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HARMFULNESS OF WHEAT YELLOW RUST AND IDENTIFICATION OF RESISTANCE GENES TO ITS HIGHLY VIRULENT RACES

Introduction. *Fungal diseases, in particular, yellow rust, are the most harmful and widespread among wheat diseases. Due to environmental and climatic changes, yellow rust (Puccinia striiformis West. f. sp. tritici) has been actively spreading and causing damage to wheat crops, particular in Ukraine. One of the aspects of overcoming this problem can be the monitoring of disease spread and the use of advanced methods of molecular genetics and breeding to create new resistant varieties.*

Problem Statement. *The specificity of the pathogen races complicates fighting against this disease, with epiphytotics leading to significant losses of the wheat yield. The application of advanced methods for identifying the genotypes that have effective Yr resistance genes to yellow rust, with the use of molecular genetic markers, will allow to avoid significant economic losses.*

Purpose. *The purpose of this research is to generalize data on the harmfulness of yellow rust and to evaluate the usability of the molecular genetic methods for resistance genes analysis.*

Material and Methods. *Ukrainian-bred wheat varieties with resistance to known races of yellow rust have been used as materials to be studied. The yellow rust resistance genes (Yr10 and Yr36) have been identified by polymerase chain reaction (PCR) with the use of our own original primers.*

Results. *The losses of the wheat crop as a result of damage by yellow rust have been shown to depend on the resistance of the variety, the period of infection, the duration of the development of the disease, and the climatic conditions. The original primers have been developed and optimal conditions for PCR have been determined. The genes for resistance to yellow rust in soft winter wheat varieties has been identified.*

Conclusions. *The results have indicated the absence of alleles that can ensure resistance to new harmful races of yellow rust in Ukrainian-bred wheat varieties. This implies the need to use sources with Yr10 and Yr36 genes in the breeding process.*

Keywords: wheat, yellow rust, harmfulness, resistance genes, molecular genetic analysis, varieties.

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According to the International Maize and Wheat Improvement Center (CIMMYT), wheat is affected by more than 20 fungal diseases, including powdery mildew and various types of rust [1]. Yellow rust is one of the most harmful diseases of wheat [2, 3]. The first mentions of yellow rust appeared in the literature in the second half of the 18th century. For a long time there were discussions about the origin of this pathogen and as late as on the verge of the 20th century, yellow rust was recognized as a separate species of cereal grass rust, and later named *Puccinia striiformis* West that has been still used so far [4]. The name of wheat yellow rust according to the International Code of Botanical Nomenclature is *Puccinia striiformis* West. f. sp. *tritici*. In recent years, yellow rust of wheat has increasingly attracted the attention of phytopathologists and breeders because of its rapidly spreading highly virulent races of Asian origin [2]. That is why the purpose of this research is to summarize modern data on the harmfulness of yellow rust of wheat, the features of its spread and forecasts of harm to wheat crops from this disease in grain-producing countries, as well as to assess the possibilities of developing methods for molecular genetic analysis of genes for resistance to yellow rust.

As a disease, yellow rust affects leaves, stems, spikes, ears, and grain either. It manifests itself as uredinio- and teliopustules with spores, which are located linearly in the form of a dotted stripe and, in large numbers, form a continuous yellow spot (Fig. 1). Later, in the affected areas, there are formed dark brown or almost black telia that do not break through the epidermis [5, 6].

