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Disease resistance and adaptation of winter wheat lines derived from wide hybridisation under arid environments

Ivan MOTSNYI¹, Mykola LYTVYNNENKO¹, Eugenia GOLUB¹, Tetiana NARGAN¹,
Mykola NAKONECHNYI¹, Saveliy LYFENKO¹, Olga MOLODCHENKOVA¹,
Yaroslav FANIN¹, Ivan MISHCHENKO², Andrii SMERTENKO³, Lidiya MISHCHENKO⁴

¹Plant Breeding and Genetics Institute – National Center of Seed and Cultivar Investigations (PBGI-NCSCI)
3 Ovidiopol'skaya, 65036 Odesa, Ukraine

²National University of Life and Environmental Sciences of Ukraine
15 Heroyiv Oborony, 03041 Kyiv, Ukraine

³Washington State University, Institute of Biological Chemistry
PO Box 646340, Pullman, WA 99164, USA

⁴Taras Shevchenko National University of Kyiv,
Educational and Scientific Centre “Institute of Biology and Medicine”
64/13 Volodymyrska, 01601 Kyiv, Ukraine
E-mail: lmishchenko@ukr.net

Abstract

A combination of fungal diseases and drought can cause significant yield losses of winter wheat (*Triticum aestivum* L.). It is known that alien traits introduced through wide hybridisation contribute to breeding of cultivars with a higher yield potential in arid environments. In this study, the impact of alien genes on the main agronomic traits in the arid environments of the Southern Steppe of Ukraine was analysed. The lines were grown under the arid conditions in 5 and 10 m² plots in the 2019–2021 growing seasons. Eight agronomic and six plant pathological traits were assessed and subjected to statistical analysis to comprehend the diversity and connections between the features. Due to the successful introgression of alien genes from all sources involved in hybridisation, most of lines were resistant to one of the rust species. The lines derived from the genotype containing the translocation 1BL.1RS in the karyotype and *Triticum timopheevii* in the pedigree were resistant to all rust species. There was a negative correlation between the protein content and grain yield in 2020 ($r = -0.40^{***}$), and a weak positive correlation was found between the grain yield and resistance to yellow rust ($R_{sp} = 0.19^*$ in 2019 and $R_{sp} = 0.26^{***}$ in 2020) or tolerance to Septoria leaf blotch ($R_{sp} = 0.27^{***}$). Under drought conditions, the grain yield reduced by 32.5% in 2020 and ca. 70% in 2021. The lines containing alien genes *Lr42* and *Hs* showed a higher grain yield than the recurrent and standard ones.

For further breeding, eighteen lines with a high TKW, protein content, and grain yield, and resistance to drought or disease were identified, and four promising drought-tolerant lines have been selected.

Keywords: disease resistance, drought, wheat lines, agronomic traits, productivity, *Triticum aestivum*.

Introduction

A significant part of the existing breeding efforts aims at improving the grain yield and quality of winter wheat (*Triticum aestivum* L.). The exploitation of available genetic diversity contributed to the increase of grain yield potential over 10 t ha⁻¹ (Morgun et al., 2014; Lytvynenko, 2016a; Lyfenko et al., 2021). For example, in experimental trials, in favourable conditions under a very high level of fertilisation, the grain yield potential of PBGI-NCSCI cultivars ‘Knyaginya Olga’ and ‘Lira’ was 11.74 and 12.57 t ha⁻¹, respectively (Lytvynenko, 2016b).

In Ukraine, cultivars ‘Smuglyanka’, ‘Zolotokolosa’, and ‘Favoritka’ showed the record grain yield between 12.40 and 13.18 t ha⁻¹ (Morgun, 2016). According to the Guinness World Records, the highest grain yield of 17.4 t ha⁻¹ recorded in the world was achieved in New Zealand in 2020. However, along with the growth of productivity in optimal environments, sustaining grain yield in response to biotic and abiotic stresses becomes an essential problem (Soko et al., 2018; Badaeva et al., 2021; Langridge, Reynolds, 2021). It is important to

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note that virus diseases also cause significant crop losses (Mishchenko et al., 2021). A significant deterioration of grain yield and quality causes the evolution of more pathogenic disease (Wellings, 2011; O'Driscoll et al., 2014; Soko et al., 2018; Mourad et al., 2021) in combination with global climate change (Juroszek, von Tiedemann, 2013; Lewis et al., 2018; Miedaner, Juroszek, 2021). Addressing this problem requires development of genotypes resistant to biotic factors and drought (Lopes et al., 2015; Lytvynenko, 2016b; Bhatta et al., 2019; Lyfenko et al., 2021). For breeding of new wheat cultivars with more superior characteristics, wide hybridisation has been successfully used (Dempewolf et al., 2017; Liu et al., 2020; Sharma et al., 2021). For example, a set of leaf rust resistant wheat cultivars such as 'Rostislav', 'Vostorg', 'Zhirovka', 'Fisht', 'Evgeniya', and others, were created using *Triticum miguschovae* Zhiron (an artificial amphidiploid of *T. militinae* Zhuk. et Migusch. \times *Ae. tauschii*) (Tverdokhle, 2009). The cultivar 'Pamyati Maystrenko' containing the genetic material of *T. timopheevii* Zhuk. \times *Ae. tauschii* has resistance to leaf and stem rusts, powdery mildew, and high protein (17.3%) and gluten (34.3%) contents as well as good bread-making qualities (flour strength, W = 600 conventional units) (Laikova et al., 2013).

