

ANALYSIS OF PHYSIOLOGICAL MECHANISMS OF ADAPTATION AND RESISTANCE OF WINTER WHEAT ACCESSIONS OF DIFFERENT GEOGRAPHICAL ORIGINS

Makaova B.Ye., Tyshchenko V.M.
Poltava State Agrarian University, Ukraine

The article presents a literature review of methods analyzing the role of morphological traits and physiological responses to climatic changes. The article covers results on 318 winter wheat accessions of different eco-geographical origins from 27 countries described by a set of morphological traits and physiological responses to environmental conditions of the Left-Bank Forest-Steppe of Ukraine in 2020–2021 and 2021–2022.

Key words: *winter bread wheat, starting material, adaptation, morphological trait.*

Introduction. Winter wheat (*Triticum aestivum L.*) is a critically important component of the global food system, providing a significant part of the world's food supply and contributing to food security in many regions [1]. Since the implementation of the Green Revolution achievements in production, the winter wheat yield has increased 2- to 4-fold, depending on cultivation regions. Today, its yield can amount to 120 t/ha under favorable environmental conditions and with state-of-art farming techniques [2]. However, high-yielding wheat varieties are less able to maintain homeostasis than highly adaptable varieties, especially when grown at drought [3], high temperatures [4], low temperatures [5] and significant disease development [6].

In Ukraine, reduced precipitation and the efficiency of its use by plants is particularly critical with regard to wheat yield losses. The average annual precipitation (for the period of 1961–1990) in Ukraine is 578 mm, whereas 700 mm and more are required for sustainable agriculture. The territory of Ukraine is mostly a risky agriculture zone (in particular, where winter wheat occupies large areas). In addition, the steppe area (zone of unstable moisture and elevated temperature) tends to enlarge. Analysis of trends in climatic changes in recent years in Europe makes it possible to assume that the weather in the cereal-growing zone of Ukraine is a future scenario that is possible in Eastern and Central European countries, which currently have favorable conditions for winter wheat growing [7].

Literature review. Today, studies of adaptation and resistance to adverse environmental factors are conducted towards adapting wheat phenology to climatic changes [8] as well as towards increasing photosynthetic activity [9] and efficiency of moisture [10] and fertilizer [11] use. However, research into resistance to adverse environmental conditions and regeneration rate after stressor action is of the greatest interest [12].

Winter wheat is a highly adaptable crop; it is grown in a wide range of environments due to diversity of genes that are responsible for phenological phases [13]. Wheat phenology and physiology allows it to counteract negative environmental phenomena by changing lengths of development phases in accordance with changes in environmental conditions [14, 15]. Productivity features is expressed precisely in association with resistance of wheat plants to negative environmental factors [16, 17].

Elucidation of mechanisms of plant resistance to extreme temperatures in recent decades has become one of the most urgent problems of plant physiology [18] and agriculture [19]. Genes and gene complexes of resistance to extreme temperatures, their expression and inheritance, which form metabolic and biochemical pathways of adaptation, are studied in breeding [20,21].

Vernalization (Vrn), photoperiod (Ppd), dwarfism (Rht), and disease resistance genes have major effects on developmental phases and, in general, on adaptation to a new cultivation site with conditions differing from those in the origin location of a genotype. It was established that genotypes with long vernalization and low photoperiod sensitivity are most suitable for the Left Bank Forest-Steppe of Ukraine [22]. Such combination ensures high winter hardiness and freezing tolerance, as well as rapid growth and development of plants in spring, so plants will have time to set seeds before drought and high temperatures.

Knowledge of physiological responses of different morphobiotypes to changes in growing conditions, their expression and inheritance is a basis for targeted breeding of valuable winter wheat genotypes upon climatic changes [15].

The coefficients of environmental plasticity and stability are classic methods to determine adaptability [23], followed by visually evaluated and laboratory tested morphological and physiological traits of collection winter wheat accessions, as such assessments are becoming widespread [24].

Use of wheat accessions of different geographical and genetic origins, which have specific morphological features and physiological responses to stressors, is important in increasing the genetic diversity, adaptability and resilience [25, 26].

For local breeding programs, traits that are statistically significantly related to productivity are markers of adaptation to specific conditions and can be determined directly in the field or by simple laboratory tests that do not require high financial costs; these traits are of great importance.

Characteristics that determine resistance to adverse conditions during germination and overwintering include a large kernel and a long coleoptile; rapid root growth in the initial phases; rapid growth of secondary roots; rapid accumulation of sugars; high or medium freezing tolerance and high winter hardiness in the field; regenerative capacity of plants [27].

If we summarize publications on basic morphological traits that ensure resistance to high temperatures and drought, they are as follows [28, 29, 30]: seed germination and energy of germination; long coleoptile; high percentage of plant coverage of the ground surface; high absorption capacity of the root system; presence of wax coating; pubescence of leaves; ability to twist leaves to reduce transpiration; early earing and flowering; large leaf and flag leaf surfaces; moderate height of plants; increased amount of chloroplasts (light-green color); stay-green character of the upper internode and flag leaf during the grain filling period; stem thickness, stem filling in the full ripeness phase (remobilization of substances).

Our purpose was to analyze the role of morphological traits and physiological responses to the conditions in the Left-Bank Forest-Steppe of Ukraine by investigating a large assortment of winter wheat collection accessions and identifying valuable accessions to involve them in breeding.

Materials and methods. This work is a continuation of the genetic diversity study on winter wheat accessions of different origins, the results of which were published earlier [31]. In total, 318 accessions of various ecological, geographical and genetic origins from 27 countries worldwide were studied. To comprehensively represent the Ukrainian genetic diversity, 145 varieties and lines bred in different years from all research-breeding institutions of Ukraine were included. The study accessions were grouped according to their geographical origins: Central and Western Europe - Austria (4 accessions), Bulgaria (4), the Czech Republic (7), Germany (30), France (15), Great Britain (2), Hungary (5), the Netherlands (2), Poland (2); Northern Europe - Estonia (7), Latvia (1), Sweden (2); Southeast Europe - Serbia (1), Croatia (2), Romania (9); Southern Europe - Turkey (37); Eastern Europe - Russia (17), Belarus (1); North America - USA (14), Canada (1); South America - Mexico (2); Central Asia - Azerbaijan (2); Kazakhstan (1), Tajikistan (1); Western Asia - Saudi Arabia (1), Iran (3). By genetic origin, the accessions belonged to the following subspecies: *Triticum aestivum* L: var. erythrospermum; var. lutescens; var. ferrugineum A1; var. album; var. milturum; var. nigro-aristatum; subs. spelt.