The infection can affect about 320 species of grasses of 50 genera, among which the main ones are *Aegilops, Agropyron, Bromus, Elymus, Hordeum*, and *Triticum*. The disease can be transmitted from plants of wild cereals in any phase of growth, from seedlings to ripening [8]. The researchers from the University of Minnesota have established that common barberry and other types of barberries are intermediate hosts of the yellow rust causative agent and can be primary sources of infection [9—11]. European barberry has historically been an important source of inoculum in North America and Europe. In Eastern Europe and Western Asia, where barberry is widespread, it can contribute to the evolution of new virulent combinations of *Puccinia striiformis* [7]. For cultivated species of *Triticum*, the main source of infection is the early crops of winter soft wheat, on which the fungus overwinters in the form of mycelium. On 1 ha, there can be formed up to 19 kg or billions of rust spores [12]. Urediniospores of the pathogen are transported over great distances, which allows it to spread in new geographical areas. In addition, the fungus has the ability to develop at a certain distance from

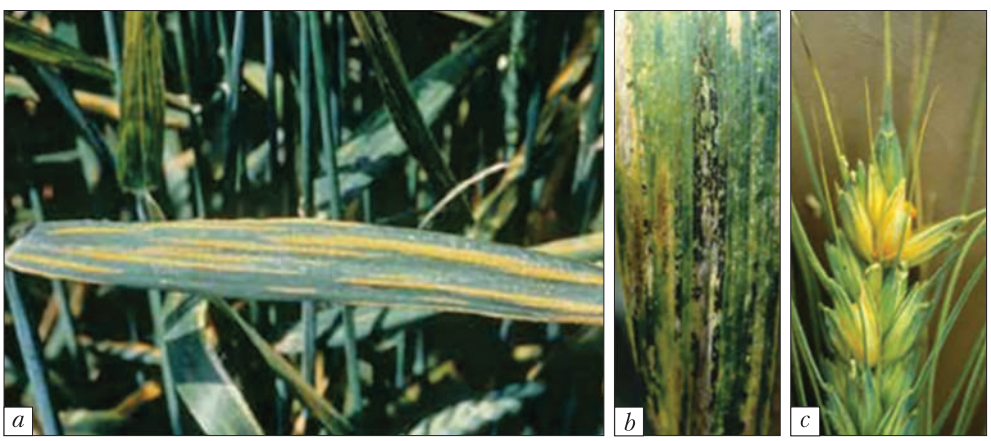

Fig. 1. *Puccinia striiformis* West. f. sp. *tritici: a, b* — on the leaves; *c* — on the spike scales [7]

the culture, forming the so-called diffuse mycelium that grows at a rate of 2.5—2.9 mm per day [13].

As a rule, the peak manifestation of the disease is observed within the period from flowering to milky-waxy grain ripeness. Under favorable weather conditions, visible signs of pathogen damage are revealed as soon as a week after its penetration into the host plant. In a leaf already damaged by other types of rust, the disease develops worse. A temperature of 11—13 °C is considered optimal for the germination of urediniospores of yellow rust, but they also germinate at a temperature close to 0 °C. The temperature maximum ranges within 23—26 °C. The best conditions for the disease development have been observed in areas with a humid climate [14, 15].

In infected plants, the assimilation surface area decreases, transpiration increases, and productivity falls significantly. Damage to the ear is especially dangerous, because as a result, the grain dries up and becomes limp and light. The bakery properties deteriorate, which is associated with the loss of glutenin components in the grain, on which the flour quality depends essentially. The breach of physiological and biochemical processes leads to the worsening adaptability, in particular, drought resistance of plants [16].

The pathogen is obligate and quite specific. It is dangerous because of its ability to mutate and rapidly change generations, which accelerates the race-forming process. The specificity of *P. striiformis* f. sp. *tritici* races that affected only certain varieties of wheat had been studied since the 1930s [17]. The result of these studies was the creation of a set of differentiating varieties for establishing the fungus races [18]. However, the efficiency of this approach to identify the pathogen physiological races varied across countries. The differentiating varieties that were used in Europe turned out to be insufficiently effective in China, where wheat genotypes designated as CYR (Chinese yellow rust) were proposed. Among the Chinese material, only one variety was included in the list of the European set of differentiating varieties. Further research and discussions of the problem have allowed the researchers to propose the two sets of differentiating varieties: the international ('Chinese 166', 'Lee', 'Heines Kolben', 'Vilmorin 23', 'Moro', 'Strubes Dickkopf', and 'Suwon 92' x 'Omar') and the European ('Hybrid 46', 'Reichersberg 42', 'Heines Peko', 'Nord Desprez', 'Compare', 'Carstens V', 'Spaldings Prolific', and 'Heines VII'). For a more accurate determination of local populations of the yellow rust causative agent, each set was allowed to be supplemented with differentiating varieties without changing the numbering of races based on the use of the binary system. Research on differentiating varieties remains relevant to this day [19, 20].

