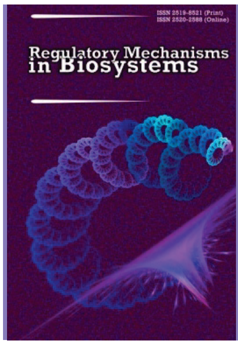

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Breeding and genetic improvement of spelt wheat (*Triticum spelta*) by interspecific hybridization

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Spelt wheat (*Triticum spelta* L.) is a high-value grain crop which is characterized by high protein, gluten and aminoacids content, high adaptive potential, resistance to diseases and high antioxidant activity. However, it is significantly inferior to soft wheat in terms of yield capacity. From crosses of spelt and soft wheat new promising genotypes can be obtained with improved quantitative traits due to introgression in the genome of spelt wheat of genetic material of soft wheat. In the research presented here based on hybridization of *Triticum spelta* L. × *Triticum aestivum* L. we obtained new forms of spelt which differ among themselves in terms of morphological characteristics, productivity and grain quality. As a result of the conducted research, a wide form-forming process in terms of plant height, ear morphology and grain threshing quality was recorded. The height of plants in F_1 hybrids is inherited by the type of dominance of high stemness or intermediate inheritance was established. In the F_2–F_4 generations, the share of obtaining short-stemmed forms of spelt wheat was higher than with the use of short-stemmed varieties of common wheat as the maternal form. In F_2 offspring, the inheritance of threshing quality by the type of dominant epistasis according to the 12 : 3 : 1 scheme was established. In $F_{3–4}$ offspring, splitting according to ear morphology occurred with the appearance of not only typical forms of spelt wheat or common wheat, but also intermediate forms with different ratios of spike length and density. High-yielding (5.75–5.79 t/ha) short-stemmed (h = 78–89 cm) spelt wheat samples 1817 and 1559 with high grain quality indicators (weight of 1000 grains 64.4 g, protein content – 21.0%, gluten – 43.7%) were identified. Sample 13, which successfully combined high grain quality indicators in particular high protein content (26.2%), gluten content (55.8%), grain hardness (66.5 units), flour strength (340 alveograph units) was selected.

Keywords: spelt wheat; plant height; inheritance; yield; threshing quality; spike morphology.

Introduction

Spelt (*Triticum spelta* L.) is one of the oldest types of wheat, which was known as early as the VII–VIII millennium BC. The center of origin of spelt is in Southwest Asia, from where it spread to Northern and Central Europe. The evolutionary histories and trajectories of spelt in Europe are the subject of long-standing debate (Levy & Feldman, 2022; Wang et al., 2024). Now is considered that Asian subspecies of spelt were probably obtained as a result of spontaneous hybridization of *Triticum turgidum* ssp. *dicoccon* and *Aegilops tauschii* ssp. *strangulata*, and later, it gave rise to gymnosperm hexaploid species, in particular, *Triticum aestivum* L. According to the genomic composition and chromosome structure of individual subgenomes, spelt is identical to common wheat (Matsuoka, 2011; Packa et al., 2019).

Spelt is characterized by a number of valuable features, in particular, a high content of protein in the grain, the presence of certain nutrients and aminoacids that do not have products of animal origin and abiotic stress tolerance (Geisslitz et al., 2019; Kraska et al., 2020; Huertas-Garcıa et al., 2023). It has recently attracted renewed interest because of its potential to satisfy current consumer preferences for healthy and diverse products (Arzani & Ashraf, 2017; Curzon et al., 2021; Langraf et al., 2022; Huertas-Garcıa et al., 2023; Longin, 2023). In addition, the spelt population shows significant genetic variation in multiple agronomic and disease resistance traits (Chrpova et al., 2021). In terms of protein content in grains spelt exceeds *Triticum aestivum* L. by 8.0–10.0%, *T. sphaerococum* Persiv. – by 3.0–8.0%. In addition, spelt contains less gluten components than soft wheat, barley, oats, which allows its use in dietary nutrition (Wiwart et al., 2023). Despite a number of advantages, spelt remains a rare species that needs breeding improvement. As a domesticated wheat, spelt exhibits certain morphological characteristics resembling those of non-domesticated grass species, including grains tightly surrounded by tenacious glumes, high stemness of plants and later flowering compared with soft wheat (Ratajczak et al., 2020; Wang et al., 2024).