The study was conducted in the experimental field of the collection nursery of Poltava State Agrarian University (soil-climatic zone – Eastern Left-Bank Forest-Steppe of Ukraine; the Vorskla River valley) in 2020–2021 and 2021–2022.

The weather in 2020–2021 and 2021–2022 was not favorable for assessing drought resistance of accessions during the generative phase. The winter weather conditions was generally favorable for winter rest of winter wheat plants; in the both growing years, there were frosts down to -15°C with a thin snow cover, which enables evaluating the genotypes for resistance to low temperatures by damage to leaves. Characterizing the weather in the study years (2020 – 2022), we should note that the average annual air temperature was $+11.2^{\circ}\text{C}$ in 2020–2021 and $+10.1^{\circ}\text{C}$ in the 2021–2022. A clear upward trend in the average annual temperature is traced. February was the coldest month in comparison with the long-term average. The precipitation amount was 549 mm and 515 mm in 2020–2021 and 2021–2022, respectively. On November 12, 2020, winter wheat plants stopped autumn vegetation, which turned out to be 10 days earlier than the average multi-year data. The winter seemed to be relatively favorable for overwintering. Plants restarted active vegetation on March 28, 2021. On November 9, 2021, winter wheat varieties stopped active autumn vegetation, which turned out to be 13 days earlier than the average multi-year data. In the spring, the vegetation recovery was recorded on April 2, 2022.

The following parameters were evaluated in the field and in the laboratory: 1) the pre-overwintering state of plants (9-point scale, where 1 point is weak tillering and low intensity of growth; 9 points is rapid growth of vegetation mass); 2) winter hardiness (9-point scale, where 1 point is complete or partial death of plants; 9 points is complete survival of plants); 3) plant regeneration rate in the spring (9-point scale, where 1 point is weak performance and low growth intensity; 9 points is rapid growth); 4) earing time (the number of days after January 1); 5) damage by foliar diseases (as percentage of affected vegetative parts of plants and resistance score on a 9-point scale). Morphological characteristics was also assessed: flag leaf width (cm), wax coating intensity (1 point – light-green vegetative organs; 9 points – dark-gray); stem thickness in the upper internode; plant height (cm). The above parameters were visually assessed in accordance with distinction, uniformity and stability tests on common wheat (*Triticum aestivum* L.) varieties recommended by UPOV and the State Service [32], physiological methods in breeding used in CIMMYT [33] and methods of wheat breeding for winter hardiness [34].

Results and discussion. In the soil and climatic conditions of the Left-Bank Ukraine, significant variations in all the studied features characterizing resistance of plants to biotic and abiotic factors of the environment (growth rate in autumn, field winter hardiness, plant regeneration rate in spring, field resistance to diseases, lodging resistance) were recorded.

Table 1 summarizes basic statistical data on the accessions evaluated for physiological characteristics by study years.

Table 1

Basic statistic data on all wheat genotypes					
Trait	Year	Mean	Min	Max	Coefficient of variation, %
Autumn growth intensity score	2021-2022	5.0	2	8	21.7
Field winter hardiness score	2020-2021	6.1	1	9	27.3
	2021-2022	5.3	1	8	26.4
Spring growth intensity score	2021-2022	5.7	1	9	26.6
Days from January 1 to the earing date	2020-2021	157.3	149	171	2.9
	2021-2022	155.1	148	166	2.2
Field resistance to <i>Septoria spp.</i> score	2020-2021	5.7	1	9	36.8
	2021-2022	7.0	2	9	19.5
Lodging resistance score	2021-2022	8.3	3	9	14.1

Comparing the study years, we should note that the overwintering conditions in 2021–2022 were harsher than in 2020–2021. The average field winter hardiness score was lower than the previous year. On the contrary, the earing onset date in 2022 was earlier than in 2021, which can be explained by warmer and drier conditions in the spring. The average field resistance to *Septoria* spp. in 2022 was higher, although other foliar diseases were more prevalent.

Autumn growth intensity. The growth rate in the (increase in vegetative mass and, as a result, accumulation of stress-protective substances) determines subsequent resistance of a genotype to adverse overwintering conditions. The weather in the 2021–2022 growing season contributed to an extended growth period, which enabled evaluating the accessions by growth intensity at the initial stages.

Most of the accessions (215 or 68%) showed a medium intensity of growth (5–6 points) and entered the winter in the state of 5–7 leaves. Eighty-eight accessions (27%) showed a low intensity of growth (3–5 leaves) at the initial stages, which generally affected their further overwintering. The following accessions showed a high intensity of growth (7–10 leaves): Oberih Myronivskiy (Ukraine) and Andrada (Romania) (8 points); Lira Odeska, Oktava Odeska, Ferrugeneum 351, Bilotserkivska 153, Podolska 1 (Ukraine), Turkuaz (Azerbaijan), Katarina (Romania), Florencia, Bernstein (Germany) varieties and T67/X84W063-9-45//Kar192/3 (Turkey), RL6043/4*Nac//Pastor/3/Babach (Mexico), Bezostaya1/Ae.cylindrica (Kazakhstan) lines (7 points).

The growth intensity in the initial stages is important in relation to plant hardening and preparing for overwintering. Active tillering contributes to an increase in the photosynthetic surface of plants and accumulation of macronutrients. Taking into account the weather conditions during the sowing periods of recent years (dry and cool autumns), the ability of plants to grow quickly gives great advantages in terms of further seed productivity. In addition, high intensity of growth at the initial stages of plant development is a marker of low or neutral photoperiod sensitivity, which is important under climatic changes.

Winter hardiness. Winter resistance includes a complex of resistances to adverse weather conditions in winter. Recent climatic changes have increased the number of undesirable weather phenomena, including thin snow cover, frequent thaws and temperature fluctuations. Low photoperiod sensitivity and long vernalization play an important role in winter hardiness of plants. Freezing tolerance is a critically important trait for overwintering, but the greatest losses are caused by unpredictable combinations of factors, such as snow and ice crust, winter duration, light mode, freeze-thaw cycles, diseases, insects, which greatly complicate selection of resistant lines in the field. We assessed the condition of plants after overwintering, i.e. survival with due account for all the adverse factors of overwintering.