Moreover, wide hybridisation contributes to increasing both pathogen resistance and also adaptation to abiotic stress factors. For example, it contributed to the transfer of genes to wheat for disease resistance (McIntosh et al., 2013; Davoyan et al., 2018), pests' tolerance (Morgounov et al., 2018), and adaptation to arid environments (Reynolds et al., 2007; Langridge, Reynolds, 2021). Thus, to date, the officially designated genes originated from wheat alien species including 17 *Yr*, 35 *Lr*, 30 *Sr*, and 41 *Pm* genes and one *Septoria* leaf blotch resistance gene (Liu et al., 2020). A number of *T. turgidum* ssp. *durum* (modern tetraploid durum wheat) \times *Ae. tauschii* hexaploids have shown resistance to major wheat diseases and tolerance to abiotic stresses such as drought, heat, water logging, salinity, and pre-harvest sprouting. High end-use quality derivatives that meet industry standards have also been developed, while recent experiments have identified synthetic wheat derivatives with a higher grain yield than that of commercial cultivars under the sufficient soil moisture content of 18–30% (van Ginkel, Ogonnaya, 2007).

The aim of the study was to analyse the resistance of lines developed from the wide hybridisation of wild relatives of wheat with cultivated wheat to common wheat diseases in the Southern Steppe region of Ukraine. Also, the effect of alien genes on agronomic traits in favourable and arid environments was evaluated.

Material and methods

Genetic background. For the arid climate zone, 153 winter wheat (*Triticum aestivum* L.) hybrid lines developed on the mixed genetic background of PBGI-NCSCI ten cultivars ('Odes'ka 267', 'Albatros', 'Selyanka', 'Gurt', and others) and a collection sample (H74/90-245), original introgression strains (E200/97-2, 592PH16, and E214/09-1), amphiploid lines derived using *Aegilops tauschii* Coss (AD Zhiron, ES4, ES17, ES20, and ES25) with a recurrent cultivar ('Odes'ka 267'), and six standard cultivars ('Antonivka', 'Kuyal'nyk', 'Mudrist', 'Vereran', 'Optima', and 'Nasnaga') were investigated. The lines correspond to different generations, degrees of saturation, and origin. General information about their

pedigree and types with a detailed description of the cross combinations and the hybridisation schemes, the status of the alien sources and a notification of the alien traits have been presented in our previous publications (Motsnyi et al., 2021 a; b). Herewith, all the experimental lines were developed with the Pedigree method because of numerous permanent individual selections starting from the first segregating generation.

Growing of plants in field experiments. In the control nursery, 144 lines were grown in 5 m² plots in 2018–2019 without repetitions in the experimental fields of PBGI-NCSCI. Due to overly hard threshing, one line was not sown next year, but nine addition lines from breeding nursery were sown. Therefore, 152 lines were grown during the 2019–2020 growing season in 10 m² plots at the PBGI-NCSCI Experimental Base "Dachna" in Dachna village, Bilyayivsk district, and in different locations in Odesa region, Ukraine, and 143 of them were grown in both seasons. Together with the standard cultivars, the data matrix for statistical analysis to determine the adaptive properties of the material consists of 152 lines in total. Moreover, 18 best lines were repeatedly grown during the 2020–2021 growing season at the Experimental Base "Dachna". The agricultural technology is typical of the South of Ukraine. There were no fungicide treatments in all trials. Sowing, plant growing, and harvesting were performed using published procedures (Motsnyi et al., 2021 a; b). Fertilisers were applied as follows: 1) during pre-sowing cultivation, 150 kg ha⁻¹ of nitroammophoska (24.0 kg of nitrogen per 1 ha) was applied; 2) early spring root fertilisation was carried out with ammonium nitrate at a dose of 150 kg ha⁻¹ (51.6 kg of nitrogen per 1 ha); 3) foliar feeding was carried out by spraying a tank mixture using urea at the rate of 7.7 kg ha⁻¹ of the nitrogen active substance.

Analysis of grain quality. Total protein content was determined by the Kjeldahl method with the analyser Kjeltex-Auto 1030 (Foss Electric, Denmark) according to Finnie and Atwell (2016). The thousand kernel weight (TKW) was measured for the conventional method (DSTU 4138-2002) with two portions in 500 kernels. Grain quality was determined by the SDS30/K sedimentation method (sodium dodecyl sulphate sedimentation method with the duration of autolysis of flour for 30 min) according to Rybalka et al. (2006). For a thorough investigation of the material by a complex of breeding traits and selection of lines with a high protein content, the additional protein criteria were calculated:

protein yield per unit area, t ha⁻¹ = (grain yield, t ha⁻¹ \times total protein content in grain, %) / 100%, and absolute protein content per thousand kernel weight, g = (TKW, g \times total protein content, %) / 100%, as reported earlier (Szulc et al., 2020; Motsnyi et al., 2021a).

Disease resistance. Resistance to common widespread diseases: powdery mildew (*Blumeria graminis* (DC) Speer f. sp. *tritici* March.) (PM), leaf (*Puccinia triticina* Erikss. & Henn.) (LR), stem (*Puccinia graminis* sp. *tritici* Erikss. & Henn.) (SR), and stripe (*Puccinia striiformis* West.) rusts, and wheat *Septoria* leaf blotch (*Septoria tritici* Rob. ex Desm.) (STB), was studied for all 153 lines under natural infection environments in 2015–2021. In parallel, in 2016–2021, the leaf and stem rust resistance was assessed against provocative backgrounds in the infectious field nursery of the Department of Phytopathology and Entomology of PBGI-NCSCI. In addition, natural infection of tan spot (*Pyrenophora tritici-repentis* Died.) (TS) and common bunt (*Tilletia caries* (DC.) Tul.) were spread in 2021.

The degree of adult plant damage was determined at the phase of maximal disease development using the 9-point integrated scale (Babayants, Babayants, 2014), developed on the modified scale of Saari and Prescott (1975). This scale allows estimating the response to mildew or Septoria leaf blotch on the basis of the vertical progression of the pathogen, and to rusts and tan spot on the basis of the top leaves damage intensity. Thus, the reaction to all the diseases was scored as follows: 1–2 – very susceptible, 3 – highly susceptible, 4 – susceptible, 5 – moderately susceptible, 6 – moderately resistant, 7 – resistant, 8 – highly resistant, 9 – immune. That allows processing the data of pathogen response uniformly in points using conventional statistical methods (Babayants, Babayants, 2014). The designations of diseases and morphological traits in the tables and text are given in accordance with the Catalogue of Gene Symbols for Wheat (McIntosh et al., 2013).

