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THE IMPACT OF LOW-TEMPERATURE TOLERANCE ON THE ENVIRONMENTAL PLASTICITY INDICATORS OF WINTER BREAD WHEAT IN THE CONTEXT OF CLIMATE CHANGE

This study examines how low-temperature tolerance influences environmental plasticity of winter bread wheat — a critical factor for crop homeostasis amid global warming challenges. Among winter wheat genotypes graded by hypothermia tolerance, 19.0% demonstrated the highest environmental plasticity for yield. Genotypes with superior genetic potential adaptability (identified by the lowest rank sums (rank sum = 2) of genotypic effect and regression coefficient (Oktava Odeska, Pontiyka, Zamolxe, NE 10507) yielded 128—148% related to the check cultivar. In the winter bread wheat cultivars under investigation, there was a moderate negative correlation between freezing tolerance of winter bread wheat leaves in early spring and rank sum of genotypic effect and yield plasticity ($r = -0.42$; $P < 0.05$) and a moderate positive correlation between tolerance to critical freezing temperatures and rank sum of genotypic effect and yield plasticity ($r = 0.41$; $P < 0.05$). The selected winter bread wheat genotypes with high genetic potentials of environmental plasticity represent high-value starting materials for breeding new wheat cultivars that would be adaptable to current climatic changes.

Key words: *freezing tolerance, genotypic effect, adaptive potential, stress tolerance, winter bread wheat.*

INTRODUCTION

Low-temperature tolerance in winter cereals, which is one of the main properties for safeguarding yield stability and genetic potential, is becoming increasingly relevant because new high-yielding cultivars are often poorly adaptable. Winter bread wheat (*Triticum aestivum* L.), which is valued for biochemical composition of grain and numerous wheat-based foods, is of global food and strategic importance and dominates vast agricultural landscapes [5, 20].

Despite a clear trend toward global warming, for many European countries, the issue of winter cereal crops' vulnerability to low temperatures and the growing negative effects on cultivars' homeostasis remains pressing and increasingly vital, since vulnerability leads to substantial yield losses and financial damages for farmers [15, 30].

Global warming is increasingly accompanied by sharp temperature fluctuations with significant precipitation variability, more extreme weather phenomena [28], frequent thaw periods, thinned snow cover in winter, and earlier onset of meteorological spring. These factors collectively reduce hardening capacity and lower stress tolerance threshold of winter cereals to critical freezing temperatures [3, 4]. Consequently, due to adverse effects of climatic/weather factors and rising annual air temperatures on agricultural crops, yield potential fulfilment, yield stability and agricultural production efficien-

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cy decline. As noted by Yu.V. Kernasiuk [14], in 2015—2020, cereal yield variability was 18.0—25.1% in some regions of the steppe zone, 19.8—21.7% in the forest-steppe and 17.2—20.8% in the woodlands.

Owing to adaptive responses, which are driven by physiological, biochemical, and molecular-genetic changes, hardened winter cereals can withstand low temperatures within their genotypic reaction norms during winter [9]. Hardening includes two phases. V.V. Morhun et al. [23] have reported that phase I occurs at daytime temperatures of 8—10 °C, when sugars accumulate in tillering nodes and they are minimally consumed for plant growth and respiration at night (0—4 °C). The content of water-soluble sugars (sucrose, fructose, raffinose, glucose, *etc.*) in tillering nodes depends on the physiological characteristics of genotypes and averages ~30% [23].

In hardening phase II, cells are dehydrated, soluble sugar concentrations rise, free water (prone to rapid freezing) amount decreases, and bound water (resistant to freezing at critical temperatures) amount increases [21]. M. Hosseinifard et al. [12] elaborated predecessors' findings and emphasized that hardening increased reserves of osmotically active compounds (*e.g.*, sugars, proline) in tillering nodes, enhancing freezing tolerance of plants. Sugars and proline are known to exert antioxidant effects, which are directly associated with genotype adaptation to low-temperature stress [8]. Sugars are multifunctional protective compounds in plants that stabilize membrane, protein, and lipid structures. However, contents of sugars and proline in leaves and shoots are not always correlated with hypothermia tolerance [16, 25].

T.V. Yurchenko et al. [34] noted that gradual air temperature decrease made hardening of winter bread wheat more effective compared to drastic temperature fluctuations. Adaptive responses of a genotype to low-temperature stress are based on complex physiological and biochemical reactions mediated by various phytohormones and hormone-like compounds, in particular brassinosteroids, polyamines, melatonin, *etc.* [11, 30, 35].

It is known that high stress tolerance of winter bread wheat to low temperatures requires both freezing tolerance and field winter hardiness combined with optimal vegetation restoration in spring. B.Ye. Makaova and V.M. Tyshchenko [22] observed correlations between field winter hardiness and autumn growth intensity (r = 0.653) and between field winter hardiness and capacity of plants for regeneration in spring (r = 0.835). Field winter hardiness is determined by a trait set ensuring overwintering success, including freezing tolerance, vernalization length and photoperiodic sensitivity [24]. A critical factor is genotypic resistance of winter bread wheat cultivars to snow mold (*Microdochium nivale* (Fr.) Samuels and I.C. Hallett), which is significant negatively correlated with rank sum of genotypic effect and yield plasticity degree (r = –0.69; P < 0.01) [32].