The permanent mutation process and the formation of more aggressive physiological races of the pathogen lead to the fact that the selection for disease resistance is continuous and requires knowledge of the composition of the pathogen population in different territories and systematic control of its changes [21—24]. The use of sets of isogenic wheat lines with known resistance genes is considered progressive. They are useful as differentiators of pathogen races, as sources of resistance, and as testers in genetic tests to study relationships in host-parasite pathosystems [25, 26].

The resistance of lines to individual races of the pathogen is called race-specific. In various countries of the world, this problem has been studied quite effectively with the use of wheat germplasm [27—32]. Race-specific resistance is determined by specific dominant genes and is ineffective against new mutant virulent races. Wheat varieties with specific resistance keep it for an average of 3—5 years. Non-specific, field resistance, as a rule, is controlled by several gene loci and is effective against many races of the pathogen. Genotypes with field resistance can resist the pathogen for a long time under various conditions, despite changes in its racial composition. However, the stable and long-term preservation of non-specific resistance depends not only on the number of genes, but also on the nature of the interaction between the parasite's virulence genes and the host's resistance genes under certain environmental conditions [33, 34].

The plant resistance to diseases and abiotic stresses has been currently relevant and widely discussed [35, 36]. It should be noted that there have been may approaches to solving these problems. One of the modern approaches to the formation of ideas about the immune response of a plant cell to pathogen attacks is based on a system for detecting signs of danger [37].

The dynamics of the spread of the yellow rust pathogen in Europe is under constant control, and official data are regularly published in the reports of the University of Aarus (Denmark) [38—43]. On the territory of Ukraine, there have been distinguished several dominant races of the causative agent of yellow rust, the main ones are OEO, 6EO, and 6E16 [44]. However, mutations and recombinations in the genomes of pathogens lead to the formation of new virulent races. Currently, against the background of global warming, yellow rust has adapted to elevated temperatures and increased its spread area. The resistance of different varieties is overcome within a short period, and the epiphytotia caused by the races tolerant to high temperatures become more aggressive [45, 46].

Yellow rust originates from Eurasia, and now it has spread over most of the Earth's territory. There has been a rapid increase in the area affected by the disease in Asia, in the last 10 years it has expanded to East Africa, with pathogen race becoming resistant to elevated temperatures. In the case of epiphytotic diseases, grain losses can reach about 1 million tons [47]. In Western, Central, and Eastern Asia, several large-scale epiphytotia were recorded in the last century; in China, yellow rust covered thousands hectares of wheat crops. The disease remains a serious problem in India and Pakistan. In South Africa, the first outbreak of the disease was caused by the lack of resistant varieties and favorable weather conditions; the grain losses were estimated at USD 2.5 million. Since 2010, new aggressive races of yellow rust have started to appear in the North Africa, as well as in the Middle East and Central Asia, spreading at a fairly fast pace, causing serious outbreaks of the disease. The AF2012 race was characteristic only for Afghanistan, but as soon as in 2016, outbreaks of yellow rust of the AF2012 race were reported in Uzbekistan and Ethiopia, where tens thousands hectares of wheat crops were damaged. In Australia, after the first case of yellow rust, AUD 40 million has been spent to protect cereals against this disease. With air masses, yellow rust spread to New Zealand, as urediniospores covered a distance of 2000 km in a year. Yellow rust causes crop losses in the USA, especially in the areas where early damage and development of the pathogen over several months is possible [48—56].

