.



Table 2. Effect of benzimidazole on infection types of wheat leaf segments after inoculation with *P. triticina* clones.

No clone	Leaf segment incubation	The clone multiplication on	Infection type					
			Zhigulevskaya	Ivolga	Pamiaty Azieva	Novosibirskaya 29	Leningradskaya 6	Nadejda Kusbassa
1	Water	Water	3	3	3	3	3	3
	Water	Benzimidazole	3	0	3	3	0	3
	Benzimidazole	Water	3	0	3	3	0	3
2	Water	Water	3	3	3	3	3	3
	Water	Benzimidazole	3	3	0	3	0	0
	Benzimidazole	Water	3	3	0	3	0	0
3	Water	Water	3	3	3	3	3	3
	Water	Benzimidazole	0	3	3	3	3	0
	Benzimidazole	Water	0	3	3	3	3	0
4	Water	Water	3	3	3	3	3	3
	Water	Benzimidazole	3	0	3	0	3	3
	Benzimidazole	Water	3	0	3	0	3	3
5	Water	Water	3	3	3	3	3	3
	Water	Benzimidazole	0	3	0	3	3	3
	Benzimidazole	Water	0	3	0	3	3	3
6	Water	Water	3	3	3	3	3	3
	Water	Benzimidazole	3	0	3	0	3	0
	Benzimidazole	Water	3	0	3	0	3	0

Table 3. Effect of nitrogen salt on infection types of wheat after inoculation with *P. triticina* clones.

No clone	Leaf segment incubation	The clone multiplication on	Infection type					
			Zhigulevskaya	Ivolga	Pamiaty Azieva	Novosibirskaya 29	Leningradskaya 6	Nadejda Kusbassa
1	Water	Water	3	3	3	3	3	3
	Water	N ₃	0	0	3	0	3	0
	N ₃	Water	0	0	3	0	3	0
2	Water	Water	3	3	3	3	3	3
	Water	N ₃	0	0	3	3	3	3
	N ₃	Water	0	0	3	3	3	3
3	Water	Water	3	3	3	3	3	3
	Water	N ₃	3	0	3	3	0	0
	N ₃	Water	3	0	3	3	0	0
4	Water	Water	3	3	3	3	3	3
	Water	N ₃	3	0	0	3	0	3
	N ₃	Water	3	0	0	3	0	3
5	Water	Water	3	3	3	3	3	3
	Water	N ₃	0	3	0	0	3	0
	N ₃	Water	0	3	0	0	3	0
6	Water	Water	3	3	3	3	3	3
	Water	N ₃	3	0	0	0	3	3
	N ₃	Water	3	0	0	0	3	3

The results of infection of leaf segments on water with *P. triticina* clones and multiplied in the presence of ammonium nitrate indicate the correctness of the first hypothesis.

For the varieties whose leaves were incubated in the presence of the factor, susceptibility to clones did not alter virulence, because of their reproduction in presence of ammonium nitrate. This indicates that NH_4NO_3 had no effect on vertical resistance of the studied wheat genotypes.

No changes were recorded in the infection

types under the influence of increased pre-inoculation temperature of seedling growth (Table 4). In 18 out of 36 pairs of interaction, leaf segments incubated at 22°C and multiplied at 2 different temperatures showed differences in the types of reactions to the infection by pathogen isolates (Table 4). This fact confirmed the earlier conclusion on the high-frequency effect of this factor on the phenotypical expression of the pathogen virulence (Tyryshkin, 2016).

In all combinations of interaction, an absolute coincidence in infection types was recorded for the leaf segments incubated at

Table 4. Effect of temperature on infection types in wheat leaf segments after inoculation with *P. triticina* clones.