Environmental plasticity plays a decisive role in a cultivar's adaptation to pedo-climatic conditions, reflecting the genotype's ability to adapt to variable environmental conditions and minimize the impact of different stressors [19].

Thus, selection of hypothermia-tolerant winter bread wheat cultivars with high environmental plasticity precedes the efficient development of superior genotypes with high adaptive potentials.

We pursued the following objectives: to determine freezing tolerance of leaves in early spring, freezing tolerance of plants and their influence on environmental plasticity indicators in wheat bread winter accessions under climate change; to identify high-yielding, low-temperature tolerance genotypes.

MATERIALS AND METHODS

Twenty-one short-stemmed winter bread wheat (*Triticum aestivum* L.) genotypes from seven countries were studied: eight Ukrainian cultivars (Pontiika, Osnova Odeska, Oktava Odeska, Peizazh, Perevaha, Poradnytsia, Zorianka, and Podilska Nyva), four German cultivars (Producent, Futurum, Tobak, and Estivus), three Romanian cultivars (Zamolxe, Fajura and FGMUT 293), two Austrian cultivars (Amandus and Palmus), two cultivars from the USA (NE 12443 and NE 10507), one French cultivar (Altigo), and one Chinese cultivar (Tianmin 366).

The study was conducted in the Laboratory of Cereal Genetic Resources of the National Center for Plant Genetic Resources of Ukraine (NCPGRU) of the Yuriev Plant Production Institute of NAAS of Ukraine in 2020—2023. The experiments were carried out in compliance with qualifying examination techniques [29]. The cultivars were sown after fallow within optimal timeframes. The seeding rate was 4.5 million seeds/ha. The experiments were replicated three times. The record plot area was 5 m². In spring, the plots were fertilized with ammonium nitrate (N_{40}). Cultivar 'Bunchuk' was taken as the check cultivar.

Freezing tolerance of leaves after spring restoration of vegetation was assessed using a 9-point scale, where 1 point — very low tolerance (massive kill; >70% of frozen vegetative mass from all plants in general); 3 points — low tolerance (considerable kill; 51—70%); 5 points — medium tolerance (moderate kill; 31—50%); 7 — high tolerance (mild kill; 10—30%); 9 — very high tolerance (negligible kill; <10%). Freezing tolerance of cultivars was evaluated under controlled conditions per State Standard of Ukraine DSTU 4749:2007 [6]. Plants were grown in vegetation boxes under natural conditions for development and hardening. Freezing was accomplished in «Danfoss Optyma» low-temperature chambers (Danfoss, Netherlands) set at −5 to −17.7 °C. Plants were kept in the chambers for 24 hours. Temperature at which at least 50% of plants were killed was defined as critical freezing temperature. After exposure to subzero temperatures in the chambers, plants were regrown in a greenhouse at 16-hour photoperiod and 15—17 °C night/22—23 °C day. Percentage of survived plants was calculated. Freezing tolerance of plants was assessed on a 9-point scale, where 9 is the highest tolerance and 1 is the lowest tolerance in comparison with the check cultivar. Environmental plasticity was determined by B.P. Huriev et al. method [13]. In this method, genotypic effect (ε_i) is a criterion of total adaptive capacity, and regression coefficient (R_i) means plasticity degree.

Here, the highest rank (rank 1) includes cultivars with strong genotypic effect and low coefficient of regression and the lowest rank (rank 3) comprises cultivars with weak genotypic effect and high coefficient of regression. The medium rank (rank 2) is assigned to cultivars with intermediate values [13].

In the work used the following analysis methods: *analysis of variance (ANOVA)* — to determine environmental plasticity for yield and significance of differences between experimental data; *correlation analysis* — to identify relationships between the studied traits; *regression analysis* — to determine the patterns of low-temperature influence on the ecological plasticity parameters of winter wheat. The significance of correlations between the studied traits was verified using the Student's t-test and F–test.

To qualitatively assess correlation coefficients, *i. e.* relationship strength between the studied traits, we used the Chaddock scale [2]. The significance of correlations between the studied traits was verified using the Student's t-test and F–test. Significance was set at $P < 0.05$. Experimental data were statistically processed by in MS Excel 2007 (Microsoft, USA) and Statistica 6.0 (StatSoft, USA).

RESULTS AND DISCUSSION

Having analyzed the weather during the growing periods in 2020—2023, we can state that both temperature and precipitation ranges significantly influenced the variability of the tolerance of winter bread wheat leaves to spring freezing, yield and environmental plasticity. According to the hydrothermal coefficient, the 2021 autumn was very dry (HTC = 0.36); the 2020 autumn was dry (HTC = = 0.46); and the 2022 autumn was water-logged (HTC = 2.84). It should be noted that the weather in the study years was not favourable for optimal pre-winter hardening of winter bread wheat. An acute water deficit and, increased temperatures in the 2020 and 2021 autumns delayed wheat growth and development; the vast majority of the accessions did not accumulate sufficient amounts of carbohydrates necessary for successful overwintering.