The weather in the both study years was generally favorable for winter wheat overwintering. It is noteworthy that the overwintering conditions in 2021–2022 were somewhat harsher; wheat plants were more exhausted because of sudden temperature rises and drops.

In 2020–2021, 24 accessions (about 10% of the total number) showed low winter hardiness (1–3 points), 96 accessions (40%) – medium winter hardiness (4–6 points) and 116 accessions – high winter hardiness (7–9 points). Of them, accessions that received 9 points stood out: breeding lines of Poltava State Agrarian University and Ustymivka Experimental Station, Tsarychanka, Kyivska 17 (Ukraine), Vekha (Russia), Ruske (Estonia) varieties. In 2021–2022, the following accessions had 8 points (high winter hardiness): Lira Odeska, Oberih Myronivskiy, Ferrugeneum 351, Natalka, Lehenda Myronivska, Bunchuk, Dykanka, PS Tashan (Ukraine), Turkuaz (Azerbaijan), Andrada (Romania) and NE10507 (USA). In 2021–2022, no genotype received 9 points (very high winter hardiness) because of exhaustion of plants during winter dormancy. One hundred and four genotypes showed low field winter hardiness, and 60 genotypes – high (7 points) winter resistance.

Complete death of plants after overwintering was recorded for the Renan (France) variety.

Ukrainian varieties and in particular breeding material of Poltava State Agrarian University demonstrated the highest winter hardiness with medium to high growth intensity in autumn under the harsh conditions of overwintering in 2021–2022.

A Romanian variety, Andrada, should be distinguished, as it showed sufficiently high winter hardiness in the two study years, as well as good regeneration in spring. Search for such accessions is an important objective in testing varieties of different origins.

Summing up, we can conclude that the highest number of highly winter-hardy accessions (7-9 points) over the two study years was recorded among accessions from Ukraine, USA, Estonia.

Spring growth intensity. Vegetative growth intensity after spring vegetation renewal depends on physiological characteristics of a genotype (winter hardiness and photoperiod sensitivity) and on environmental factors (soil and air temperature, moisture). Vegetative growth intensity in spring (tillering intensity and rate of transition to the generative phase) indicates how adaptable the genotype is to environmental conditions and how big yield is going to be harvested. Genotypes that can quickly reinstate growth after adverse overwintering conditions are of particular importance.

Thirty-two of the studied accessions (10%) had low regenerative capacity (1–3 points), 169 accessions – medium (4–6 points), and 118 accessions – high (7–9 points). The highest regenerative capacity was recorded for Ferrugeneum 351 (Ukraine) and T67 (Turkey).

The growth intensity in the autumn and spring periods was found to be closely correlated with winter hardiness. The correlation coefficient (r) between the field winter hardiness and autumn growth intensity was 0.653, while $r = 0.835$ for the “field winter hardiness – spring regeneration ability” correlation.

Accessions that combine high winter hardiness in the field and high regeneration ability in spring, especially under arid conditions, are of high value in breeding for adaptability to climatic changes. Such accessions included both Ukrainian varieties (Lira Odeska, Oberih Myronivskiy, Dykanka) and foreign varieties (Turkuaz (Azerbaijan), Andrada (Romania)). In addition, the following accessions showed increased winter hardiness (7-8 points) and good regeneration in the spring (8-9 points): Oktava Odeska, Harantiia Odeska, Natalka, Zolotava Nosivska, Lehenda Myronivska, Bunchuk, Orzytsia Nova, PS Tashan (Ukraine), T67/ X84W063-9-45//Kar192/3 (Turkey), AR800-1-3-1/NW97S320, and NE10507 (USA).

Earing date. Earing date is an important physiological marker that indicates both suitability of a genotype for growing conditions (corresponding ripeness group) and signs of photoperiod sensitivity. Wheat anthesis length is determined by growing period; it is when plants transit from nutrient consumption to nutrient accumulation; finally it influences seed yield and productivity traits.

The earing date varied from May 29 to June 20 in 2021 and from May 27 to June 15 in 2022. The early-ripening group over the two study years mainly comprises Ukrainian, Turkish, and Southern European varieties. In 2021, the earliest earing date (May 29) was intrinsic to the following accessions: Monterey 2 and Podilska Niva (Ukraine); Donskaya Polukarlikovaya and Grom (Russia); ATTILA/BABAX//PASTOR/4/TAST (Turkey); Bodycek (France); Daria (Croatia); Seilar (Germany); NE 12443 (USA); and Amandus (Austria). In 2022, the earliest earing date was recorded for Shestopalivka, Monterey 2, Plyska, Natalka, Buh, Ruta, 6180-06, Orzytsia Nova (Ukraine); Felix (Romania); Isfara (Tajikistan); OK82282/SNB//AGRI/NAC/3/SHA (Turkey); Mason/Jagger (USA); and Avenue (France). Representatives of European breeding pool (Germany, Czech Republic, Austria) mainly belonged to the late-ripening group. Of the Ukrainian varieties, Podilska Niva, which is close to the European ecotype in its characteristics, had the latest earing phase onset.

There was a weak inverse correlation between the field winter hardiness and the earing phase onset ($r = -0.21$).

Resistance to diseases. There were significant variations in damage to genotypes by diseases: from complete absence of damage signs to 90% of affected plant parts. The greatest loss of yield was caused by viral diseases. When considerably damaged, plants had no spikelets or significantly lost productive stems. The Septoria tritici blotch prevailed in 2021, while in 2022 other leaf diseases (brown and yellow rusts) were predominant.

In 2021, German accessions (Patras, Centurion, Florencia, Tobak, Vilejka, Arctis, Oksal, Mulan, Apertus, Estivus, and AR800-1-3-1/NW97S320 as well as GA951079-3-5/Neuse (USA) were highly resistant to *Septoria* spp. (9 points). Of the Ukrainian accessions, Raihorodka, Spivanka Poliska, Bohdana, Magnatka, Podilska Niva, and Kraievyd should be distinguished.