Starting from the second half of the 19th century and to this day, spelt is used as a source of the hereditary basis of a number of economic and valuable traits (Curzon et al., 2021; Huertas-Garcıa et al., 2023). During the 20th century in Central Europe, local varieties from Austria and Germany were grown, as well as created by simple selection from the varieties and lines of Oberkulmer Rotkorn, Schwabenkorn, Bauerlaender, Ostro, Holstenkorn, Frankenkorn, Nirvana, NSS 3/01, NSS 6/01, NSS 1/02, B1030, S2013, S2070, P12, Heritage and yari CDC Nexon, CDC Origin, CDC Zorba, Lentz Spelt. Currently, a small number of spelt varieties are grown in production, and the existing genetic diversity of this crop is limited to local forms of folk breeding (Diordiieva et al., 2022; Wang et al., 2024). Therefore, spelt cannot compete with common wheat in yield. The main obstacles to its wide implementation in agricultural production are low productivity, tendency to lodging, complicated threshing of grain from the ear (Ratajczak et al., 2020; Diordiieva et al., 2022). In this regard, the search for effective ways to eliminate deficiencies is an urgent task of spelt breeding. By crossing *Triticum spelta* L. with *Triticum aestivum* L. it is possible to obtain new hybrid forms of spelt with improved quantitative and qualitative indicators due to the introgression of common wheat genetic material into their genome. The height of plants in wild forms of spelt wheat can reach 130 cm. In selected varieties, this indicator is slightly lower (115–120 cm), but this does not change its tendency to lodging, which, in turn, leads to a decrease in yield and product quality (Grant et al., 2018). Low threshing quality (about 60–70%) leads to a lack of harvest and additional costs during harvesting. Creating short stem forms of spelt with improved threshing quality is an effective way to increase its productivity, which will increase the demand for spelt among agricultural producers. For successful selection of spelt to reduce the height of plants by short-stemmed donors, it is worth involving varieties of soft winter wheat. In hybrid generations, it is necessary to carry out an analysis of the inheritance of selection traits and the selection of promising short-stem genotypes, taking into account the morphology of the ear.

The purpose of our research was to obtain new valuable forms of spelt wheat by hybridizing *Triticum spelta* L. × *Triticum aestivum* L. to create new valuable initial material with high productivity and grain quality and introduce them into breeding schemes for creating high-yielding varieties of spelt.

Materials and methods

The study was conducted in the in the research field of the Department of Genetics, Plant Breeding and Biotechnology of Uman National University of Horticulture, located in Uman, Cherkasy region, the zone of the Right Bank Forest-Steppe of Ukraine (Fig. 1).

Fig. 1. Experimental breeding plots of spelt wheat

The region belongs to the subzone of unstable humidity (there are droughts once in 2–3 years). The average long-term precipitation rate for the region is 586 mm, the average annual air temperature is + 7.8 ^{0}C. The soil of the experimental field is heavy loamy chornozem. In the studies, the generally accepted technology of growing winter grain crops was used. Sowing was carried out in the optimal time for the zone – the third decade of September. The work used a systematic method of placing plots with four repetitions. Numbered plants were placed in blocks with plant density 400 thousand units per hectar.

To create short-stem forms of spelt wheat, interspecies hybridization of short-stemmed soft winter wheat varieties (Panna, Podolyanka, Kryzhynka, Farandol, Kharus, Yermak) with spelt wheat (sample from Carpathian region and variety Zoria Ukrainy) was carried out. A number of reciprocal crosses were carried out according to the scheme ♀ common wheat (low stem) × ♂ spelt (high stem), ♀ spelt (high stem) × ♂ common wheat (low stem). Hybridization was carried out by manual castration of the flowers of the mother form and subsequent forced pollination with the pollen of the parent form by the limited freedom method under a parchment insulator.