In 2022, proper hardening of plants was hindered by an autumn extended drought, which delayed germination. It should be noted that vegetation ceased within the first 10 days of November in 2021 and 2022 during the phenological phases of two and three leaves, respectively. In 2020, vegetation ceased within the second 10 days of November during the phenological phase of two leaves.

In general, the 2020/2021 and 2021/2022 winters were favorable for overwintering of winter cereals, but variations in leaf tolerance to spring freezing were observed. It should be noted that the unstable weather in February 2023 was characterized by wet-snow accretions, blizzards and glaze frost, which negatively affected plants' overwintering driven by resistance of plants to the snow mold pathogen (*M. nivale* (Fr.) Samuels and I.C. Hallett). The springs were extended and cool throughout all years of the study. Vegetation resumed within the third 10 days of March in 2021 and 2022 and within the first 10 days of April in 2023.

Analyzing the HTCs of the spring-summer periods in the study years, we found that the 2022 spring was dry (HTC = 0.59); the 2021 spring had sufficient precipitation (HTC = 1.46) and the 2023 spring was waterlogged (HTC = 1.61). The summer months in 2022 (HTC = 1.17) and 2023 (HTC = = 1.23) were sufficiently wetted, while the summer month in 2021 were moderately dry (HTC = 0.64).

In 2022, the weather factors were most favorable for producing high yield by the studied cultivars. In the other years, the yield potentials of the genotypes under investigation were less fulfilled in most cases.

It should be noted that the significant amplitudes of variation of ambient temperature in the winter-spring periods negatively affected plant homeostasis, enhancing gradation of the winter bread wheat accessions in terms of freezing tolerance of leaves in early spring. For example, the weather factors in 2021 were most favourable for identification of genotypes of freezing tolerance of leaves; the standard deviation (SD) of the average monthly temperature (°C) during the January-April period had the widest limits: SD = 12.3—14.9 (Table 1).

The temperature variation amplitude ranged from 22.8 to 31.9 °C in 2021. The conditions in the 2023 winter-spring period turned out to be least favorable for gradation of the studied genotypes in terms of leaf tolerance to freezing. The temperature profiles experienced the smallest fluctuations that year (SD = 0.7—2.9 °C), with the ambient temperature ranging 1.4 to 5.8 °C.

Thus, the weather fluctuations during the winter-spring periods in 2020—2023 enabled to grade the wheat varieties by leaf tolerance to freezing in early spring and to select high-yielding genotypes that are adapted to the pedo-climatic conditions of the eastern forest-steppe of Ukraine.

In 2020—2023, the tolerance of leaves to freezing in early spring varied from 1 to 9 points in the studied winter bread wheat cultivars. We identified 11 winter bread wheat genotypes (52.4%) with strong expression of this trait (from 7.0 points to 8.7 points): Pontiika, Osnova Odeska, Oktava Odeska, Peizazh, Perevaha, and Poradnytsia, Zamolxe and Fajura, Producent, NE 12443 and NE 10507 as well as Bunchuk (check cultivar; 6.8 points).

Medium tolerance of leaves to freezing in early spring (4.3—6.7 points) was intrinsic to several genotypes: Zorianka and Podilska Nyva, FGMUT 293, and others; the share of such genotypes was 42.9%. Tianmin 366 showed poor tolerance (3.0 points) (its share was 4.8%).

It is noteworthy that the amplitude of variation (A_m) of the «tolerance of leaves to freezing in early spring» trait in the short-stemmed winter bread wheat genotypes under investigation ranged from 1 to 8 points. Cultivars Pontiika, Oktava Odeska and Zamolxe turned out to be the most valuable genotypes, as their leaves were highly tolerant to freezing in early spring and this trait was characterized by low variability and the smallest amplitude (A_m = 1). The greatest amplitude was noted in cvs. Palmus (A_m = 8), Amandus (A_m = 6) and Producent (A_m = 5) (Fig. 1).

From coefficient of variation CV, it is seen that the variability of tolerance of leaves to freezing in early spring ranged from 6.7 to 96.1%. Analyzing the limits of variation of this trait, we found that low variability (CV ≤10.0%) was intrinsic to cvs. Pontiika ‘Oktava Odeska and Zamolxe, their share was 14.3%. Seven accessions (33.3%) were characterized by medium variability (CV = 11.0—20.0%):

Table 1. **Statistical analysis of the temperature during the winter-spring periods, 2021—2023**

Temperature, °C	Month			
	January	February	March	April
2021				
X_{min}	−21.8	−19.8	−10.2	−3.3
X_{max}	6.6	12.1	12.6	21.3
$\bar{X}$	0.1	−4.8	1.4	8.7
A_m	28.4	31.9	22.8	24.6
SD	14.9	15.9	11.4	12.3
2022				
X_{min}	−4.9	−10.0	−7.0	2.0
X_{max}	−1.2	6.0	9.0	17.0
$\bar{X}$	−3.3	0.3	2.0	12.0
A_m	3.7	16.0	16.0	15.0
SD	1.9	8.1	8.0	7.6
2023				
X_{min}	−3.1	−3.2	2.1	10.1
X_{max}	−1.7	−1.1	7.9	11.6
$\bar{X}$	−2.6	−2.0	4.8	10.9
A_m	1.4	2.1	5.8	1.5
SD	0.7	1.1	2.9	0.8
Average monthly temperature	−6.5	−5.8	−0.3	9.6

Note: X_{min} — minimum; X_{max} — maximum; X — mean; A_m — amplitude of variation ($A_m = X_{max}—X_{min}$); SD — standard deviation. Compiled by the authors from data of the Kharkiv Regional Center for Hydrometeorology.