In recent years, as a result of warming and climate change, the disease has been spreading in Ukraine. Due to its biological features, the pathogen has the best conditions for development in areas with a humid climate: in Lviv, Ternopil, Khmelnytskyi, Kyiv, and Sumy regions, as well as in the northern part of Kharkiv region. In these regions, the infection develops on crops of sensitive wheat varieties, forming foci of severely affected plants. This contributes to the further spread of the disease, and moderate epiphytotia have been also found in the steppe zone [57]. In 2020, yellow rust was reported in Volhynian and Kirovohrad regions, up to 12% of the plants in the studied areas were affected for 5% [58]. In June 2022, yellow rust was detected in the farms of Cherkasy region, where it covered up to 6% of winter wheat plants on 1.5% of the studied areas [59]. According to the simulation results that were considered at the 41st session of the European Commission on Agriculture [60], in Europe, the number of cases of wheat damage by the most common pathogens, in particular *P. striiformis*, would increase and might reach 100% in some areas (Fig. 2).

The creation and introduction of resistant varieties is currently the only ecologically clean and economically justified means of combating diseases. After all, genotypes with mutations of resistance to fungicides accumulate in pest populations, which reduces the effectiveness of the use of known drugs and requires the development of

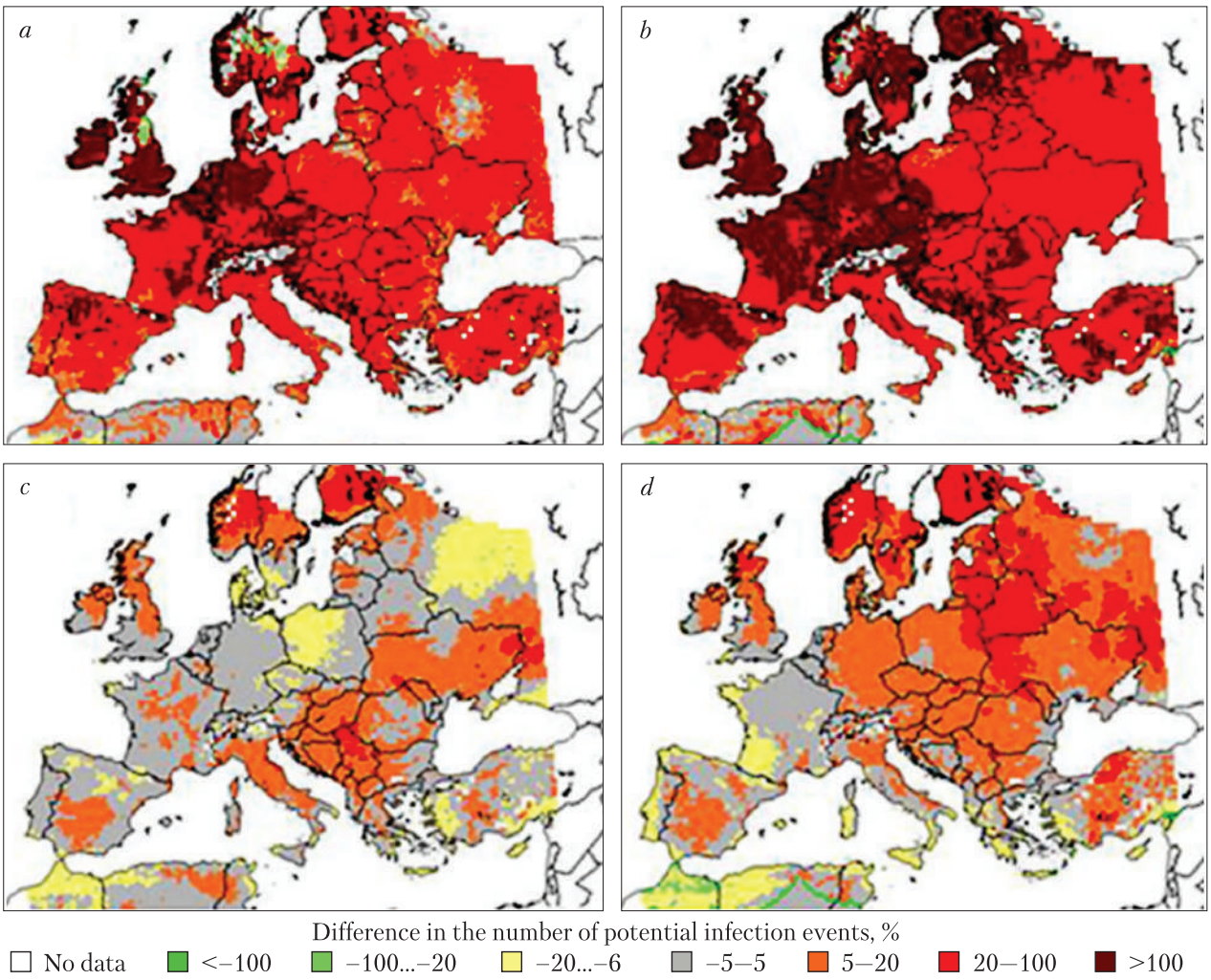

Fig. 2. Forecast of potential cases of infection with rust given the climatic zones as compared with 1993—2007, % (S. Bregaglio et al., 2013): *a, b — Puccinia recondita* (*a* — 2030, *b* — 2050); *c, d — P. striiformis* (*c* — 2030, *d* — 2050) [60]

new ones. The use of the gene pool of resistant forms as a source of genetic diversity is the key to success in creating disease-resistant varieties. Therefore, genotyping of both local wheat varieties and samples of different geographical origins is of great importance [61—63].

Varieties and variety samples that carry genes for resistance to fungal diseases, including yellow rust, can be recommended for use in breeding programs as starting material for the creation of modern high-yielding wheat varieties with increased resistance. According to Ukrainian researchers [64], the domestic highly resistant wheat varieties are 'Akter', 'Dobirna', 'Kyivska 7', 'Kyivska 8', 'Lasunya', 