It should be noted that the *Septoria tritici* blotch intensity in 2022 was lower than in 2021. In 2021-2022, 41 accessions were highly resistant to *Septoria* spp. (9 points). Among the Ukrainian accessions, no *Septoria tritici* blotch symptoms was recorded in Spivanka Poliska, Nadezhda, Halytska, Mahnatka, Kraievyd, Zenitka, Lelostanka 74, and Erythrospermum 7488.

Kraievyd, Mahnatka, Spivanka Poliska (Ukraine), Arctis (Germany), Apertus (Austria), and AR800-1-3-1/NW97S320 (USA) were highly resistant over the two study years; hence they can be classed as sources of resistance to *Septoria* spp.

No symptoms of viral diseases were recorded in most of the studied accessions. It should be noted that, in the 2021–2022 conditions, there were more accessions had symptoms of viral diseases. This can be explained by both temperature and post-overwintering weakening of plants.

Lodging resistance. The main factors related to lodging resistance include morphological and anatomical characteristics of plants.

In 2022, plants were assessed for lodging resistance. The weather and late sowing did not induce lodging, so most of the accessions (209) were highly resistant to lodging. Old Ukrainian varieties showed low lodging resistance: Ferrugeneum 351, Krakov, Yurievka 676, Durabl, Nadezhda, Erythrospermum 2704, Amerykanka, Tryumf Podolii. All accessions with low lodging resistance had increased plant height (more than 100 cm).

Morphological traits that can be markers of resistance to high temperatures and drought according to literature data were also evaluated. However, the weather in the study years did favor assessments of resistance to high temperatures or drought.

Wax coating. Accessions with the greatest wax coating (8-9 points) were found in the studied sample: Bernstein, Zeppelin, Oksal, Linus, Mulan, Cubus, KWS Ronin (Germany), Apertus, Estivus (Austria), MV 29-98 (Hungary), Beauford (England), Azano (Sweden), Bezosta 1, Duplet (Russia), and Augustina (Belarus). Ukrainian accessions were characterized by light-green color, so they are more adaptable to the sunlight duration and intensity.

Stem thickness. We selected accessions with increased thickness (2.5-3 cm) of the stem in the upper internode site: lines Admis/Milan/Ducula (Mexico), KRASNODAR/FRTL/6/NGDA146/4, KS920709-B-5-1-1/ Burbot-4 (Turkey), and Tsapki/Farmec (USA). Among the Ukrainian accessions, old varieties had the thickest stems: Luhanskaia 2, Zoria, Yurievka 676, Podilska Niva.

Stem filling. Accessions with filled stems were found: Erythrospermum 7488 (Ukraine), Athlon (Germany), Vilejka (Czech), AR800-1-3-1/NW97S320, Kambara1/Zander-17, and Isfara (Tajikistan).

Flag leaf width. Accessions with a wide flag leaf (more than 2 cm) were found: Podilska Niva, Zoriana (Ukraine), Patras, Tobak (Germany), Vilejka (Czech Republic), Bezostaya1/Ae.cylindrica (Kazakhstan).

Green coloration of the upper internode and flag leaf during the grain filling period. This trait allows extending the photosynthetic activity period in wheat plants during the grain filling phase. Accessions that maintained green color as of July 6, 2022 were identified: Patras, Athlon, Florencia, Zeppelin, Tobak, Bernstein, Oksal, Linus, KWS Emil, Matrix, Frisky, LG Egmont, LG Initial, Julius (Germany), Spivanka Podilska (Ukraine), Beauford (England), Augustina (Belarus), and Duplet (Russia). It should be noted that most of the accessions with this trait are late-ripening varieties. Of them, only few Ukrainian varieties (Kraievid, Vinok Podillia, Kyivska, Svitiaz) were classed as mid-ripening.

Conclusions. Analysis of temperature in recent years indicates changes in the autumn and winter periods of wheat vegetation in the Left-Bank Forest-Steppe of Ukraine. For adaptation of wheat plants to the weather in recent years, not only freezing tolerance but also winter hardiness in combination with intensive growth in the initial stages and good regeneration in spring is important.

We selected accessions with high winter hardiness and high intensity of spring regeneration: Lira Odeska, Oberih Myronivskiy, Dykanka (Ukraine); Turkuaz (Azerbaijan); Andrada (Romania). The following accessions showed increased winter hardiness (7-8 points) and good regeneration in spring (8-9 points): Oktava Odeska, Natalka, Zolotava Nosivska, Lehenda Myronivska, Bunchuk, Orzytsia Nova, PS Tashan (Ukraine), T67/X84W063-9-45//Karl92/3 (Turkey), AR800-1-3-1/NW97S320, and NE10507 (USA). According to the results on resistance to *Septoria tritici* blotch over the two study years, the following resistant accessions can be used as sources of resistance: Kraievyyd, Mahnatka, Spivanka poliska (Ukraine), Arctis (Germany), Apertus (Austria), and AR800-1-3-1/NW97S320 (USA).

There was a correlation between winter hardiness in the field and growth intensity in the autumn ($r=0.653$) and between winter hardiness in the field and regenerative capacity of plants in the spring ($r=0.835$).