Meteorological conditions. The environments, in which plants were grown, differed between years very much. The 2018–2019 growing season was characterised as moderately drought but was mostly favourable with the total rainfall of 172 mm (Sidorenko, Chebotar, 2020). The 2019–2020 growing season was a durable strong drought with the total precipitation of 26 mm during winter and no productive precipitation in spring. The lack of rain in the autumn of 2020–2021 growing season with the exception of 23 mm on 4–5 September together with high air temperatures (up to 31°C in September and 24°C in October) resulted in a severe drought. Almost no moisture reserves were detected in the arable (0–20 cm) soil layer throughout October–December. Being sown on 10–12 October, seeds lost energy of germination, and young growth was observed in January but was weak and sparse. The plant development was following the spring habit: overwintering in the spike phase and spring weak tillering. Plentiful spring and summer rains contributed to the growth of the vegetative mass of surviving crops but not to the grain yield. Thus, the drought resistance index was calculated as the fraction of grain yield in the severe drought of the 2020 or 2021 growing season compared to the yield in the satisfactory season of 2019:

drought resistance index, % = (grain yield in 2020 or in 2021, t ha⁻¹ / grain yield in 2019, t ha⁻¹) × 100%.

Contrary to Motsnyi et al. (2021a), the index being calculated in that formula is directly proportional to the level of drought resistance.

Statistical analysis was performed with the correlation and analysis of variance (ANOVA) using the software *Statistica* (StatSoft Inc.). Before the data analysis, the percentage values of drought resistance index were converted to the Fisher's angular coefficient (ϕ) in radians for the normalisation of frequency distribution.

For quantitative scores, Spearman's nonparametric rank correlation coefficient (R_{sp}), and for point scores, the Pearson's linear correlation coefficient (r) were calculated. To compare the means and analyse the variability of the values, the least significant difference (LSD) test of an appropriate confidential level, the mean values (MV), standard deviation (SD), limits of variation (LV), and the level of statistical significance (p) were used. The unified notations of the confidential levels of indicators, criteria, and coefficients defined by us or taken from the literature have been reported in the tables and text: *, **, and *** – significant at the $p < 0.05$, 0.01, and 0.001 probability levels, respectively.

Results and discussion

The genetic background and environment play important roles in the phenotypic variation for disease resistance (Mourad et al., 2021) and defining the contribution of alien genes to grain yield (Morgun, 2016; Bhatta et al., 2019; Yang et al., 2021). The plant pathological evaluation of the genetically diverse lines has revealed a wide variability pathogenesis by powdery mildew, leaf, and yellow rusts, and Septoria leaf blotch across the years. The correlation between resistance to the same disease in different years scored $R_{sp} = 0.42^{***}$ for powdery mildew (between 2016 and 2019 years), varied from $R_{sp} = 0.45^{***}$ to 0.71^{***} for leaf rust (between 2016, 2018, ^{sp} and 2019 years), and were $R_{sp} = 0.22^{**}$ for yellow rust (between 2015 and 2016 years^{sp}) and $R_{sp} = 0.31^{***}$ for Septoria leaf blotch (between 2016 and 2019 years). This may be due to changes in the racial composition of pathogen populations (Wellings, 2011; Babayants, Babayants, 2014; Soko et al., 2018; Mourad et al., 2021). Another explanation could be the presence of unidentified ineffective race specific genes for resistance. However, the reaction to stem rust was the most constant over the years (Motsnyi et al., 2021b). The studied lines differed more depending on the origin of material than the year conditions. This is probably due to the presence of the permanent artificial infectious background of the disease with the same racial composition across the years.

Most of the lines were found to be resistant to one of the rust species that was due to a successful introgression of the alien *Lr*, *Yr* or *Sr* genes from all sources involved in hybridisation (Table 1). There were fewer lines resistant to powdery mildew (Table 1, Figure 1A), but resistance to Septoria leaf blotch was not observed (Figure 1B); the best lines showed a moderate susceptibility at the level of standard cultivars. The lines resistant to stem rust were often also resistant to leaf but not to yellow rust. Several lines were resistant to all rust species (E212/09, AIL87PH18, and AIL341/18). The most resistant were the derivatives of the collection

Table 1. Average disease resistance scores in the years 2015–2021 and correlations between the grain yield and resistance of 153 winter wheat lines

Disease	% lines with reaction, points					Statistical parameter				
	susceptible		resistant							
	1–2	3–4	5	6–7	8–9	MV	SD	LV	R_{sp} 2019	R_{sp} 2020
PM	1.3	58.2	25.5	13.7	1.3	4.3	1.25	1–8	–0.04	0.11
LR	3.3	37.3	4.6	51.6	3.3	5.4	1.72	2–8	–0.08	–0.07
YR	4.6	45.8	3.9	44.4	1.3	5.1	1.63	2–8	0.19*	0.26***
SR	33.3	25.5	10.5	27.5	3.3	4.0	2.25	1–8	–0.08	0.07
STB	3.9	88.2	7.8	–	–	3.7	0.67	2–5	0.14	0.27***

PM – powdery mildew, LR – leaf rust, YR – yellow rust, SR – stem rust (artificial infection), STB – Septoria tritici blotch; MV – mean value of the trait on the lines, SD – standard deviation, LV – limits of variation (min–max); R_{sp} – Spearman's nonparametric coefficient; *, *** – significant at $p < 0.05$ and < 0.001 , respectively.