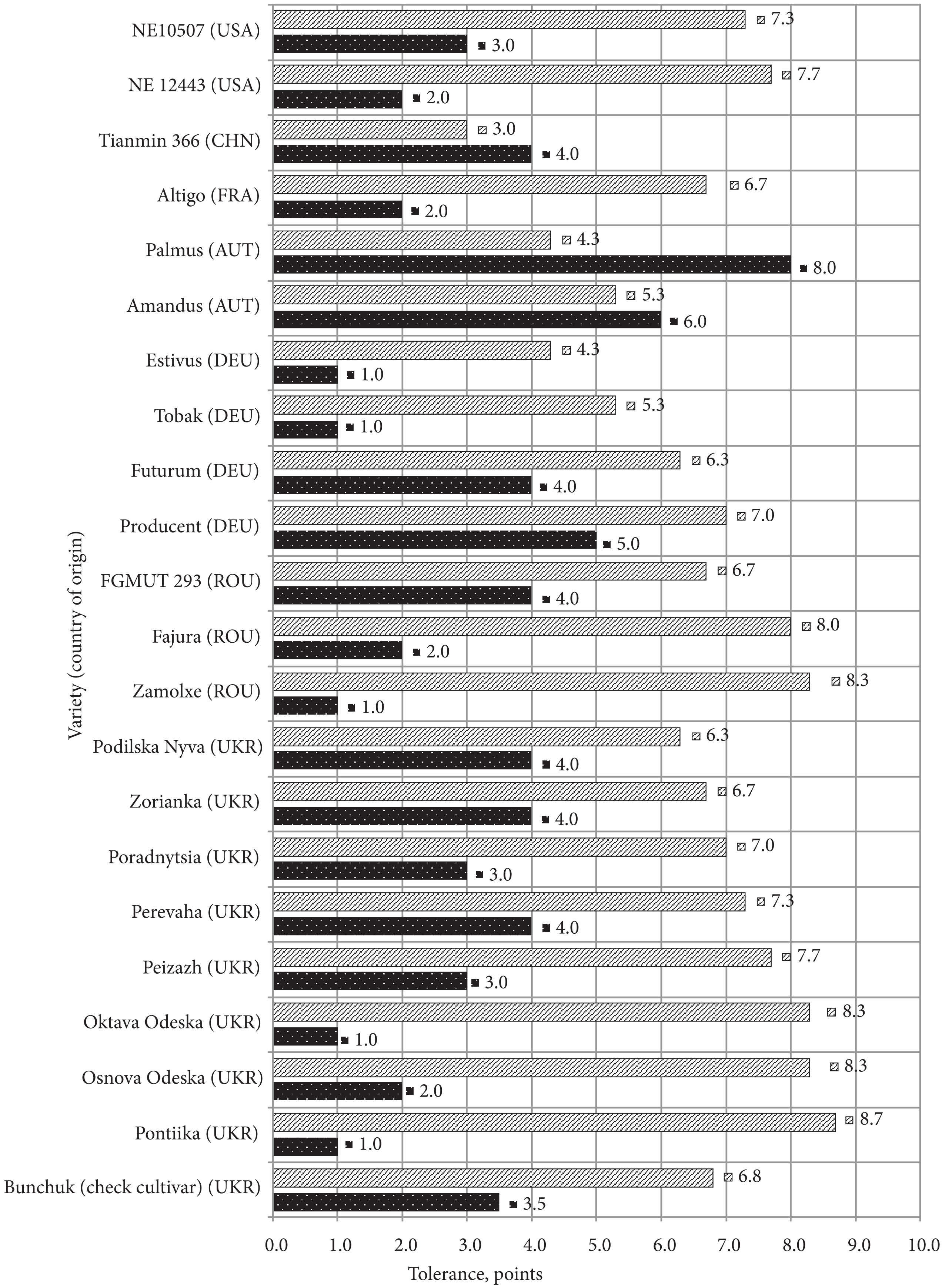

Fig. 1. Tolerance to winter bread wheat leaves to freezing in early spring, 2020—2023. ■ — average value in points (X); □ — amplitude of variation (A_m), points