No clone	Temperature of seedlings growth (°C)	Temperature of leaf segments incubation (°C)	Temperature of the clone multiplication (°C)	Infection type					
				Zhigulevskaya	Ivolga	Pamiaty Azieva	Novosibirskaya 29	Leningradskaya 6	Nadejda Kusbassa
1	22	22	22	3	3	3	3	3	3
		22	28	3	3	0	3	0	3
		28	22	3	3	0	3	0	3
2	22	22	22	3	3	3	3	3	3
		22	28	0	0	3	0	3	0
		28	22	0	0	3	0	3	0
3	22	22	22	3	3	3	3	3	3
		22	28	3	0	3	3	0	3
		28	22	3	3	3	3	3	3
4	22	22	22	3	3	3	3	3	3
		22	28	0	0	3	0	3	0
		28	22	0	0	3	0	3	0
5	22	22	22	3	3	3	3	3	3
		22	28	3	3	0	0	3	0
		28	22	3	3	0	0	3	0
6	22	22	22	3	3	3	3	3	3
		22	28	0	0	3	3	0	3
		28	22	0	0	3	3	0	3
		22	22	3	3	3	3	3	3
		22	28	3	3	3	3	3	3
		28	22	3	3	3	3	3	3



28°C, infected with *P. triticina* isolates, and multiplied at 22°C, and the leaf segments incubated at 22°C, infected with pathogen isolates, and multiplied at 28°C, (Table 4). This fact proves that in wheat varieties under study, temperature has no effects on vertical resistance to given *P. triticina* clones. In the case of such influence, lower infection types must be observed in the first treatment in comparison with the second, at least for some combination of variety – isolate.

Theoretically, the changes in the degree of leaf rust development on wheat varieties seedlings under the influence of the environmental factors could be explained also by changes in plant race-nonspecific resistance and/or changes in the aggressiveness of *P. triticina*.

To verify these hypotheses, 6 artificial subpopulations of the rust pathogen were created multiplying initial complex *P. triticina* population on leaves of two wheat varieties under the influence of abiotic environmental factors. As a result, each subpopulation represented a mixture of the rust isolates virulent to a certain variety in the presence of specific factor (avirulent under certain conditions isolates were discarded during the multiplication). These subpopulations, multiplied under control conditions (leaf segments on water, 22°C), were used to infect leaf segments on water at 22°C and leaf segments incubated in the presence of the studied factors. Additionally, leaf segments on water were inoculated with suspensions of uredospores from the same subpopulations but multiplied in the presence of a specific factor. Before inoculation, the spores' concentrations in the two suspensions used for inoculation in each experiment were equaled.

Significant differences in the rust development under the influence of 3 abiotic environmental factors were found after inoculation with mixture of *P. triticina* clones virulent to wheat genotypes under specific conditions. On average, for the two wheat varieties, the number of pustules per leaf surface unit decreased by 58.7, 51.2 and 40.8% compared to the control in the variants of seedling segments incubation in the

presence of benzimidazole, ammonium nitrate, and at increased temperature, respectively. Compared to the control, the average number of uredospores in pustule in these variants decreased by 31.4, 39.6, and 27.6%, respectively (Table 5).

Thus, the studied factors reduced 2 indexes of rust development on 2 wheat varieties under study, after infection with rust subpopulations represented by mixture of pathogens genotypes virulent to these plant genotypes. It is obvious that, in this case, the decrease cannot be due to a change in virulence of some isolates in the subpopulations, but theoretically, it can be explained by the influence of a factor on the aggressiveness of pathogens and/or on the horizontal resistance of the varieties. Reduction of indexes of rust development in the variant of infection of leaves, not exposed to the factors, with the parasite subpopulations multiplied at their presence (Table 5), indicates the influence of the three studied abiotic factors on the aggressiveness of the pathogen subpopulations.

No significant differences were found in wheat varieties for leaf rust development between the variants of infection of leaf segments, incubated in the presence of a factor and infected with subpopulation of pathogen multiplied in the absence of this factor, and leaf segments incubated in water at 22°C and infected with subpopulation multiplied in the presence of the factor (Table 5).

This fact indicates the absence of significant influence of nitrogen salt, benzimidazole, and high temperature directly on the change in race-nonspecific resistance in the studied wheat varieties. If such an effect had been observed, the number of pustules and/or the number of spores in pustules, would have been different in the different variants of experiments (at least for one factor).