'Compliment', 'Columbia', 'Myronivska 65', 'Vdala', 'Pyvna', 'Zolotokolosa', 'Myronivska 66', 'Krasunia Odeska', 'Smuglyanka', 'Favorite', 'Snizhana'; the resistant varieties are 'Kolos Myronivshchyny', 'Skarbnytsia', 'Svitanok', 'Cinderella', and 'Pereyaslavka', 'Khersonska 99' are moderately resistant. The presented varieties are included in the State Register of plant varieties suitable for distribution in Ukraine [65].

At the same time, recent studies have indicated the spread of the highly virulent strains of yellow

rust of Asian origin as they have displaced the less pathogenic European races of *P. striiformis* [66]. It is most likely that most of the Ukrainian and foreign bred varieties grown in Ukraine are sensitive to new highly virulent races, so the identification among the collections of wheat varieties of those that have genes for resistance to yellow rust should become an important part of breeding programs to ensure food security of the state. The key to progress in this field can be the practice of using advanced innovation technologies for identifying and pyramiding the genes, which is associated with the presence of molecular markers and the possibility of their use in marker-assisted selection (MAS) [67—70].

The search for genomic sequences and the development of molecular markers for wheat resistance genes have been quite actively used in global practice. In our research, wheat varieties have been analyzed in order to identify the wheat genotypes with *Yr* resistance genes to new Asian races of yellow rust [71], using both newly created and already known molecular genetic markers. To identify and determine the allelic status of resistance genes, the *Yr5*, *Yr10*, *Yr15*, and *YrSp* genes, which provide race-specific resistance to genotypes, and the *Yr36* gene that provides general moderate resistance to known pathotypes of yellow rust have been selected at the initial stages of the research. Further, original primers for the *Yr10* and *Yr36* genes have been designed for wheat genome studies, as these genes are known to provide reliable resistance to a large number of yellow rust races. The highly virulent races of yellow rust from Tibet have been reported to spread on the European continent and to replace the local races of yellow rust [66], so in the future, they may reach Ukraine. The varieties with a certain allelic state of the *Yr36* and *Yr10* genes are invulnerable to these races and have been used in agriculture.