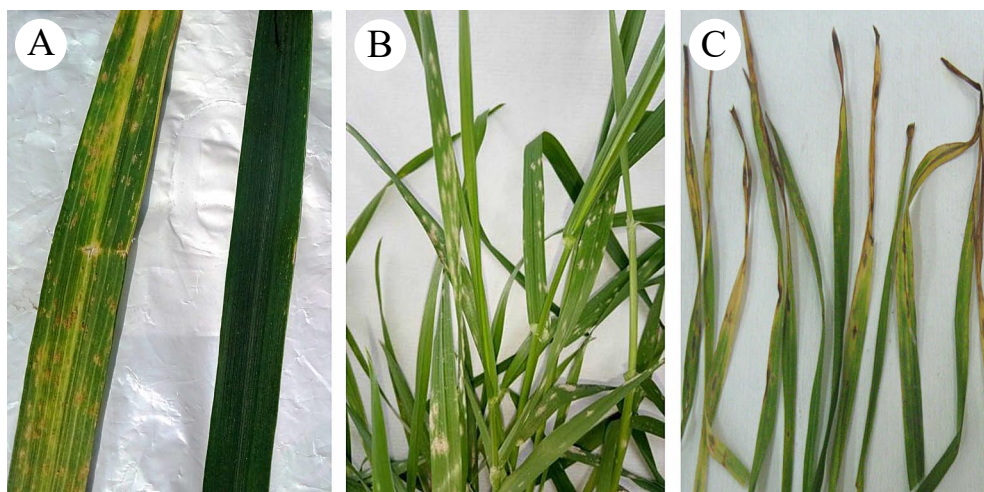


Figure 1. Winter wheat line E212/09 resistant to powdery mildew (A, right) and the standard cultivar 'Kuyal'nyk' (A, left) affected by powdery mildew (B), and the introgression lines affected by Septoria leaf blotch (C)

sample H74/90-245 from Bulgaria. It is known that combining alien resistance genes from different sources resulted in donors with a high resistance to rust diseases (Motsnyi et al., 2021a).

The wheat-rye translocation 1BL.1RS of 'Aurora' type was determined using the electrophoresis of storage protein in the sample H74/90-245 and some of its derivatives (Motsnyi et al., 2021b). Resistant lines in their progeny studied in the current experiment likely inherited the translocation. The 1RS arm of this translocation is known to carry the *Lr26/Sr31/Yr9/Pm8* gene complex (McIntosh et al., 2013). The effectiveness of the resistance genes in this locus is partly lost due to the emergence of new races of pathogens. However, some positive effect of the translocation 1BL.1RS on the economically valuable and adaptive traits depends on the genetic and environmental background (Davoyan et al., 2018; Pershina et al., 2018; Shamanin et al., 2020). In particular, the *Sr31* and *Yr9* genes were reported to be effective for the pathogen resistance in Ukraine (Babayants, Babayants, 2014; Morgun, 2016).

The resistance level of the best lines cannot be determined only by the translocation 1BL.1RS (Table 1). Some effective *Lr* and *Sr* genes could be derived from the amphiploid AD (*T. timopheevii* × *Ae. tauschii*), which is a part of the sample H74/90-245 (Motsnyi et al., 2021b). Alien species, particularly the tetraploid (A'A'GG) wheat wild relatives (Badaeva et al., 2021), are known to provide diversity for new wheat genes and are useful hybridisation partners for wheat improvement (Liu et al., 2020; Shamanin et al., 2020; Sharma et al., 2021).

To determine the impact of alien genes on the pathogen resistance, the correlation analysis was performed using the data matrix from the overall values per each line and the nonparametric Spearman's coefficient (R_{sp}). The analysis showed a weak positive correlation of grain yield with resistance to yellow rust and Septoria leaf blotch in 2020 (Table 1). Probably, these diseases appear to be most harmful in the South of Ukraine. The absence of a correlation between grain yield and resistance to powdery mildew, leaf or stem rust agrees with our previous data (Motsnyi et al., 2021b) and suggests that resistance is associated with weak natural backgrounds of those diseases. Moreover, stem rust occurs in Odesa only after artificial infection, and yellow rust and Septoria leaf blotch become important in

individual years with favourable conditions (mild winters, cool and humid spring, and summer) for the diseases. In another study (Motsnyi et al., 2021a), a weak positive correlation ($R_{sp} = 0.34^{**}$) was revealed between grain yield and stem rust resistance and explained by a positive effect of the translocation 1BL.1RS on both traits. The absence of such correlation in the current (Table 1) and previous (Motsnyi et al., 2021b) studies could be due to another set of introgression lines (a small proportion of the lines with the translocation) or somewhat different environments.

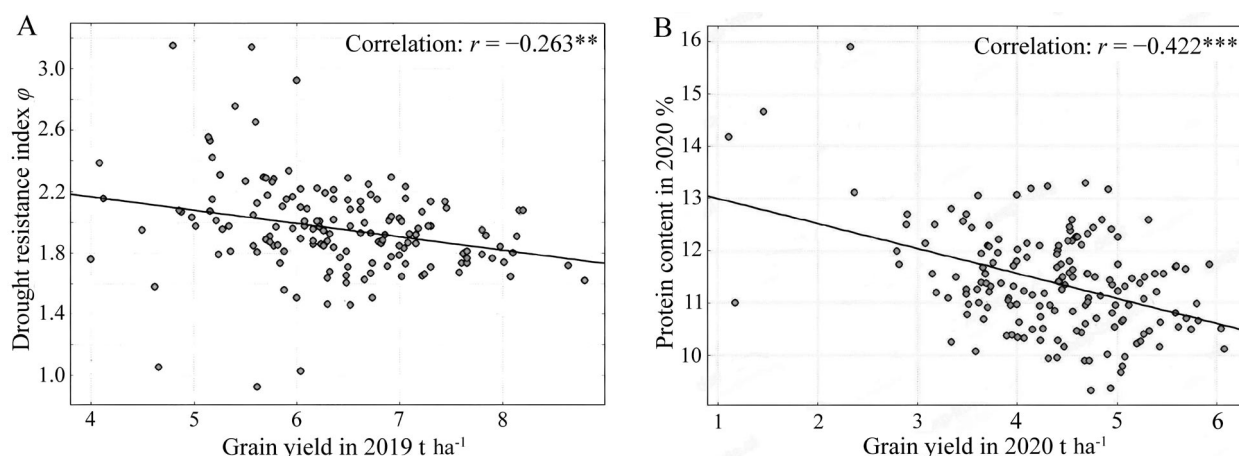
The lack of rain in the spring 2020 shortened the heading time by the average of 0.4 days and reduced the plant height by 16 cm compared to 2019. TKW and protein content varied in each line over the ten years resulting in different ranking. Nevertheless, on the average both parameters were slightly higher in the drier season of 2020. Protein yield was much higher in 2019 than in 2020 (0.68 vs 0.49 t ha⁻¹). This parameter was mainly influenced by the total grain yield, which was also much higher in the more favourable weather of the growing season 2019 than in 2020 (6.40 vs 4.32 t ha⁻¹). However, the absolute protein content per TKW was in 2019 than in 2020 (3.94 g vs 4.41 g). Differences between mean values for all parameters were significant at $p < 0.001$ with the exception of the heading date (Table 2).