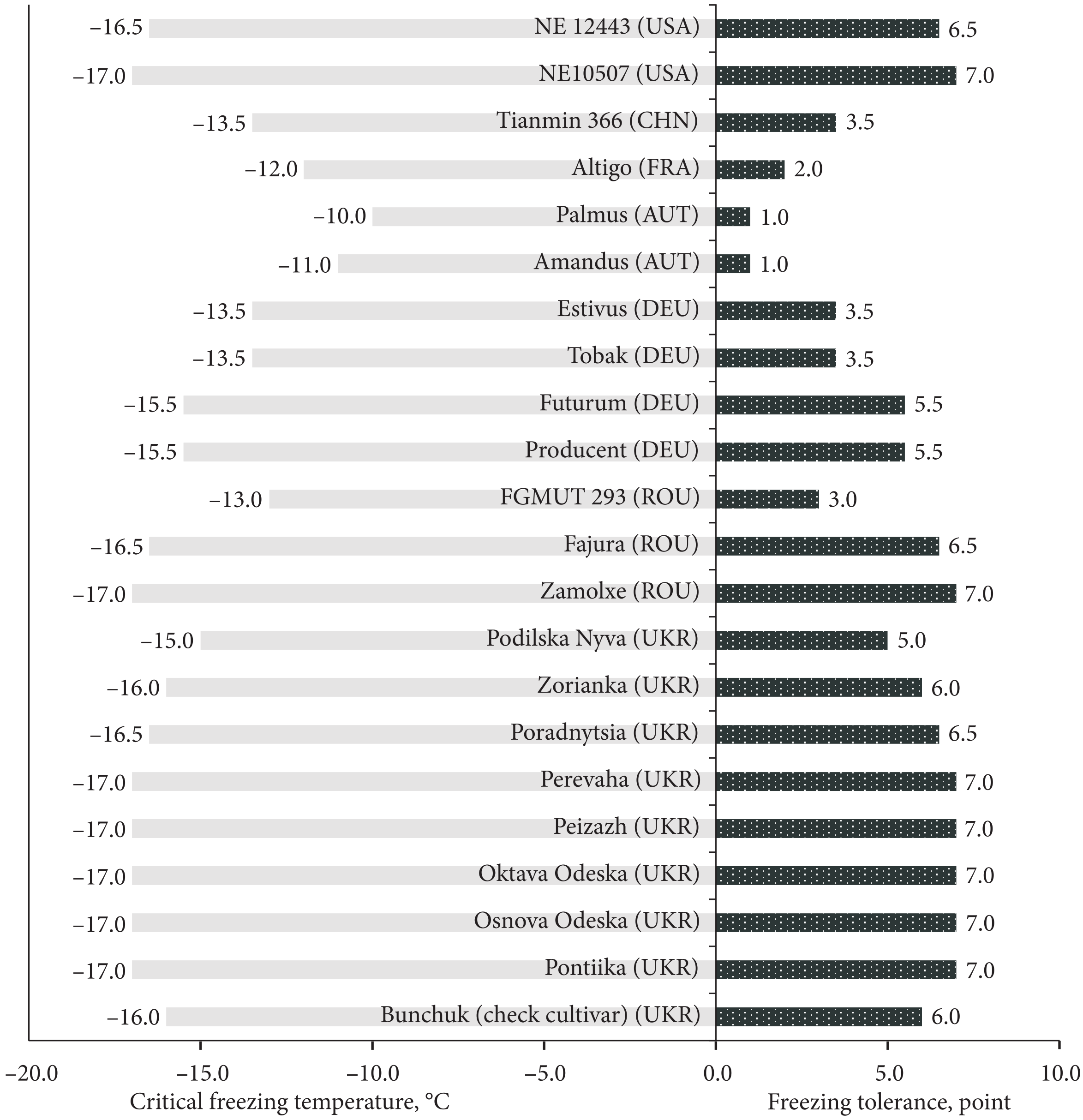

Fig. 2. Freezing tolerance of the winter bread wheat accessions graded by tolerance of their leaves to freezing in early spring, 2020—2023. ▢ — temperature, °C; ■ — freezing tolerance, points

Osnova Odeska, Peizazh, Fajura, Tobak, Estivus, Altigo and NE 12443. High variability (CV >20.0%) of leaf tolerance to freezing was observed in 52.4% of the studied cultivars: Poradnytsia, Producent, Amandus and others. The variability of this trait in the check cultivar, Bunchuk, was high (CV = = 27.7%).

Investigating tolerance of winter bread wheat to low-temperature tolerance, we assessed and graded the sample by tolerance to critical freezing temperatures. The critical freezing temperature in the sample varied from high (–10.0 °C) to low (–17.0 °C). Seven accessions (33.3%) were distinguished by high tolerance to critical freezing temperature (7 points): Pontiika, Osnova Odeska, Oktava Odeska, Peizazh, Perevaha, Zamolxe and NE 10507, the critical freezing temperature in these cultivars was –17.0 °C. The following accessions were characterized by above-average freezing tolerance of plants (5.5—6.5 points) with a critical freezing temperature of –15.5—–16.5 °C: cvs. Poradnytsia, Zorianka, Fajura, Futurum, Producent and NE 12443, their share was 28.6%. The medium freezing tolerance of plants (5 points) with the critical freezing temperature of –15.0 °C was noted for cv. Podilska Nyva. Among the studied accessions, the lowest freezing tolerance of 1.0—3.5 points, with the critical freezing temperature varying within –10.0—

−13.5 °C, was observed in seven accessions: cvs. Tobak, Estivus, Amandus, Palmus, Tianmin 366, Altigo, FGMUT 293. The check cultivar Bunchuk showed freezing tolerance of 6 points (Fig. 2).