CONCLUSIONS

A study of the effect of benzimidazole, ammonium nitrate, and increased temperature on the results of infection with

Table 5. Effect of abiotic environmental factors on average *P. triticina* pustules number per leaf and their productivity after inoculation with virulent subpopulations of the pathogen.

Leaf segments incubation on	Subpopulation multiplication	Variety			
		Zhigulevskaya		Leningradskaya 6	
		Pustules number	Uredospores number in pustule	Pustules number	Uredospores number in pustule
Factor-Benzimidazole					
Water	Water	19.6	1380.0	20.1	1420.0
	Benzimidazole	8.6	980.0	7.8	940.0
Water	Benzimidazole	8.4	960.0	8.3	980.0
LSD		4.1	120.0	3.8	120.0
Factor-N ₃					
Water	Water	23.5	1300.0	18.3	1380.0
N ₃	Water	10.5	820.0	9.9	800.0
Water	N ₃	10.4	820.0	8.7	840.0
LSD		4.2	105.0	2.1	100.0
Factor-Temperature					
22°C	22°C	18.5	1320.0	18.3	1360.0
28°C	22°C	13.9	900.0	7.9	1040.0
22°C	28°C	13.7	920.0	8.1	1100.0
LSD		4.4	110.0	3.9	125.0

leaf rust pathogen showed a change in the degree of the disease development on seedlings of 6 wheat varieties under the influence of these abiotic factors. No influence of the 3 factors on the changes in specific (vertical) and non-specific (horizontal) seedling resistance to the rust was revealed. Evidently, it cannot be concluded that such influence does not exist at all. It is obvious that a significant decrease in the development of the disease under the influence of the studied abiotic factors is related first of all (and highly likely it is the only reason), to their effect on the modification and variability of the virulence and aggressiveness of the pathogen.

ACKNOWLEDGEMENTS

The research was performed within the framework of the State Task according to the theme plan of VIR, Project № 0481-2022-0001 “Structuring and disclosing the potential of hereditary variation in the global collection of cereal and goat crops at VIR for the development of an optimized

genebank and its sustainable utilization in plant breeding and crop production”.

REFERENCES

1. Atiq, M., Javed, N., Urooj, S., Bukhari, A. A., Ali, Y., Zeeshan, A., Shahid, A., Ali, S., Jabbar, A. and Wasi-ud-Din. 2017. Management of Leaf Rust of Wheat through Different Levels of NPK and Sowing Times. *Advances in Zoology and Botany*, **5**: 39-44.
2. Bromfield, K. R. 1961. The Effect of Postinoculation Temperature on Seedling Reaction of Selected Wheat Varieties to Stem Rust. *Phytopathology*, **51**: 590-593.
3. Browder, L. E. and Eversmeyer, M. G. 1986. Interaction of Temperature and Time with Some *Puccinia recondita*: *Triticum* Corresponding Gene Pairs. *Phytopathology*, **76**: 1286-1288.
4. Bryant, R. 2013. Effects of Temperature on Wheat-Pathogen Interactions. A Thesis for the Degree of Doctor of Philosophy. John Innes Centre.
5. Dordas, C. 2008. Role of Nutrients in Controlling Plant Diseases in Sustainable Agriculture. A Review. *Agron. Sustain. Dev.*, **28**: 33-46.