Except for two lines, the overall grain yield was higher in 2019 than in 2020. Line AIL391/18 (Kuyal'nyk/4/Od.267/H74/90-245 F₂ // Od.267^{*4}/3/Selyanka F₇/5/Vatazhok F₆) had almost the same grain yield in both growing seasons: 5.56 and 5.59 t ha⁻¹ in 2019 and 2020, respectively. Only line PIL906/16 (Selyanka/ES20 F₇//Od.267 F₈) was more productive in the dry season of 2020 (5.80 t ha⁻¹), but less productive in the season of 2019 (4.80 t ha⁻¹). Lower grain yield in 2019 was most likely due to the reasons accounted for in the experimental design. Consequently, the drought resistance index in some lines exceeded 100% ($\varphi > 3.142$) with the overall range between 19.8% and 120.8% for the experimental lines and between 63.3% and 83.1% for the standard cultivars (Figure 2A). The minimal drought resistance index corresponding to the worst drought resistance was in the line MA1 (24.2%), which has a modified translocation of 1BL.1RS_m in the genetic background of the spring wheat cultivar 'Pavon 76' (Lukaszewski, 2000) as well as in its derivatives. The

Table 2. Effect of drought on the main agronomic traits of winter wheat lines in 2020 compared to the more favourable growing season of 2019

Agronomic trait	Growing season		Effect of drought	
	2018–2019	2019–2020	absolute values	%
Date of heading, May	12.4 ± 1.99 (8–17)	12.0 ± 1.76 (9–17)	–0.4	–3.2
Plant height cm	104.8 ± 10.2 (73–140)	88.8 ± 7.3 (60–115)	–16.0***	–15.3
Grain yield t ha ^{–1}	6.40 ± 0.93 (4.00–8.80)	4.32 ± 0.86 (1.11–6.08)	–2.08***	–32.5
Protein content %	10.6 ± 0.78 (8.6–13.6)	11.4 ± 0.99 (9.3–15.9)	+0.83***	+7.8
Protein yield t ha ^{–1}	0.68 ± 0.11 (0.43–1.02)	0.49 ± 0.09 (0.13–0.70)	–0.19***	–27.7
Thousand kernel weight (TKW) g	37.2 ± 3.14 (23.4–47.0)	38.7 ± 3.72 (23.1–51.5)	+1.45***	+3.9
Absolute protein content per TKW g	3.94 ± 0.42 (3.06–5.47)	4.41 ± 0.55 (3.33–6.75)	+0.47***	+12.0

Mean ± standard deviation and limits of variation (in parenthesis), *** – significant at $p < 0.001$

**Figure 2.** Correlation between the drought resistance index (percentage values converted to the angular coefficient ϕ) and winter wheat grain yield (in 5 m² plots) in the control nursery in 2018–2019 (A) and between the protein content and grain yield (in 10 m² plots) in the control nursery in 2019–2020 (B) growing seasons

drought resistance index in 11.2% of the experimental lines exceeded that of the standard cultivars.

The drought resistance index correlated with the grain yield in the arid conditions in 2020 ($r = 0.69^{***}$). This outcome is consistent with the fact that drought tolerance is determined by the productivity under sub-optimal soil moisture content. However, the index was also inversely proportional to the grain yield values ($r = -0.26^{**}$) under favourable conditions (Figure 2A). Interestingly, the lines with a lower grain yield in 2019 had a smaller one reduction in arid 2020 and thus were allegedly classified as lines having a higher drought resistance. This outcome indicates that drought tolerance traits can negatively impact the grain yield under these conditions. Furthermore, except for three lines with a high and three lines with a low drought resistance index, the vast majority of cases on the scatterplot fitted the general trend. Therefore, the drought resistance index is determined not only by grain yield in drought conditions but also by one under favourable environments.

A correlation between the drought resistance index and protein yield ($r = -0.25^{**}$ in 2019 and $r =$

0.69^{***} in 2020) signifies the contribution of grain yield to this trait. Interestingly, a correlation ($r = -0.17^{*}$) was also observed between the drought resistance index and protein content in 2020. Apparently, this is due to the negative correlation between the line grain yield and protein content ($r = -0.42^{***}$) in 2020 (Figure 2B). The correlation between the drought resistance index and TKW as well as the protein content and absolute protein content per TKW in 2019 was insignificant (Table 3).

According to the 2019 and 2020 data, 18 introgression lines with a different level of resistance to powdery mildew or rusts were picked out and sown for the next 2020–2021 growing season (Table 4). In the dry season of 2020, these lines combined a high productivity and the highest drought resistance index. Six of them were the advanced lines derived from the sample H74/90–245. Based on the apparent resistance to stem rust, these lines might carry the translocation 1BL.1RS from the cultivar ‘Aurora’. Except for NIL4 (Od.267/E124/03//Od.267^{*10} F₇), none of those lines showed the alien morphological traits.