Inheritance of plant height in different generations of spelt wheat hybrids was determined by the formula of Griffing (1950). The ranking of the created materials according to the degree of dominance (hp) was carried out according to the gradation of Beil & Atkins (1965): 1) hp < –1 – negative overdominance (negative heterosis, or depression); 2) –1 < hp < –0.5 – negative dominance; 3) –0.5 < hp < 0.5 – intermediate inheritance; 4) 0.5 < hp < 1 – positive dominance; 5) hp > 1 – positive overdominance (positive heterosis). The correspondence between the actual and expected splitting of F_2 hybrids was evaluated by the χ^2 criterion.

All phenological observations, analysis of crop structure indicators were carried out according to the "Methodology of conducting a qualification examination of plant varieties of the group of grain, grain and leguminous crops for suitability for distribution in Ukraine" (2016). Grouping of wheat samples by plant height was carried out according to the modified scale of Orliuk et al. (2006). Plant biometrics was determined in 50 plants, selected from each plot in two nonadjacent repetitions. Quality indicators (protein and gluten content, flour strength, grain hardness) were determined by the infrared spectroscopy method using the Infratec™ Nova device (FOSS Analytical, Sweden). The ranking of samples by flour strength was carried out on a scale: > 500 alveograph units (a. u.) – excellent improver, 400–500 a. u. – good improver, 280–400 a. u. – satisfactory improver, 260–280 a. u. – valuable wheat, 240–260 a. u. – good filler, 180–240 a. u. – satisfactory filler, < 180 a. u. – weak wheat. According to grain hardness, wheat samples were divided into three categories: > 60 units of the device – hard grain type, 54–60 units – medium hard grain type, < 54 units – soft grain type.

After carrying out all the calculations and analyses, the grain was threshed and the yield was determined. Threshing quality was determined by the percentage of fully threshed grain to the total amount of grain. Ecological plasticity was estimated by the regression coefficient (b_i) using the method of Eberhart & Russell (1966). Statistical analysis of the research data was performed using Statistica 12 software (StatSoft, Inc., USA). Results are expressed as means ± standard deviation. The differences between samples were determined using Tukey's test, where the differences were considered significant at P < 0.05.

Results

Inheritance of stem height and ear morphology in hybrid populations F_1–F_4 *Triticum aestivum* L. × *Triticum spelta* L. The initial form of spelt wheat used for hybridization was high-stemmed (h = > 120 cm), had a long (20 cm), loose, narrow, brittle, membranous, thornless, white spike without wax coating. During ripening, the ear broke into separate segments and was characterized by heavy, complicated grain threshing due to the presence of coarse, dense ear scales. Its yield was at the level of 4.50 t/ha, protein content – 25.0%, gluten content – 50.0–52.0%. The initial varieties of common wheat were characterized by short stems (h = 85–100 cm) and high productivity (over 6.0 t/ha).

The F_1 hybrids were of the same type according to the morphological structure of the ear and were characterized by an elongated ear, red color of the ear scales, and spinelessness. In generations F_3–F_4, the splitting of the ear into spelt (Fig. 2a), speltoids (Fig. 2b), forms with a typical soft wheat ear (Fig. 2c), squareheads (Fig. 2d), subcompactoids (Fig. 2e) and compactoids (Fig. 2f) was fixed.

a *b* *c* *d* *e* *f*

Fig. 2. Splitting of F_{2-4} *Triticum spelta* L. × *Triticum aestivum* L. hybrids by ear morphology: *a* – spelt; *b* – spelt-like (intermediate) form; *c* – a typical ear of soft wheat; *d* – squarehead; *e* – subcompactoid; *f* – compactoid

Further breeding work was carried out directly among spelt (long, loose ear with tough glume and difficult grain threshing of the ear) and spelt-like (elongated, loose or medium dense ear with difficult grain threshing) samples. In the F_{3-4} generations, a number of highly productive, low-stemmed hybrid populations with improved grain threshing were isolated.

A comparative analysis of the created samples of spelt and the original forms indicates a different nature of plant height inheritance from typical intermediate inheritance to depression and dominant tallness. Hybrids of the first generation were mostly medium- or high-stemmed (h = 110–120 cm), regardless of the height of the plants of the mother form. When hybridizing short-stemmed forms of common wheat (♀) with spelt (♂), the dominance of high-stemmed forms was observed in 44.4% of first-generation hybrids, intermediate inheritance – 55.6%, and no short-stemmed forms were detected (Table 1). When hybridizing high-stemmed forms of spelt wheat (♀) with short-stemmed forms of common wheat (♂), the share of high-stemmed offspring was significantly higher and reached 76.3% in F_1 hybrids with the dominance of high-stemmed.