Список використаних джерел

1. Curtis T., Halford N.G. Food security: the challenge of increasing wheat yield and the importance of not compromising food safety. *Ann Appl Biol.* 2014. № 164(3). P. 354–372. DOI: <https://doi.org/10.1111/aab.12108>.
2. Guarin J.R., Martre P., Ewert F., Webber H., Dueri S., Calderini D., Reynolds M., et al. Evidence for increasing global wheat yield potential. *Environmental Research Letters.* 2022. № 17. P. 124. DOI: <https://doi.org/10.1088/1748-9326/aca77c>.
3. Jatayev S., Sukhikh I., Vavilova V., Gupta N.K., Jacobs B., de Groos S., et al. Green revolution ‘stumbles’ in a dry environment: Dwarf wheat with Rht genes fails to produce higher grain yield than taller plants under drought. *Plant Cell Environ.* 2020. № 43. P. 2355–2364. DOI: <https://doi.org/10.1111/pce.13819>.
4. Rousi E., Kornhuber K., Beobide-Arsuaga G., Luo F., Coumou D. Accelerated western European heatwave trends linked to more-persistent double jets over Eurasia. *Nat. Commun.* 2022. № 13. P. 3851. DOI: <https://doi.org/10.1038/s41467-022-31432-y>.
5. Olgun M., Yildirim T., Turan M. Adaptation of wheat genotypes (*Triticum aestivum* L.) to cold climate. *Acta Agriculturae Scandinavica. Section B - Soil & Plant Science.* 2005. Vol. 55, № 1. P. 9–15. DOI: <https://doi.org/10.1080/09064710510008757>.
6. Figueroa M., Hammond-Kosack K.E., Solomon P.S. A review of wheat diseases-a field perspective. *Mol Plant Pathol.* 2018. № 19(6). P. 1523–1536. DOI: <https://doi.org/10.1111/mpp.12618>.
7. Arora N.K. Impact of climate change on agriculture production and its sustainable solutions. *Environmental Sustainability.* 2019. № 2. P. 95–96. DOI: <https://doi.org/10.1007/s42398-019-00078-w>.
8. Du X., Gao Z., Sun X., Bian D., Ren J., Yan P., Cui Y. Increasing temperature during early spring increases winter wheat grain yield by advancing phenology and mitigating leaf senescence. *Sci Total Environ.* 2022. № 15. P. 812. DOI: <https://doi.org/10.1016/j.scitotenv.2021.152557>.
9. Kubar M.S., Alshallash K.S., Asghar M.A., Feng M. et al. Improving Winter Wheat Photosynthesis, Nitrogen Use Efficiency, and Yield by Optimizing Nitrogen Fertilization. *Life.* 2022. № 12. P. 1478. DOI: <https://doi.org/10.3390/life12101478>.
10. Berca M., Robescu V., Horoias R. Winter wheat crop water consumption and its effect on yields in southern Romania, in the very dry 2019-2020 agricultural year. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca,* 2021. № 49(2). DOI: <https://doi.org/10.15835/nbha49212309>.
11. Tabak M., Lepiarczyk A., Filipek-Mazur B., Lisowska A. Efficiency of Nitrogen Fertilization of Winter Wheat Depending on Sulfur Fertilization. *Agronomy.* 2020. № 10(9). P. 1304. DOI: <https://doi.org/10.3390/agronomy10091304>.
12. Semenov M.A., Stratonovitch P., Alghabari F., Gooding M.J. Adapting wheat in Europe for climate change. *Journal of Cereal Science.* 2014. № 59(3). P. 245–256. DOI: <https://doi.org/10.1016/j.jcs.2014.01.006>.

13. Balfourier F., Bouchet S., Robert S., De Oliveira R., Rimbart H., Kitt J., Choulet F. Worldwide phylogeography and history of wheat genetic diversity. *Science Advances*, 2019. № 5(5). P. 1–16. DOI: <https://www.science.org/doi/10.1126/sciadv.aav0536>.
14. Cann D., Hunt J.R., Porker K.D., Harris F., Rattey A., Hyles J. The role of phenology in environmental adaptation of winter wheat. *European Journal of Agronomy*. 2023. № 143. P. 126686. DOI: <https://doi.org/10.1016/j.eja.2022.126686>.
15. Reynolds M., Langridge P. Physiological breeding. *Current Opinion in Plant Biology*. 2016. № 31. P. 162–171. DOI: <https://doi.org/10.1016/j.pbi.2016.04.005>.
16. Hyles J., Bloomfield M.T., Hunt J.R. et al. Phenology and related traits for wheat adaptation. *Heredity*. 2020. № 125. P. 417–430. DOI: <https://doi.org/10.1038/s41437-020-0320-1>.
17. Khomenko L. Creation of winter wheat source material with increased adaptive potential to adverse environmental conditions. *EUREKA: Life Sciences*. 2021. № 6. P. 25–33. DOI: <https://doi.org/10.21303/2504-5695.2021.002188>.
18. Kolupaev Y.E., Yemets A.I., Yastreb T.O., Blume Y.B. The role of nitric oxide and hydrogen sulfide in regulation of redox homeostasis at extreme temperatures in plants. *Frontiers in Plant Science*. 2023. № 14. DOI: <https://doi.org/10.3389/fpls.2023.1128439>.
19. Beillouin D., Schauburger B., Bastos A., Ciais P., Makowski D. Impact of extreme weather conditions on European crop production in 2018. *Phil. Trans. R. Soc. B*. 2022; 375. DOI: <https://doi.org/10.1098/rstb.2019.0510>.
20. Babben S., Schliephake E., Janitzka P. et al. Association genetics studies on frost tolerance in wheat (*Triticum aestivum* L.) reveal new highly conserved amino acid substitutions in CBF-A3, CBF-A15, VRN3 and PPD1 genes. *BMC Genomics*. 2018. № 19. P. 409. DOI: <https://doi.org/10.1186/s12864-018-4795-6>.
21. Vapela T., Shimelis H., Tsilo T.J., Mathew I. Genetic Improvement of Wheat for Drought Tolerance: Progress, Challenges and Opportunities. *Plants (Basel)*. 2022. № 11(10). P. 1331. DOI: <https://doi.org/10.3390/plants11101331>.
22. Тищенко В.Н., Чекалин Н.М. Генетические основы адаптивной селекции озимой пшеницы в лесостепи. Полтава: Зб. наук. праць. ДАУ, 2005. 270 с.
23. Yarosh A.V., Riabchun V.K., Riabchun N.I. Adaptability of winter bread wheat by environmental plasticity and stability. *Plant Breeding and Seed Production*. 2022. № 121. P. 75–83. DOI: <https://doi.org/10.30835/2413-7510.2022.260998>.
24. Austin RB, Bingham J, Blackwell RD, Evans LT, Ford MA, Morgan CL and Taylor M. Genetic Improvements in Winter Wheat Yields Since 1900 and Associated Physiological Changes. *The Journal of Agricultural Science*. 1980. № 94. P. 675–689. DOI: <https://doi.org/10.1017/S0021859600028665>.
25. Galluzzi G., Seyoum A., Halewood M., López Noriega ., Welch E.W. The Role of Genetic Resources in Breeding for Climate Change: The Case of Public Breeding Programmes in Eighteen Developing Countries. *Plants*. 2020. № 9. P. 1129. DOI: <https://doi.org/10.3390/plants9091129>.
26. Molero G., Coombes B., Joynson R. et al. Exotic alleles contribute to heat tolerance in wheat under field conditions. *Commun Biol*. 2023. № 6. P. 21. DOI: <https://doi.org/10.1038/s42003-022-04325-5>.
27. Jaškūnė K., Armonienė R., Liatukas Ž., Statkevičiūtė G., Cesevičienė J., Brazauskas G. Relationship between Freezing Tolerance and Leaf Growth during Acclimation in Winter Wheat. *Agronomy*. 2022. № 12(4). P. 859. DOI: <https://doi.org/10.3390/agronomy12040859>.
28. Sarto M.V.M., Sarto J.R.W., Rampim L., Bassegio D., da Costa P.F., Inagaki A.M. Wheat phenology and yield under drought: a review. *Aust. J. Crop Sci*. 2017. № 11. P. 941–946. DOI: <https://doi.org/10.21475/ajcs.17.11.08.pne351>.
29. Khadka K., Earl H.J., Raizada M.N., Navabi A.A. Physio-Morphological Trait-Based Approach for Breeding Drought Tolerant Wheat. *Frontiers in plant science*. 2020. № 11. DOI: <https://doi.org/10.3389/fpls.2020.00715>.