Table 3. Correlation between the drought resistance index and agronomic traits of winter wheat introgression lines and standard cultivars in the control nursery (n = 152)

Growing season	Date of heading	Plant height	Grain yield	Protein content	Protein yield	Thousand kernel weight (TKW)	Absolute protein content per TKW
2018–2019	0.26**	–0.13	–0.26**	–0.05	–0.25**	0.15	0.09
2019–2020	0.30***	0.02	0.69***	–0.17*	0.69***	0.13	–0.01

*, **, *** – significant at $p < 0.05$, < 0.01 , and < 0.001 , respectively

Table 4. Resistance and performance (visual evaluation of productivity before harvesting) of the selected winter wheat lines

Line / cultivar	Resistance to diseases, points						Drought resistance index		Performance points ¹
	PM	LR	YR	SR	STB	TS	2020 ²	2021 ²	
Od.267 (rec)	3–4 ¹	3–5	4–5	1–2	4–6	5	61.5	32.2	4...5–
NIL2	3–4	6–8	4–5	1–2	4–7	5	66.3	26.9	4+
NIL4	4	3–4	4–5	1–2	4–5	7	74.1	32.4	4+...5–
E212/09	7–8	5–7	6–7	5	3–4	4	80.6	34.1	4+...5+
E214/09-7	4–5	2–4	4–7	4–6	4–5	4	77.3	22.0	5+...2–
E2776/14	5	3–6	5–7	2–3	4–5	5	74.9	21.0	4–...4+
E2778/14	6–8	3–6	5–7	3	4–5	7	73.6	30.6	4...5+
PIL860/16	6	3–5	6–7	2	4	4	98.8	24.8	5–...5+
PIL906/16	6–8	7–8	4–7	2	4–5	4	120.8	34.4	5+...2–
BL1015/16	3	3–5	6	2–3	3–5	6	69.6	30.1	4+...5–
BL1024/16	5	3–5	4	2–4	4–5	8	72.4	34.4	4...5–
BL1025/16	4–5	3–5	4	2–4	4–5	6	82.8	42.8	4...5–
AIL327/18	5	3–4	4–7	2–3	4–5	5	74.1	23.4	4–...5–
AIL341/18	4	6–7	4–7	7	4–5	4	77.5	20.2	4...5–
AIL391/18	4	3–5	5–7	5–7	5	5	100.5	23.6	4–...5–
AIL890/18	5	3–4	4	2–4	3–4	4	79.9	38.2	5...5+
AIL87PH18	4	5–7	5–7	6–8	3	6	85.9	13.0	4+...5+
AIL236PH18	4–6	5–7	5–6	6–8	3–5	4	76.6	9.5	5+...2–
PIL355PH18	4	6–7	7	2	5	6	76.7	29.5	4...5–
Kuyal'nyk (st)	3–4	3–4	4–5	2–3	3–6	4	74.1	37.4	4...5
Nasnaga (st)	3–4	3–4	3	2–3	4–5	4	70.4	37.9	4...5

Note. rec – recurrent, st – standard; NIL – near isogenic line, E – erythrosporum, PIL – primitive introgression line, BL – breeding line, AIL – advanced introgression line, PH – line from the field infectious nursery of the Department of Phytopathology and Entomology of PBGI-NCSCI; the lines selected for further breeding are marked in bold; PM – powdery mildew, LR – leaf rust, YR – yellow rust, SR – stem rust, STB – Septoria tritici blotch, TS – tan spot; the points correspond to the intensity of damage in percentages: 1 – to 100%, 2 – to 90%, 3 – to 65%, 4 – to 40%, 5 – to 25%, 6 – to 15%, 7 – to 10%, 8 – to 5%, and 9 – to 0%; defeat of infection accumulators and high disease susceptibility indicators – 1 point each year; ¹ – range of variation in scores across the years; ² – grain yield percentage from the yield in 2019.

In general, the picked-out lines eared later and were lower or higher than the standard cultivars (Table 5). The near isogenic line NIL2 (Od.267/PEAG//Od.267^{*10} F₇) carries the gene *Lr42* from the amphiploid PEAG (*T. dicoccum* Schuebl. × *Ae. tauschii* Coss.) in the genetic background of cultivar 'Odes'ka 267'. This line flowered earlier and was shorter than the recurrent cultivar and had slightly higher grain yield, protein content, TKW, and sedimentation values than the standard ones.

However, the drought resistance index was not significantly different. Line NIL4 with pubescence of the lower part of the stem (leaf sheaths) regularly exceeded the productivity of the recurrent and standard cultivars (Figure 3). The alien trait was transferred from the primitive introgression line E124/03 and originated by outcrosses probably from *Aegilops cylindrica* Host, which was widely spread among the hybrids. According to Vdovichenko et al. (2001), the trait is controlled by 4D chromosome and may be used as its morphological marker. The presence of a segment of the alien 4D chromosome according to literature (Li et al., 2011) and our preliminary data (not shown) had a positive effect on increasing the tiller number per plant that probably might provide some advantages under dry conditions.

The lines NIL2, E2776/14, PIL860/16, BL1015/16, AIL341/18, AIL391/18, AIL87PH18, and AIL236PH18 were severely sparse, and the lines E214/09-7, BL1015/16, and AIL236PH18 were struck by common bunt and were culled. The line PIL906/16 having the highest drought resistance index in 2020

**Figure 3.** Hairiness of leaf sheaths in winter wheat line NIL4

had a low breeding performance, was unnecessarily dwarfed, and had a low grain yield (1.65 t ha⁻¹) in 2021. Notably, the line E2776/14 (Vigen/Od.267//Selyanka F₆) known for a high productivity and protein content, in the previous study (Motsnyi et al., 2021a), showed no tolerance to a severe drought in the autumn of 2020 (grain yield 1.57 t ha⁻¹ in 2021 and protein content at the level of standard cultivars). Furthermore, the line PIL355PH18 (Selyanka/ES20 F₂//Od.267 F₅/3/Gurt F₄), previously selected for a high grain yield and protein content and large grains (Motsnyi et al., 2021b), had the highest TKW but the average grain yield and protein content (Table 5).