6. Dospikhov, B. A. 1979. Field Experience Technique. Moscow. (in Russian)
7. Dyck, P. L. and Johnson, R. 1983. Temperature Sensitivity of Genes for Resistance in Wheat to *Puccinia recondita*. *Can. J. Plant Pathol.*, **5**: 229-234.
8. Feng, J., Zeng, H., Fengtao, W. and Lin, R. 2019. Identification of Temperature Sensitive Resistance to *Puccinia striiformis* f. sp. *tritici* in Wheat Differential Hosts and Its Potential Applications in Resistance Breeding. *Int. J. Plant Sci. Hor.*, **1**: 163-172.
9. Flor, H. H. 1956. The Complementary Genetic System in Flax and Flax Rusts. *Adv. Genet.*, **8**: 29-54.
10. Flor, H. H. 1971. Current Status of the Gene-for-Gene Concept. *Ann. Rev. Phytopathol.*, **9**: 275-296.
11. Forsyth, F. R. and Samborski, D. J. 1958. The Effect of Various Methods of Breaking Resistance on Stem Rust Reaction and Content of Soluble Carbohydrate and Nitrogen in Wheat Leaves. *Can. J. Bot.*, **36**: 717-723.
12. Goncharova, E. A., Shchedrina, Z. A., Makarova, N. A. and Makeeva, A. A. 2005. Resistance of Spring Barley to Abiotic and Biotic Environmental Factors Depending on Mineral Nutrition. In *Pr°C.: New and Untraditional Plants and the Prospects for Their Use*. Moscow, **I**: 231-233. (in Russian).
13. Gousseau, H. D. M. and Deverall, B. J. 1987. Manipulation of the Temperature-Sensitive Expression of the *Sr15* Allele Conditioning Resistance to Stem Rust in Wheat. *Physiol. Mol. Plant Pathol.*, **30**: 157-165. (doi: 10.1016/0885-5765(87)90030-0).
14. Howard, D. D., Chambers, A. Y. and Logan, J. 1994. Nitrogen and Fungicide Effects on Yield Components and Disease Severity in Wheat. *J. Prod. Agr.*, **7**: 448-454.
15. Mains, E. B. and Jackson, H. S. 1926. Physiologic Specialization in Leaf Rust of Wheat, *Puccinia triticina*, Erikss. *Phytopathology*, **16**: 89-120.
16. Makarova, N. A. 2005. The Role of Mineral Nutrition in the Expression of *Lr*-Genes for Resistance of Spring Soft Wheat to Brown Rust. In *Pr°C.: New and Untraditional Plants and the Prospects for Their Use*. Moscow, **I**: 309-311. (in Russian)
17. Martens, J. W., McKenzie, R. I. H. and Green, G. J. 1967. Thermal Stability of Stem Rust Resistance in Oat Seedlings. *Can. J. Bot.*, **45**: 451-458.
18. Mascagni Jr., H. J., Harrison, S. A., Russin, J. S., Desta, H. M., Colyer, P. D., Habetz, R. J., Hallmark, W. B., Moore, S. H., Rabb, J.L., Hutchinson, R. L. and Boquet, D. J. 1997. Nitrogen and Fungicide Effects on Winter Wheat Produced in the Louisiana Gulf Coast Region. *J. Plant Nutr.*, **20**: 1375-1390.
19. McIntosh, R. A., Wellings, C. R. and Park, R. F. 1995. Wheat Rusts: An Atlas of Resistance Genes. CSIRO Press, Melbourne.
20. Peresyphkin, V. F. 1989. Agricultural Phytopathology. Moscow. (in Russian)
21. Ramage, R. A. and Sutherland, M. W. 1995. High and Low Pre-In°Culation Temperatures Decrease the Effectiveness of the *Lr 20* and *Sr 15* Rust Resistance Genes in Wheat. *Plant Pathol.*, **44**: 772-778.
22. Shkalikov, V. A. , Beloshapkina, O. O., Bukreev, D. D., Gorbachev, I. V., Dzhililov, F. S.-U., Korsak, I. V., Minaev, V. Y. and Stroykov, Y. M. 2010. Plants Protection from Disease. Moscow. (in Russian).
23. Stakman, E. C. and Aamodt, O. S. 1924. The Effect of Fertilizers on the Development of Stem Rust of Wheat. *J. Agr. Res.*, **27**: 341-379.
24. Sweeny, D. W., Granade, G. V., Eversmeyer, M. G. and Whitney, D. A. 2000. Phosphorus, Potassium, Chloride, and Fungicide Effects on Wheat Yield and Leaf Rust Severity. *J. Plant Nutr.*, **23**: 1267-1281.
25. Tyryshkin, L. G. 2016. Modification Variability of Virulence and Aggressiveness of Cereals Phytopathogens: Conclusions, Consequences, Possibilities of Practical Application: Monograph. St. Petersburg. (in Russian)
26. Tyryshkin, L. G., Ershova, M. A. and Tyryshkina, N. A. 2005. Influence of Benzimidazole on Wheat Resistance to Diseases. *Mycology and Phytopathology*, **39**: 93-99. (in Russian).
27. Tyryshkin, L. G., Kolesova, M. A., Kurbanova, P. M., Kurkiyev, K. U. and Sarukhanov, I. G. 2008. Genotype-Specific Induction of Cereal Resistance to Leaf Rust under the Effect of Benzimidazole. *Vestnik of the Russian Agricultural Science*, **6**: 61-63. (in Russian).
28. Vavilov, N. I. 1918. *Immunitetrastenii k infektzionnyrn zabolevaniyam. [Plant Immunity to Infectious Diseases]*. Works of the Petrovsky Agricultural Academy 1-4, 240 PP. (in Russian)