In most cases, molecular markers are known to be DNA sequences linked to the genes of interest, because they are located next to these genes and can be inherited together with them. Marker sequences are analyzed with the use of such advanced molecular genetic methods as SSR, AFLP, SNP, and others. At the same time, molecular markers, despite their relevance and practical importance, have certain limitations in their use. Among the disadvantages of molecular markers there are insufficient efficiency and informativeness when they are used for the analysis of genes of interest in plant samples with a genomic structure that has not yet been investigated.

The identification of genes in the genotypes of varieties is based on their already known molecular structure and the polymerase chain reaction (PCR), for which selected specific fragments of the sequences of these genes serve as primers. To date, urediniospore cDNA libraries have been created, whole-genome sequencing of yellow rust races has been done, and the genes associated with resistance to *P. striiformis* have been sequenced [72, 73]. These data can be used to develop our own molecular markers for resistance genes and to study cultivars and varieties for which information on these genes is missing.

Most of the existing molecular markers [74—79] are linked to traits, only some of them represent sequences of the genes of interest. We have developed our own molecular markers for *Yr10* and *Yr36* genes based on their sequences. In practice, such approaches with high probability and accuracy allow analyzing the wheat varieties that have already passed previous phytopathological tests, but not tested for the presence of resistance genes. Accordingly, the sequences of *Yr10* and *Yr36* genes and their allelic variants have been obtained from databases (NCBI, EnsemblePlants). The primers for the identification of the *Yr10* gene have been designed on the basis of its known sequence, with the use of homologues from wheat and *Aegilops tauschii*. The sequence has been aligned with the use of *ClustalOmega* program. The resulting primer sequences have been tested for self-complementarity and the ability to form hairpins with the use of *Oligoanalyzer 3.1* program. The annealing temperature of primer pairs is chosen with the use of the same program.

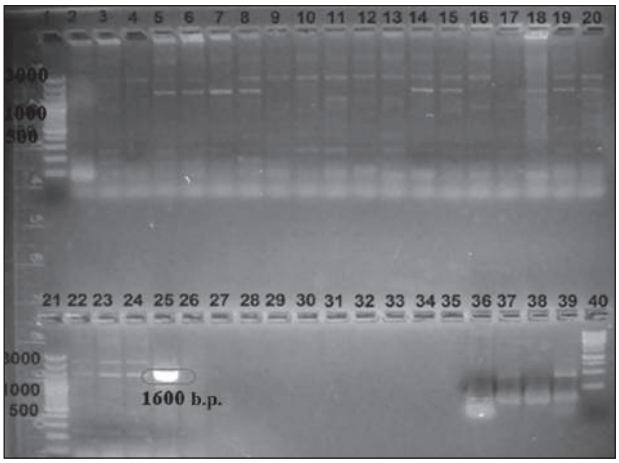

Fig. 3. Electrophorogram of PCR products, the reaction mix of which contains the Yr10_R3 and Yr10_F primers. Wells: 1, 21 — DNA marker; 2—20, 22—24, 27—40 — analyzed varieties of Ukrainian-bred wheat; 25 — reference *Ae. tauschii*; 26 — negative reference