30. Kandic V., Dodig D., Jovic M., Nikolic B., Prodanovic S. The importance of physiological traits in wheat breeding under irrigation and drought stress. *Genetika*. 2009. № 41. P. 11–20. DOI: <http://dx.doi.org/10.2298/GENSR0901011K>.
31. Makaova B.E., Tyshchenko V.M., Kryvoruchko L.M. Genetic diversity analysis of winter wheat accessions of different geographical origins by PCA. *Breeding and seed production*. 2022. № 121. P. 41–50. DOI: <https://doi.org/10.30835/2413-7510.2022.260994>.
32. Методика експертизи сортів зернових і зернобобових культур на придатність до поширення в Україні. ред. від Ткачик С.О. Вінниця. 2016. 82 с.
33. Pask A.J.D., Pietragalla J., Mullan D.M., Reynolds M. *Physiological Breeding II: A Field Guide to Wheat Phenotyping*. Mexico D.F.: CIMMYT. 2012. 133 p. URL: <http://hdl.handle.net/10883/1288>.
34. Fowler D.B., Gusta L.V. Selection for Winterhardiness in Wheat. I. Identification of Genotypic Variability. *Crop Science*. 1979. № 19. P. 769–772. DOI: <https://doi.org/10.2135/cropsci1979.0011183X001900060005x>.

References

1. Curtis T., Halford N.G. Food security: the challenge of increasing wheat yield and the importance of not compromising food safety. *Ann Appl Biol*. 2014; 164(3): 354–372. DOI: <https://doi.org/10.1111/aab.12108>.
2. Guarin J.R., Martre P., Ewert F., Webber H., Dueri S., Calderini D., Reynolds M., et al. Evidence for increasing global wheat yield potential. *Environmental Research Letters*. 2022; 17: 124. DOI: <https://doi.org/10.1088/1748-9326/aca77c>.
3. Jatayev S., Sukhikh I., Vavilova V., Gupta N.K., Jacobs B., de Groos S., et al. Green revolution ‘stumbles’ in a dry environment: Dwarf wheat with Rht genes fails to produce higher grain yield than taller plants under drought. *Plant Cell Environ*. 2020; 43: 2355–2364. DOI: <https://doi.org/10.1111/pce.13819>.
4. Rousi E., Kornhuber K., Beobide-Arsuaga G., Luo F., Coumou D. Accelerated western European heatwave trends linked to more-persistent double jets over Eurasia. *Nat. Commun*. 2022; 13: 3851. DOI: <https://doi.org/10.1038/s41467-022-31432-y>.
5. Olgun M., Yildirim T., Turan M. Adaptation of wheat genotypes (*Triticum aestivum* L.) to cold climate. *Acta Agriculturae Scandinavica. Section B - Soil & Plant Science*. 2005; 55: 15–19. DOI: <https://doi.org/10.1080/09064710510008757>.
6. Figueroa M., Hammond-Kosack K.E., Solomon P.S. A review of wheat diseases-a field perspective. *Mol Plant Pathol*. 2018; 19(6): 1523–1536. DOI: <https://doi.org/10.1111/mpp.12618>.
7. Arora N.K. Impact of climate change on agriculture production and its sustainable solutions. *Environmental Sustainability*. 2019; 2: 95–96. DOI: <https://doi.org/10.1007/s42398-019-00078-w>.
8. Du X., Gao Z., Sun X., Bian D., Ren J., Yan P., Cui Y. Increasing temperature during early spring increases winter wheat grain yield by advancing phenology and mitigating leaf senescence. *Sci Total Environ*. 2022; 15: 812. DOI: <https://doi.org/10.1016/j.scitotenv.2021.152557>.
9. Kubar MS, Alshallash KS, Asghar MA, Feng M. et al. Improving Winter Wheat Photosynthesis, Nitrogen Use Efficiency, and Yield by Optimizing Nitrogen Fertilization. *Life*. 2022; 12: 1478. DOI: <https://doi.org/10.3390/life12101478>.
10. Berca M., Robescu V., Horoias R. Winter wheat crop water consumption and its effect on yields in southern Romania, in the very dry 2019–2020 agricultural year. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*. 2021; 49(2). DOI: <https://doi.org/10.15835/nbha49212309>.
11. Tabak M., Lepiarczyk A., Filipek-Mazur B., Lisowska A. Efficiency of Nitrogen Fertilization of Winter Wheat Depending on Sulfur Fertilization. *Agronomy*. 2020; 10(9): 1304. DOI: <https://doi.org/10.3390/agronomy10091304>.