Table 5. Mean values of important agronomic traits of winter wheat lines in the 2019–2021 growing seasons

Line / cultivar	Heading date, May	Plant height cm	Grain yield t ha ⁻¹	Protein content %	Protein yield per area kg ha ⁻¹	Thousand kernel weight (TKW) g	Absolute protein content per TKW g	Sedimentation ml
Od.267 (rec)	18.3	100.0	5.21	11.1	587	38.9	4.32	57
NIL2	17.3	94.3	5.24	11.3	597	43.6	4.91	74
NIL4¹	19.3	101.7	5.61	10.9	624	40.1	4.37	62
E212/09	18.3	82.3	5.12	11.5	579	44.0	5.09	56
E214/09-7	18.3	85.0	4.50	11.0	477	41.1	4.55	54
E2776/14	18.3	84.3	4.87	11.1	513	38.2	4.26	62
E2778/14	18.7	87.7	5.20	11.2	434	43.3	5.04	55
PIL860/16	17.0	98.3	4.47	10.8	479	38.1	4.09	64
PIL906/16	21.7	72.7	4.08	10.6	432	42.0	4.46	44
BL1015/16	17.7	84.0	4.86	11.0	517	43.9	4.85	57
BL1024/16	19.0	90.3	4.77	10.8	502	40.7	4.42	62
BL1025/16	18.7	85.3	4.89	10.9	524	39.4	4.32	58
AIL327/18	16.3	92.3	5.40	10.9	592	40.3	4.40	55
AIL341/18	19.3	97.0	4.65	11.9	564	35.7	4.23	57
AIL391/18	21.3	87.0	4.15	11.7	478	37.4	4.37	64
AIL890/18	17.3	84.0	4.62	9.8	438	40.1	3.93	60
AIL87PH18	18.0	87.0	3.95	11.2	440	35.4	3.98	58
AIL236PH18	17.3	81.7	4.62	10.2	471	38.4	3.92	51
PIL355PH18	15.7	89.7	5.02	11.0	544	45.4	5.04	51
Kuyal'nyk (st)	16.8	90.8	4.83	10.5	434	37.5	3.94	62
Nasnaga (st)	17.1	90.5	5.08	10.4	527	37.1	3.86	54
LSD _{0.05}	1.4	7.4	1.0	0.6	78	3.4	0.32	–

Note. Explanation under Table 4; ¹ – the lines selected for further breeding are marked in bold; LSD_{0.05} – significant at $p < 0.05$.

A severe drought in the autumn of the 2020–2021 growing season caused ca. 70% grain yield losses in all lines (Table 4). Therefore, despite the high potential of the picked-out lines, there was a stagnation of the grain yield under the stress (Table 5). The differentiation between the lines was almost absent under such environments, and only few lines differed from the standard cultivars. The same trend was reported in other regions (Langridge, Reynolds, 2021) necessitating an identification of new sources of genes for disease resistance or tolerance to abiotic stress (Reynolds et al., 2007). Some traits including the date of heading, plant height, grain protein content, TKW, and absolute protein content per TKW differed between some lines and the standard cultivars.

The lack of significant differences between the lines in protein yield per area is explained by the strong variation of both components (grain yield and protein content) of the trait depending on the year environments. As a result, for preliminary trials, four promising drought-tolerant lines: NIL4, E212/09 (H242/97-1/Od.267*₃//Kuyal'nyk F_∞), E2778/14 (Vigen/Od.267//Selyanka F₆), and AIL890/18 (Kuyal'nyk/B241/09 F₄), were selected. These lines scored the highest grain yield (above the nearest standard) in 2021, were not affected by common bunt, and had sedimentation values similar to those in the standard cultivars. Although the line AIL890/18 did not exceed the average grain yield of the standard cultivars, had low protein content, and was susceptible to diseases, it showed one of the best breeding performance and the highest drought resistance indices next to the line BL1025/16 (Table 4).

It is known that *T. timopheevii* has a complex immunity to fungal diseases (Badaeva et al., 2021). Synthetic hexaploids *T. timopheevii* × *Ae. tauschii*

are commonly used in hybridisation (Brown-Guedira et al., 1996; Tverdokhle, 2009; Davoyan et al., 2018). However, their leaf rust resistance is mainly controlled by the gene combination of *Lr39* from *Aegilops* and *Lr26* from rye (Davoyan et al., 2018) but not by elements of tetraploid A'A'GG. This above gene pool is commonly ignored (Badaeva et al., 2021) due to the inefficiency of introgression processes: the chromosomes of the specific subgenomes A' and G are structurally different from the genome of wheat (Brown-Guedira et al., 1996) that complicates the introgression of resistance genes. The genetic material of the A' and G subgenome chromosomes is transferred to wheat usually by translocations of large segments or substitutions of whole chromosomes. The presence of such amounts of alien chromatin causes a decrease in the productivity of the introgression material. For this reason, the number of commercial cultivars with A'G genome elements is generally very small (Laikova et al., 2013), though many introgression lines were generated using *T. timopheevii* (Brown-Guedira et al., 1996; McIntosh et al., 2013). Nevertheless, such genetic material is carried by the cultivar 'Pamyati Maystrenko' containing 2G and 3G chromosomes of *T. timopheevii* and 1D chromosome of *Ae. tauschii* (Laikova et al., 2013).

Therefore, studies of alien traits are crucial for both improving the genetic potential of winter wheat and developing new effective breeding strategies for drought tolerance (Motsnyi et al., 2021a; Sharma et al., 2021; Yang et al., 2021). More successful exploitation of the alien resistance genes from the A'G genome as well as from the 1BL. 1RS translocation could be achieved by inducing of wheat-alien allosyndesis (Lukaszewski, 2000) or developing transgenic wheat lines (Yu et al., 2021).