In the studied varieties, we identified high-yielding genotypes; they yielded 118—148% related to the check cultivar. These accessions included the following cultivars: Oktava Odeska, Pontiika, Perevaha, Peizazh, Zorianka, Osnova Odeska, Poradnytsia, Zamolxe, Fajura, Producent, Estivus, Palmus, Altigo, NE 12443, and NE 10507. The check cultivar Bunchuk yielded 4.92 t/ha (Table 2). Nine varieties (42.9%) showed a strong genotypic effect (rank 1) for yield, viz. cvs. Oktava Odeska, Pontiika, Perevaha, Zamolxe, Fajura, Producent, Palmus, NE 12443, and NE 10507.

Medium genotypic effects (rank 2) were intrinsic to cvs. Peizazh, Zorianka, Osnova Odeska, Poradnytsia, Estivus, Futurum and Altigo; their proportion was 33.3%. Five varieties (23.8%) showed weak genotypic effects (rank 3); they were cvs. Podilska Nyva FGMUT 293, Tobak, Amandus and Tianmin 366. The check cultivar Bunchuk showed a weak genotypic effect for yield (rank 3).

We found that the genotypic effect (ε_i) for yield ranged from −1.33 to 1.31 in the sample varieties graded by tolerance to low temperatures.

As to plasticity degree (R_i), there were eight homeostatic varieties (38.1%), which produced stable yields (rank 1), viz. cvs. Poradnytsia, Oktava Odeska, Pontiika, Zamolxe, Tobak, Estivus, Futurum and NE 10507. Yields of five accessions (23.8%)

Table 2. **Environmental plasticity of the winter bread wheat varieties graded by tolerance to critical freezing temperatures, tolerance of leaves to freezing in early spring and yield, 2020—2023**

Variety	Country of origin	Yield, t/ha		Genotypic effect		Coefficient of regression (plasticity degree)		Environmental plasticity, rank
		$\overline{X}$	Related to the check cultivar, %	ε_i	Rank	R_i	Rank	
Bunchuk *	UKR	4.92	100	−1.03	3	1.31	3	6
Oktava Odeska #	UKR	6.82	139	0.87	1	0.75	1	2
Pontiika #	UKR	6.48	132	0.53	1	0.59	1	2
Perevaha	UKR	6.40	130	0.45	1	1.50	3	4
Peizazh	UKR	6.23	127	0.28	2	1.34	3	5
Zorianka	UKR	6.17	125	0.22	2	1.36	3	5
Osnova Odeska	UKR	6.11	124	0.16	2	0.86	2	4
Podilska Nyva	UKR	5.56	113	−0.39	3	1.11	2	5
Poradnytsia	UKR	5.82	118	−0.13	2	0.69	1	3
Zamolxe #	ROU	7.26	148	1.31	1	0.55	1	2
Fajura	ROU	6.37	129	0.42	1	1.48	3	4
FGMUT 293	ROU	5.19	105	−0.76	3	1.41	3	6
Producent	DEU	6.32	128	0.37	1	1.67	3	4
Estivus	DEU	5.92	120	−0.03	2	0.14	1	3
Futurum	DEU	5.69	116	−0.26	2	0.44	1	3
Tobak	DEU	4.93	100	−1.02	3	0.72	1	4
Palmus	AUT	6.44	131	0.49	1	1.19	3	4
Amandus	AUT	4.62	94	−1.33	3	1.20	3	6
Altigo	FRA	6.12	124	0.17	2	0.96	2	4
Tianmin 366	CHN	4.85	99	−1.10	3	0.92	2	5
NE 12443	USA	6.40	130	0.45	1	1.17	2	3
NE 10507 #	USA	6.31	128	0.36	1	0.66	1	2
$LSD_{0.05}$		0.31	—	—	—	—	—	—
min		4.62	94	−1.33	1	0.14	1	1
max		7.26	148	1.31	3	1.67	3	3

Note: * — check cultivar; # — genotypes with the highest genetic potential for adaptability and the ability to form high yields.

were moderately sensitive to changes in growing conditions (rank 2); these genotypes were cvs. Osnova Odeska, Podilska Nyva, Altigo, Tianmin 366, and NE 12443. Among the short-stemmed accessions under investigation, eight cultivars that were highly sensitive to limiting environmental factors (rank 3) were identified, viz. cvs. Zorianka, Producent, Amandus, *etc*; they accounted for 38.1% of the sample. The check cultivar Bunchuk was highly sensitive to growing conditions (rank 3).