12. Semenov M.A., Stratonovitch P., Alghabari F., Gooding M.J. Adapting wheat in Europe for climate change. *Journal of Cereal Science*. 2014; 59(3): 245–256. DOI: <https://doi.org/10.1016/j.jcs.2014.01.006>.
13. Balfourier F., Bouchet S., Robert S., De Oliveira R., Rimbart H., Kitt J., Choulet F. Worldwide phylogeography and history of wheat genetic diversity. *Science Advances*, 2019; 5(5): 1-16. DOI: <https://www.science.org/doi/10.1126/sciadv.aav0536>.
14. Cann D, Hunt JR, Porker KD, Harris F, Rattey A, Hyles J. The role of phenology in environmental adaptation of winter wheat. *European Journal of Agronomy*. 2023. 143: 126686. DOI: <https://doi.org/10.1016/j.eja.2022.126686>.
15. Reynolds M, Langridge P. Physiological breeding. *Current Opinion in Plant Biology*. 2016, 31: 162–171. DOI: <https://doi.org/10.1016/j.pbi.2016.04.005>.
16. Hyles J., Bloomfield M.T., Hunt J.R. et al. Phenology and related traits for wheat adaptation. *Heredity*. 2020; 125: 417-430. DOI: <https://doi.org/10.1038/s41437-020-0320-1>.
17. Khomenko L. Creation of winter wheat source material with increased adaptive potential to adverse environmental conditions. *EUREKA: Life Sciences*. 2021; 6: 25–33. DOI: <https://doi.org/10.21303/2504-5695.2021.002188>.
18. Kolupaev Y.E., Yemets A.I., Yastreb T.O., Blume Y.B. The role of nitric oxide and hydrogen sulfide in regulation of redox homeostasis at extreme temperatures in plants. *Frontiers in Plant Science*. 2023; 14. DOI: <https://doi.org/10.3389/fpls.2023.1128439>.
19. Beillouin D., Schauburger B., Bastos A., Ciais P., Makowski D. Impact of extreme weather conditions on European crop production in 2018. *Phil. Trans. R. Soc. B*. 2022; 375. DOI: <https://doi.org/10.1098/rstb.2019.0510>.
20. Babben S., Schliephake E., Janitza P. et al. Association genetics studies on frost tolerance in wheat (*Triticum aestivum* L.) reveal new highly conserved amino acid substitutions in CBF-A3, CBF-A15, VRN3 and PPD1 genes. *BMC Genomics*. 2018; 19: 409. DOI: <https://doi.org/10.1186/s12864-018-4795-6>.
21. Bapela T., Shimelis H., Tsilo T.J., Mathew I. Genetic Improvement of Wheat for Drought Tolerance: Progress, Challenges and Opportunities. *Plants (Basel)*. 2022; 11(10): 1331. DOI: <https://doi.org/10.3390/plants11101331>.
22. Tyshchenko V.N., Chekalin N.M. Genetic basics of adaptive breeding of winter wheat in the forest-steppe. *Poltava. RVV Polt. DAA*. 2005. 270 p.
23. Yarosh A.V., Riabchun V.K., Riabchun N.I. Adaptability of winter bread wheat by environmental plasticity and stability. *Plant Breeding and Seed Production*. 2022; 121: 75–83. DOI: <https://doi.org/10.30835/2413-7510.2022.260998>.
24. Austin R.B., Bingham J., Blackwell R.D., Evans L.T., Ford M.A., Morgan C.L., Taylor M. Genetic Improvements in Winter Wheat Yields Since 1900 and Associated Physiological Changes. *The Journal of Agricultural Science*. 1980; 94: 675–689. DOI: <https://doi.org/10.1017/S0021859600028665>.
25. Galluzzi G., Seyoum A., Halewood M., López Noriega I., Welch E.W. The Role of Genetic Resources in Breeding for Climate Change: The Case of Public Breeding Programmes in Eighteen Developing Countries. *Plants*. 2020; 9: 1129. DOI: <https://doi.org/10.3390/plants9091129>.
26. Molero G., Coombes B., Joynson R. et al. Exotic alleles contribute to heat tolerance in wheat under field conditions. *Commun Biol*. 2023; 6: 21. DOI: <https://doi.org/10.1038/s42003-022-04325-5>.
27. Jaškūnė K., Armonienė R., Liatukas Ž., Statkevičiūtė G., Cesevičienė J., Brazauskas G. Relationship between Freezing Tolerance and Leaf Growth during Acclimation in Winter Wheat. *Agronomy*. 2022; 12(4): 859. DOI: <https://doi.org/10.3390/agronomy12040859>.
28. Sarto M.V.M., Sarto J.R.W., Rampim L., Bassegio D, da Costa P.F., Inagaki A.M. Wheat phenology and yield under drought: a review. *Aust. J. Crop Sci*. 2017; 11: 941–946. DOI: <https://doi.org/10.21475/ajcs.17.11.08.pne351>.

29. Khadka K., Earl H.J., Raizada M.N., Navabi A.A. Physio-Morphological Trait-Based Approach for Breeding Drought Tolerant Wheat. *Frontiers in plant science*. 2020; 11. DOI: <https://doi.org/10.3389/fpls.2020.00715>.
30. Kandic V., Dodig D., Jovic M., Nikolic B., Prodanovic S. The importance of physiological traits in wheat breeding under irrigation and drought stress. *Genetika*. 2009; 41: 11–20. DOI: <http://dx.doi.org/10.2298/GENSR0901011K>.
31. Makaova B.E., Tyshchenko V.M., Kryvoruchko L.M. Genetic diversity analysis of winter wheat accessions of different geographical origins by PCA. *Breeding and seed production*. 2022; 121: 41–50. DOI: <https://doi.org/10.30835/2413-7510.2022.260994>.
32. Methods of examination of cereal and legume varieties for suitability to dissemination in Ukraine. Ed. by Tkachik S.O. Vinnytsia. 2016. 82 p.
33. Pask A.J.D., Pietragalla J., Mullan D.M., Reynolds M. *Physiological Breeding II: A Field Guide to Wheat Phenotyping*. Mexico D.F.:CIMMYT. 2012. 133 p. URL: <http://hdl.handle.net/10883/1288>.
34. Fowler D.B., Gusta L.V. Selection for Winterhardness in Wheat. I. Identification of Genotypic Variability. *Crop Science*. 1979; 19: 769–772. DOI: <https://doi.org/10.2135/cropsci1979.0011183X001900060005x>.

АНАЛІЗ ФІЗІОЛОГІЧНИХ МЕХАНІЗМІВ АДАПТАЦІЇ ТА СТІЙКОСТІ СОРТІВ ОЗИМОЇ ПШЕНИЦІ РІЗНОГО ГЕОГРАФІЧНОГО ПОХОДЖЕННЯ

Макаова Б.Є., Тищенко В.М.