Although crossbreeding with wild wheat ancestors or related species remains an attractive option for developing advanced breeding lines, this strategy requires a careful choice of the modern cultivar parent as well as a sufficient number of backcrosses. This is because each modern cultivar comprises a unique association of genes for grain quality and adaptation to specific growing conditions, which results from a centuries-long breeding. Hybridisation, especially wide, disrupts the established genetic balance. Therefore, the limited number of useful traits contributed by the wild wheat ancestors (such as disease resistance) can be outweighed by many polygenic undesirable traits. For example, a significant disadvantage of high-yielding introgression lines remains grain yield instability in different environments (Motsnyi et al., 2021b). Therefore, only a few of such lines become cultivars (Babayants, Babayants, 2014; Lytvynenko, 2016b; Morgun, 2016; Pershina et al., 2018; Shamanin et al., 2020). Restoring this balance can only be achieved through numerous saturating crosses with modern high-productive cultivars. A subsequent selection for the desired phenotype helps to establish unique gene associations and eliminate harmful traits.

Conclusions

The analysis of the agronomic effects of an alien genetic material using the experimental lines derived from the wide hybridisation of different sources of alien variability with the established winter wheat cultivars lead to the following conclusions:

1. The resistance to powdery mildew, leaf and yellow rusts, and Septoria leaf blotch varied across the years. However, the tolerance to stem rust was the most constant and correlated with the line pedigree rather than the climate conditions.

2. Disease resistance depends on the pathogen species and the source of alien genetic variability. Resistance to one of rust species has been successfully transferred from all sources involved in the hybridisation but to all rusts – mainly from the collection sample H74/90-245 containing the whole (unmodified) translocation 1BL.1RS in the karyotype and *Triticum timopheevii* in the pedigree. Fewer lines were resistant to powdery mildew, and no resistance was found to Septoria leaf blotch.

3. The drought reduced the plant height, grain yield, and protein yield but increased the thousand kernel weight (TKW) and protein content. The grain yield reduction was 32.5% in 2020 and ca. 70% in 2021 compared to 2019 with a good precipitation. The experimental lines differ in the date of heading, plant height, TKW, total protein content, and absolute protein content per TKW. There were no significant differences of the grain yield and protein yield among the lines due to the severity of drought. Some advanced lines, which combined a high productivity in dry seasons with the highest drought resistance index, were not resistant or resistant only to one disease.

4. The best results in terms of both disease resistance and adaptation were obtained among the advanced lines derived from the sample H74/90-245. The worst results were of the lines with any morphological features of wild species. The near isogenic lines with the alien genes *Lr42* and *Hs* in the genetic background

of cultivar ‘Odes’ka 267’ showed the tendency to have a higher grain yield under drought conditions than the recurrent and standard cultivars.

5. Eighteen lines with disease resistance, high values of TKW, protein content, grain yield or drought resistance were picked out, and four promising drought-tolerant lines have been selected for further breeding studies.

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Tolimosios hibridizacijos būdu gautų žieminių kviečių veislių atsparumas ligoms sausringomis sąlygomis

I. Motsnyi¹, M. Lytvynenko¹, E. Golub¹, T. Nargan¹, M. Nakonechnyy¹, S. Lyfenko¹,
O. Molodchenkova¹, Y. Fanin¹, I. Mishchenko², A. Smertenko³, L. Mishchenko⁴

¹Nacionalinio augalų sėklų ir veislių tyrimo centro Augalų auginimo ir genetikos institutas, Ukraina

²Ukrainos nacionalinis gyvybės ir aplinkos mokslų universitetas

³Vašingtono valstybinio universiteto Biologinės chemijos institutas, JAV

⁴Taraso Ševčenkos nacionalinio Kijevo universiteto Švietimo ir mokslo centras „Biologijos ir medicinos institutas“, Ukraina

Santrauka

Grybelinės ligos ir sausra gali sukelti žymius žieminių kviečių derliaus nuostolius. Yra žinoma, kad dėl tolimosios hibridizacijos atsiradusios naujos augalo savybės gali padidinti augalų derlių sausringomis sąlygomis. Tyrimo metu analizuota įdiegtų naujų genų įtaka pagrindinėms agronominėms savybėms sausose Ukrainos pietinėse stepėse. 2019–2021 m. žieminiai kviečiai buvo auginti 5 ir 10 m² sklypuose sausros sąlygomis. Buvo įvertintos 8 agronominės bei 6 augalų patologijos savybės ir atlikta jų statistinė analizė įvairovei bei tarpusavio ryšiai nustatyti. Dėl sėkmingos naujų genų iš visų hibridizacijos šaltinių introgresijos dauguma veislių buvo atsparios vienai kviečių rūdžių rūšiai. Veislės, gautos iš genotipo, turinčio translokaciją 1BL.1RS kariotipe ir *Triticum timopheevii* genealogijoje, buvo atsparios visų rūdžių rūdims. Nustatytas neigiamas ryšys tarp baltymų kiekio bei grūdų derliaus 2020 m. ($r = -0,40^{***}$) ir silpnas teigiamas ryšys tarp grūdų derliaus bei atsparumo geltonosioms rūdims ($R_{sp} = 0,19^*$ 2019 m. ir $R_{sp} = 0,26^{***}$ 2020 m.) arba lapų septoriozės toleravimo ($R_{sp} = 0,27^{***}$). Esant sausrui, 2020 m. grūdų derlius sumažėjo 32,5 %, 2021 m. – apie 70 %. Naujus *Lr42* ir *Hs* genus turinčių linijų žieminių kviečių grūdų derlius buvo didesnis už rekurentinių ir kontrolinių linijų derlių.

Tolesnei selekcijai atrinkta 18 linijų, kurios turi didelę 1000 grūdų masę, didelį kiekį baltymų, duoda gerą grūdų derlių ir yra atsparios sausrui bei ligoms, taip pat 4 perspektyvios sausrui atsparios linijos.

Reikšminiai žodžiai: atsparumas ligoms, sausra, kviečių veislės, agronominės savybės, produktyvumas, *Triticum aestivum*.