Based on the results of the impact analysis of low temperatures on the environmental plasticity indicators in winter bread wheat, *i. e.* analyzing the rank sum of genotypic effect (ε_i) and regression coefficient (R_i) for yield, we selected four varieties (19.0%) with the highest genetic potential of adaptability (rank sum = 2) to changes in growing conditions and high tolerance to critical freezing temperatures. These genotypes were cvs. Oktava Odeska (ε_i = 0.87; R_i = 0.75), Pontiika (ε_i = 0.53; R_i = = 0.59), Zamolxe (ε_i = 1.31; R_i = 0.55), and NE 10507 (ε_i = 0.36; R_i = 0.66). A somewhat lower environmental plasticity (rank sum = 3) was observed in cvs. Poradnytsia (ε_i = –0.13; R_i = 0.69), Futurum (ε_i = –0.26; R_i = 0.44), Estivus (ε_i = –0.03; R_i = 0.14), and NE 12443 (ε_i = 0.45; R_i = 1.17). 33.3% of the cultivars had the rank sum of 4: cvs. Perevaha (ε_i = 0.45; R_i = 1.50), Osnova Odeska (ε_i = 0.16; R_i = 0.86), Fajura (ε_i = 0.42; R_i = 1.48), Producent (ε_i = 0.37; R_i = 1.67), Tobak (ε_i = –1.02; R_i = 0.72), Palmus (ε_i = 0.49; R_i = 1.19) and Altigo (ε_i = 0.17; R_i = 0.96). The rank sum of 5 was recorded for cvs. Peizazh (ε_i = 0.28; R_i = 1.34), Zorianka (ε_i = 0.22; R_i = 1.36), Podilska Nyva (ε_i = –0.39; R_i = 1.11), and Tianmin 366 (ε_i = –1.10; R_i = 0.92). The following varieties turned out to be least adapted to environmental stressors (rank sum = 6): FG-MUT 293 (ε_i = –0.76; R_i = 1.41) and Amandus (ε_i = –1.33; R_i = 1.20); their share in the studied sample was 9.5%. As to environmental plasticity of the check cultivar Bunchuk (ε_i = –1.03; R_i = 1.31), the rank sum was 6.

Having analyzed relationships between the studied traits, we found that amplitude of tolerance to leaf freezing in early spring was significantly positively correlated with rank sum of genotypic effect and yield plasticity degree (r = 0.55) in the winter bread wheat cultivars (Table 3).

There was a moderate negative correlation between tolerance of leaves to freezing in early spring and rank sum of genotypic effect and yield plasticity degree (r = –0.42); there was also a moderate positive correlation between tolerance of plants to critical freezing temperatures with rank sum of genotypic effect and yield plasticity degree (r = 0.41). Both correlations were significant at 95% (P <0.05).

Therefore, among tolerances to abiotic factors, which are limiting environmental factors, tolerance of leaves to freezing in early spring and tolerance of plants to critical freezing temperatures had moderate negative and positive effects on yield and its stability, respectively.

Through the lens of global warming, air temperature, being one of the main environmental factors affecting the functioning of systems and viability of living organisms, draws growing attention of researchers and predetermines in-depth research into adaptation of winter bread wheat, as a food crop, to changing environmental conditions.

There were numerous studies investigating which factors influence the environmental plasticity of winter bread wheat. Our results indicate that tolerance to low temperatures in *T. aestivum*, in the context of global warming, moderately affects environmental plasticity. The correlations between tolerance of leaves to freezing in early spring and tolerance of plants to critical freezing temperatures and environmental plasticity of yield are of considerable practical value, as they are a basis for determining mainstreams in breeding for adaptability. Chinese scientists Y. Wu et al. [31] worked on predicting winter wheat yield losses because of damage caused by critical freezing temperatures in the central part of the Huang-Huai Plain and, in contrast to our results, noted that insufficient tolerance to hypothermia led to a significant decrease in yield (p < 0.05) and environmental plasticity. However,

Table 3. **Correlations between environmental plasticity (rank sum of genotypic effect and plasticity degree) of yield and low-temperature tolerance in the winter bread wheat cultivars, 2020—2023**

Trait	Environmental plasticity of yield, t/ha
Score of tolerance of leaves to freezing in early spring, points	–0.42 *
Amplitude of tolerance of leaves to freezing in early spring, A_m	0.55 *
Freezing tolerance of plants (tolerance to critical freezing temperature, °C)	0.41 *

Note: * — P < 0.05.

Ukrainian scientists S.P. Lyfenko et al. [20] argue that to enhance adaptive potentials of new cultivars, it is worth paying attention to both freezing tolerance/winter hardiness and drought tolerance of starting materials, instead of focusing only on tolerance to hypothermia as the main limiting factor of adaptability.

In general, significant difficulties often arose in the breeding of genotypes with high adaptability and yield. For example, A. Ferrante et al. [7], studying yield formation in 12 wheat cultivars bred in 1973—2015, concluded that breeding for increased yields did not improve freezing tolerance. The researchers revealed that, when spring frosts were prevented using mobile heating chambers, the yield was increased by 47.5% compared to the control without protection against low temperatures. The yield in those experiments ranged from 179 ± ± 20.1 g/m^2 to 264 ± 13.3 g/m^2 [7]. However, our findings prove that, in the winter bread wheat gene pool, there are genotypes with tolerance to hypothermia, high genetic potentials for adaptability (rank sum = 2) and high yield capacities (over 128% related to the check cultivar). A genotype's tolerance to hypothermia is significantly affected by peculiarities of hardening period. A strong inverse correlation was reported between freezing tolerance and temperature during the hardening period (r = –0.77) [34].