Полтавський державний аграрний університет, Україна

Мета дослідження: Аналіз ролі ознак морфотипу та фізіологічних реакцій в адаптації до умов Лівобережного Лісостепу України шляхом вивчення широкого набору колекційних зразків пшениці озимої різного еколого-географічного походження за комплексом морфологічних ознак та фізіологічних особливостей, що визначають адаптивність до умов дослідного середовища та виявлення цінних зразків з метою подальшого залучення їх у селекційний процес.

Матеріали і методи: У статті наведено результати досліджень 318 зразків озимої пшениці різного еколого-географічного походження з 27 країн світу за комплексом морфологічних ознак і фізіологічних реакцій на умови Лівобережного Лісостепу України в 2020–2021 та 2021–2022 вегетаційних роках. Польову оцінку проводили за наступними параметрами: оцінка стану рослин перед перезимівлею; оцінка польової зимостійкості; оцінка швидкості відновлення рослин навесні; фіксація дати колосіння; оцінка пошкодження листя хворобами. Оцінку морфологічних ознак проводили відповідно до методики дослідження сортів пшениці м'якої (*Triticum aestivum* L.) на ВОС-тест, методики фізіологічних досліджень у селекції СІММУТ та методика відбору зимостійких генотипів пшениці.

Обговорення результатів: Виявлена значна варіація за всіма досліджуваними ознаками. Аналіз температурних показників останніх років свідчить про зміни умов проходження вегетації осіннього та зимового періодів. Погодні умови обох років досліджень були в цілому сприятливими для перезимівлі рослин озимої пшениці. Варто зазначити, що умови перезимівлі у 2021–2022 вегетаційному році були дещо складнішими, рослини пшениці були більш виснаженими через наявність різких підвищень та понижень температури. Виявлено, що для адаптації рослин пшениці до погодних умов важливою є не лише морозостійкість, а й польова зимостійкість у поєднанні з високим рівнем росту на початкових етапах і хорошим відновленням у весняний період. Встановлено кореляційний зв'язок між ознаками польової зимостійкості та інтенсивністю росту в осінній період ($r = 0,653$) та з регенеративною здатністю рослин у весняний період ($r = 0,835$).

Висновки: Виявлено зразки з високою зимостійкістю та високою інтенсивністю весняного відновлення – Ліра одеська, Оберіг Миронівський, Диканька (Україна) та сорти іноземного походження – Turkuaz (Азербайджан) та Andrada (Румунія). Підвищеною зимостійкістю (7–8 балів) і хорошим відновленням навесні (8–9 балів) володіли зразки: Октава одеська, Наталка, Золотава носівська, Легенда Миронівська, Бунчук, Оржиця нова, ПС Ташань (Україна) T67/X84W063-9-45//Karl92/3 (Туреччина), AR800-1-3-1/NW97S320, NE10507 (США). За результатами дворічної оцінки стійкості генотипів до плямистості *Septoria tritici* як джерела стійкості можуть бути використані наступні зразки – Краєвид, Магнатка, Співанка польська (Україна), Arctis (Німеччина), Apertus (Австрія), AR800-1-3-1/NW97S320 (США).

Ключові слова: м'яка озима пшениця, вихідний матеріал, адаптація, морфологічна ознака.

ANALYSIS OF PHYSIOLOGICAL MECHANISMS OF ADAPTATION AND RESISTANCE OF WINTER WHEAT ACCESSIONS OF DIFFERENT GEOGRAPHICAL ORIGINS

Makaova B.Ye., Tyshchenko V.M.
Poltava State Agrarian University, Ukraine

Purpose: To analyze the role of morphological traits and physiological responses to the conditions in the Left-Bank Forest-Steppe of Ukraine by investigating a large assortment of winter wheat collection accessions and identifying valuable accessions to involve them in local breeding programs.

Materials and methods: The article contains the results of evaluating 318 winter wheat accessions of different eco-geographical origins from 27 countries for a set of morphological traits and physiological responses to the environmental conditions in the Left-Bank Forest-Steppe of Ukraine in the 2020–2021 and 2021–2022 growing seasons. The following parameters were evaluated in the field (visual scores): pre-overwintering state of plants, winter hardiness, plant regeneration rate in the spring, earing date, and damage by foliar diseases. Morphological traits were assessed in accordance with DUS tests on common wheat (*Triticum aestivum* L.) varieties for recommended by UPOV and the State Service, physiological methods in breeding used in CIMMYT and methods of wheat breeding for winter hardiness.

Results and discussion: Significant variations were observed for all the studied traits. Analysis of temperature in recent years indicates changes in the autumn and winter periods of wheat vegetation in the Left-Bank Forest-Steppe of Ukraine. The weather in the both study years was generally favorable for overwintering of winter wheat plants. It is worth noting that the overwintering conditions in 2021–2022 were somewhat harsher; wheat plants were more exhausted due to sudden temperature rises and drops. It was established that, for adaptation of wheat plants to the weather conditions, not only freezing tolerance but also winter hardiness in combination with intensive growth in the initial stages and good regeneration in spring was important. There was a correlation between winter hardiness in the field and growth intensity in the autumn ($r = 0.653$) and between winter hardiness in the field and regenerative capacity of plants in the spring ($r = 0.835$).

Conclusions: We selected accessions with high winter hardiness and high intensity of spring regeneration: Lira Odeska, Oberih Myronivskyi, Dykanka (Ukraine), Turkuaz (Azerbaijan), and Andrada (Romania). The following accessions showed increased winter hardiness (7–8 points) and good regeneration in spring (8–9 points): Oktava Odeska, Natalka, Zolotava Nosivska, Lehenda Myronivska, Bunchuk, Orzytsia Nova, PS Tashan (Ukraine), T67/X84W063-9-45//Karl92/3 (Turkey), AR800-1-3-1/NW97S320, and NE10507 (USA). According to the two-year result on resistance of genotypes to *Septoria tritici* blotch, the following accessions can be used as sources of resistance: Kraievyd, Mahnatka, Spivanka Poliska (Ukraine), Arctis (Germany), Apertus (Austria), and AR800-1-3-1/NW97S320 (USA).

Key words: winter bread wheat, starting material, adaptation, morphological trait.