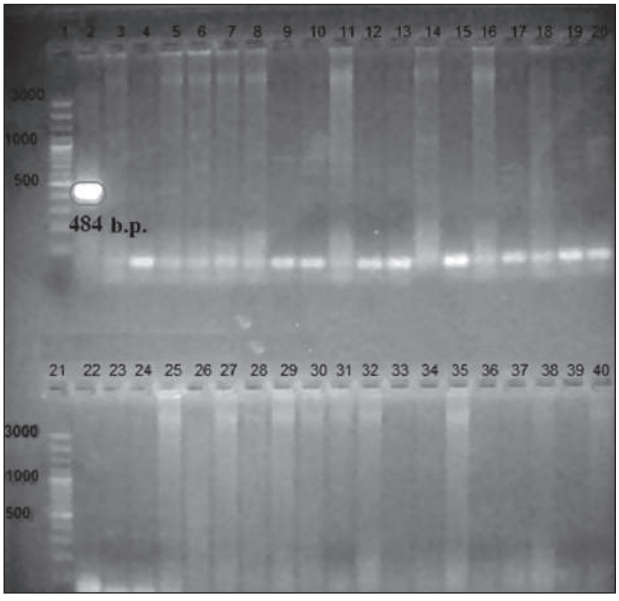

Fig. 4. Electrophorogram of PCR products, the reaction mix of which contains the *Yr36* gene primer. Wells: 1 and 21 — DNA-marker; 2 — reference *T. dicoccoides* (the expected fragment length is 484 b.p.); 3—40 — tested samples of Ukrainian-bred wheat varieties

The sequences of the primers designed by us and used to identify the *Yr10* gene are as follows:

Yr10_F 5′ — GTAGCTAAAGAGTGCTCAA AGCACA — 3′

Yr10_R1 5′ — TT GGA GAG ACA GTC GAC GGA TCT T – 3′

Yr10_R2 5′ — AAG CTG CTC ATG GTT GGC ATT G – 3′

Yr10_R3 5′ — CTT CTT GAC TTG GGA TTA TAC CAC GA – 3′

The Yr10_F primer is common to the sequence of the *Yr10* gene and its homologues. The Yr10_R1 primer has 5 mismatches with wheat homologues, the Yr10_R2 primer has 3 mismatches, and the Yr10_R3 primer is complementary only to the sequence of the *Yr10* gene and its homologue from *Ae. tauschii*.

The size of the calculated PCR product for the Yr10_F and Yr10_R1 primer pair for the *Yr10* gene and its homologue from *Ae. tauschii* is 854 b.p., for wheat homologues in case of successful annealing it is 853 b.p. For the pair of primers Yr10_F — Yr10_R2 for the *Yr10* gene and its homologue from *Ae. tauschii* is 900 b.p. while for its wheat homologues in case of successful annealing it is 899 b.p. The amplicon generated during PCR with the primer pair Yr10_F — Yr10_R3 for the *Yr10* gene and its homologue from *Ae. tauschii* is 1630 b.p., whereas for wheat homologues there is no PCR product. Different samples of *Ae. tauschii* and *Ae. speltoides* are used as references (Fig. 3).

It should be noted that unlike other combinations, the combination of the Yr10_F and Yr10_R3 primers allows identification of the *Yr10* gene. At the same time, there has been found no specific PCR product with a size of about 1600 b.p. for any analyzed soft wheat varieties during amplification, except the positive reference (*Ae. tauschii)* for which the presence of such a fragment has been shown.

To identify the *Yr36* gene, primers have been designed based on the sequences of its allelic variants, designated as P0, P1, P2, and P3. It has been determined that the varieties with allelic variants P0, P1, and P3 show resistance to yellow rust, while the varieties with allelic variant P2 are not resistant. The yellow rust susceptibility allele P2, unlike the other alleles studied, does not contain a BbsI restriction endonuclease site.

This fact can be used as a test to confirm the results obtained by PCR.

The sequences of the primers of our own design for the identification of the *Yr36* gene are as follows:

Yr36_R 5′ — CTC TAA AGC AGC ATC ACA TGG TCA — 3′

Yr36_F 5′ — GAG GTT ACA TGG ATC CAG AAC ACA T — 3′

In this case, the size of the calculated PCR product is 484 b.p. To determine whether it belongs to the resistance allele or the sensitivity allele, the PCR product (484 b.p.) shall be treated with the BbsI restriction endonuclease. If, after restriction, it is divided into two fragments having a size of 364 b.p. and 137 b.p., then it can be said that it belongs to the allele of resistance, if it remains intact, then it belongs to the allele of sensitivity (Fig. 4). Based on the results of the experiments, it has been established that among the studied Ukrainian wheat varieties, there are no such ones that have a fragment (484 b.p.) of the *Yr36* gene that is inherent in the resistant varieties.