High and stable yields are determined by different genotypic features, in particular the ability to withstand the impact of abiotic [15, 18] and biotic stressors [33]. Scientists from different countries think that plant tolerance to abiotic stresses is sustained by antioxidant activity, largely by catalase (CAT) activity, the enzyme, which is very effective in neutralizing hydrogen peroxide (H_2O_2) in high concentrations [10]. Among resistances to biotic factors, resistance of winter bread wheat to common pathogens is becoming increasingly important for genotypes' environmental plasticity. It was shown that resistance of *T. aestivum* cultivars to the pathogens of brown leaf rust and tan spot was significantly negatively correlated with rank sum of genotypic effect and of yield plasticity degree (r = = –0.65, P < 0.01 and r = –0.58, P < 0.01, respectively) [33].

Despite the fact that there are various factors limiting environmental plasticity, most scientists emphasize that gradation of starting materials by yield and adaptability under specific agroecological growing conditions is quite important and relevant [17, 27], especially through the lens of climate change [1, 14, 15]. Persistent work on improving stress tolerance of winter bread wheat resulted in the selection of a gene pool with high adaptability, in particular UK 2621/18 (homeostaticity (Hom = = 1,416.0) and UK 9855/18 (Hom = 1,008.0), which is noticeable for tolerance to low temperatures, drought tolerance and group resistance to common pathogens [15].

Thus, tolerance to low temperatures is among the main features of a cultivar that determine its yield and adaptability and it is affected by combinations of factors within limits of inter-cultivar physiological differences. Despite a lot of studies conducted by our predecessors, our findings on patterns of low-temperature impact on the environmental plasticity indicators of winter bread wheat are unique and contribute to the creation of varieties with increased adaptability.

In-depth research into genomics and metabolomics of the short-stemmed winter bread wheat graded by the analyzed traits is planned in further studies; this will supplement the results of this study with molecular-genetic and biochemical features inextricably associated with adaptation of winter bread wheat to low temperatures.

CONCLUSIONS

Among the winter bread wheat varieties graded by low-temperature tolerance, genotypes with the highest genetic potentials for adaptability (rank sum = 2), tolerance to low temperatures and yields of over 127% related to the check cultivar were identified based on rank sums of genotypic effect (ε_i) and regression coefficient (R_i) of yield: cvs. Oktava Odeska (ε_i = 0.87; R_i = 0.75), Pontiika (ε_i = = 0.53; R_i = 0.59), Zamolxe (ε_i = 1.31; R_i = 0.55), and NE10507 (ε_i = 0.36; R_i = 0.66). Thus, the selected varieties are the most valuable starting materials for efficient breeding for adaptability in the context of climate change.

Winter bread wheat genotypes showing high tolerance of their leaves to freezing in early spring and tolerance to critical freezing temperatures were selected: cvs. Pontiika, Osnova Odeska, Oktava Odeska, Peizazh, Perevaha, Zamolxe and NE 10507.

The genotypic effect (ε_i) for yield in the winter bread wheat varieties graded by tolerance to hypothermia was demonstrated to range from –1.33 to

1.31, and the regression coefficient (R_i) — from 0.14 to 1.67, affecting the environmental plasticity variations, as its rank sum ranged from 2 to 6.

It was found that, in the winter bread wheat accessions under investigation, tolerance of leaves to freezing in early spring was moderately negatively correlated with rank sum of genotypic effect and yield plasticity degree ($r = -0.42$; $p < 0.05$) and tolerance of plants to critical freezing temperatures was moderately positively correlated with rank sum of genotypic effect and yield plasticity degree ($r = 0.41$; $p < 0.05$).

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ВПЛИВ СТІЙКОСТІ ДО НИЗЬКИХ ТЕМПЕРАТУР НА ПОКАЗНИКИ ЕКОЛОГІЧНОЇ ПЛАСТИЧНОСТІ ПШЕНИЦІ М'ЯКОЇ ОЗИМОЇ В КОНТЕКСТІ ЗМІН КЛІМАТУ

У роботі досліджено вплив стійкості до низьких температур на показники екологічної пластичності пшениці м'якої озимої як одного із лімітуючих факторів гомеостазу сільськогосподарських культур, що зумовлено викликами сьогодення в умовах глобального потепління. Визначено, що серед диференційованих сортів пшениці м'якої озимої за стійкістю до гіпотермії частка генотипів з найвищою екологічною пластичністю за врожайністю становила 19,0 %. При цьому генотипи з найвищим генетичним потенціалом адаптивності за найменшою сумою рангів (сума рангів 2) генотипового ефекту та коефіцієнтом регресії (Октава одеська, Понтійка, Zamolxe та NE 10507) формували врожайність 128—148 % відносно стандартних значень. Встановлено, що у сортів пшениці м'якої озимої існують помірна негативна кореляція між стійкістю до підмерзання листя у ранньовесняний період та сумою рангів генотипового ефекту і ступенем пластичності врожайності ($r = -0{,}42$, $P < 0{,}05$) та помірна позитивна кореляція між стійкістю до критичних температур вимерзання та сумою рангів генотипового ефекту і ступенем пластичності врожайності ($r = 0{,}41$, $P < 0{,}05$). Виділені генотипи пшениці м'якої озимої з високим генетичним потенціалом екологічної пластичності є цінним вихідним матеріалом для створення нових сортів, адаптованих до кліматичних змін сьогодення.

Ключові слова: морозостійкість, генотиповий ефект, адаптивний потенціал, стресостійкість, пшениця м'яка озима.