29. Waterhouse, W. L. 1929. Australian Rust Studies. I. *Proceedings of the Linnean Society of New South Wales*, **54**: 616-680.
30. Wilcoxon, R. D. 1980. Effects of Fertilizers on Slow Rusting in Wheat. *Phytopathology*, **70**: 930-932.

تأثیر احتمالی عوامل محیطی غیرزیستی بر تغییرات مقاومت گندم به زنگ قهوه ای (زنگ برگ)

م. ا. کلسوا، و. گ. زاخارو، و ل. گ. تریشکین

چکیده

در این پژوهش، تأثیر احتمالی 3 عامل محیطی غیرزیستی (دما، نمک نیتروژن و بنزیمیدازول) بر مقاومت گندم به *Puccinia triticina* مطالعه شد. تحت تأثیر این عوامل، کاهش معنی دار آماری در توسعه و گسترش بیماری زنگ برای 6 رقم گندم بررسی شد. تغییرات خاصی از شدت بیماری زایی در 6 جدایه تکجوش (monopustule) بیمارگر تحت تأثیر عوامل مزبور با فرکانس بالا مشاهده شد. تحت تأثیر یک عامل خاص، مشاهدات ما حاکی از همزمانی مطلق انواع آلودگی گیاهچه‌های آلوده به کلون‌های بیماری زای زنگ که در شرایط نبود این عامل تکثیر شده بود و انواع آلودگی برگ‌ها که در غیاب عامل مزبور خوابانده (انکوباسیون) شده بود، اما آلوده به جدایه‌هایی بود که در حضور این عامل تکثیر شده بود. شش زیرجمعیت (subpopulation) از پاتوژن که نماینده مخلوطی از ژنوتیپ‌های بدخیم (با بیماری زایی زیاد) برای 2 رقم گندم در شرایط خاص بود ایجاد شد. ما دو شاخص توسعه بیماری (تعداد جوش‌ها (pustules) و تعداد اوردیواسپور در جوش‌ها) در نظر گرفتیم ولی تفاوت معنی داری در این دو شاخص بین گیاهچه‌های تحت تأثیر یک عامل و آلوده به زیرجمعیت‌های تکثیر شده در غیاب عامل مزبور با برگ‌هایی که تحت تأثیر این عامل قرار نداشت اما با جمعیت‌های فرعی تلقیح شده بود که در حضور این عامل تکثیر شده بود پیدا نکردیم. با توجه به نتایج، تأثیر عوامل مورد مطالعه بر بیان مقاومت ویژه (عمودی) و غیر اختصاصی (افقی) گیاهچه گندم به زنگ دیده نشد. بدیهی است که کاهش قابل توجه در گسترش زنگ تحت تأثیر عوامل محیطی مطالعه شده، در درجه اول (اگر نه تنها) به تأثیر آنها بر شدت بیماری زایی و قدرت تهاجمی بیمارگر (پاتوژن) مربوط می‌شود.