To identify the *Yr36* gene, the possibility of using PCR results with the Inter_WKS1 and Start_WKS primers has been also analyzed. The analysis of the amplification products has allowed us to conclude that all analyzed varieties of soft winter wheat contain Start-domain sequences, but none of them contain the Inter-domain sequence that is typical for the functional variants of the *Yr36* gene (unpublished data).

Thus, in general, it can be stated that the marker analysis results have demonstrated the presence of *Yr5*, *Yr15*, and *YrSp* genes in the genomes of Ukrainian-bred wheat varieties that are resistant to known races of yellow rust. However, the molecular genetic analysis with the use of the markers for the *Yr10* and *Yr36* genes, which were designed by us, has indicated the absence of alleles that provide resistance to the new harmful races of yellow rust in the analyzed varieties. Among the studied Ukrainian varieties, there is not a single one that contains the "resistance" allele of at least one of these genes in its genotype. This indicates the need to use sources that are carriers of the *Yr10* and *Yr36* genes in the appropriate allelic state in the breeding process. Although yellow rust has not yet significantly threatened the agricultural sector of Ukraine, the lack of individual effective genes for resistance to this pathogen in modern domestically-bred varieties is a negative factor that may manifest itself in the future.

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ШКОДОЧИННІСТЬ ЖОВТОЇ ІРЖІ ПШЕНИЦІ ТА ІДЕНТИФІКАЦІЯ ГЕНІВ СТІЙКОСТІ ДО ЇЇ ВИСОКОВІРУЛЕНТНИХ РАС

Вступ. Грибні хвороби, зокрема, жовта іржа, є найбільш шкодочинними і широко розповсюдженими серед захворювань пшениці. Через екологічні та кліматичні зміни збудник жовтої іржі (*Puccinia striiformis* West. f. sp. *tritici*) активно поширюється і завдає шкоди посівам пшениці, зокрема й в Україні. Одним з аспектів подолання цієї проблеми може бути моніторинг розповсюдження хвороби та використання сучасних методів молекулярної генетики і селекції для створення нових стійких сортів.

Проблематика. Специфічність рас патогена ускладнює боротьбу з грибним захворюванням, а епіфітотії призводять до значних втрат врожаю пшениці. Уникнути суттєвих економічних збитків дозволить застосування сучасних способів виявлення генотипів з ефективними генами стійкості *Yr* до жовтої іржі за допомогою молекулярно-генетичних маркерів.

Мета. Узагальнення даних щодо шкодочинності жовтої іржі пшениці та оцінювання можливостей використання методів молекулярно-генетичного аналізу генів стійкості.

Матеріали й методи. Матеріалом слугували сорти пшениці української селекції, стійкі до відомих рас жовтої іржі. Ідентифікацію генів стійкості до жовтої іржі (*Yr10* та *Yr36*) здійснювали з використанням власних оригінальних праймерів методом полімеразної ланцюгової реакції (ПЛР).

Результати. Показано, що втрати врожаю пшениці за ураження рослин жовтою іржею залежать від стійкості сорту, періоду зараження, тривалості розвитку хвороби, кліматичних умов вирощування. На основі молекулярно-біологічних підходів розроблено оригінальні праймери та підібрано оптимальні умови для проведення ПЛР, які дозволяють здійснювати ідентифікацію генів стійкості до жовтої іржі в сортах пшениці м'якої озимої.

Висновки. Отримані результати свідчать про відсутність у проаналізованих сортів пшениці української селекції алелів, які можуть забезпечити стійкість до нових шкодочинних рас жовтої іржі. Це потребує залучення у селекційний процес джерел, що є носіями генів *Yr10* та *Yr36*.

Ключові слова: пшениця, жовта іржа, шкодочинність, гени стійкості, молекулярно-генетичний аналіз, сорти.