In the F_{2-4} generations, the range of variability in plant height was 52–129 cm. The created samples were divided into high-stemmed (h = > 120 cm), medium-stemmed (h = 105–119 cm), short-stemmed (h = 85–104 cm), semi-dwarf (h = 60–84 cm) and dwarf (h = < 60 cm). In the F_{3-4} generations, a number of short-stemmed hybrid populations were isolated. The vast majority of them were obtained by hybridization of ♀ short-stem varieties of common wheat × ♂ spelt.

In the hybridization of spelt wheat and soft wheat significant differences in grain threshing quality were recorded in the offspring, which in wheat is controlled by the *Q/q* and *Tg/tg* genes. For the formation of a phenotype with free threshing of grain, it is necessary to have dominant alleles QQ and recessive alleles *tgtg* in the genotype, which is typical for common wheat. The genotype of spelt wheat is *qqTgTg*. F_1 hybrids had the *QqTgtg* genotype, the phenotype of which was characterized by a speltoid type of ear with complicated grain threshing. Their self-pollination resulted in 12 parts of plants with complicated grain threshing (with different saturation of dominant Q alleles), three parts with free threshing and one part with hard threshing.

A hybridological analysis of the splitting of F_2 offspring according to the nature of grain threshing shows that this trait is inherited by the type of dominant epistasis according to the 12 : 3 : 1 scheme (Table 2).

Table 1
Ratio for plant height of spelt wheat samples in generations F_{1-4}, obtained by reciprocal crosses of short stem forms of common wheat with spelt, 2014–2017 (%, x ± SD, n = 4)

Generation	Dominance of high stem (hp = 0.5 < 1.0)	Intermediate inheritance (hp = -0.5 < 0.5)	Dominance of short stem (hp = –1.0 < –0.5)	Depression (hp = < –1.0)
Hybridization was carried out according to the scheme ♀ short-stem varieties of common wheat × ♂ spelt				
F_1	44.41 ± 2.12 ^{b}	55.59 ± 3.58 ^{a}	0.00 ^{c}	0.00 ^{c}
F_2	46.59 ± 2.58 ^{a}	46.71 ± 2.64 ^{a}	6.70 ± 0.54 ^{b}	0.00 ^{c}
F_3	37.72 ± 1.95 ^{a}	33.33 ± 1.85 ^{a}	24.42 ± 1.74 ^{b}	4.53 ± 0.52 ^{c}
F_4	37.72 ± 1.95 ^{a}	33.33 ± 1.85 ^{a}	24.42 ± 1.74 ^{b}	4.53 ± 0.52 ^{c}
Hybridization was carried out according to the scheme ♀ spelt × ♂ short-stem varieties of common wheat				
F_1	76.33 ± 4.25 ^{a}	23.67 ± 1.88 ^{b}	0.00 ^{c}	0.00 ^{c}
F_2	60.48 ± 3.87 ^{a}	39.52 ± 2.12 ^{b}	0.00 ^{c}	0.00 ^{c}
F_3	52.58 ± 2.95 ^{a}	39.51 ± 2.05 ^{b}	7.91 ± 0.58 ^{c}	0.00 ^{d}
F_4	52.58 ± 2.95 ^{a}	39.51 ± 2.05 ^{b}	7.91 ± 0.58 ^{c}	0.00 ^{d}

Note: different letters indicate values that are significantly different within one line according to results of the Tukey test (P < 0.05).

In subsequent generations, offspring with free threshing of grain were stabilized by self-pollination and analyzed according to the level of manifestation of other economic and valuable traits. Descendants with complicated threshing were self-pollinated or repeatedly crossed with the original forms of soft wheat, as a result of which a wide form-forming process was observed according to a number of breeding and morphological features, in particular, according to the specifics of threshing quality, plant height, ear morphology.

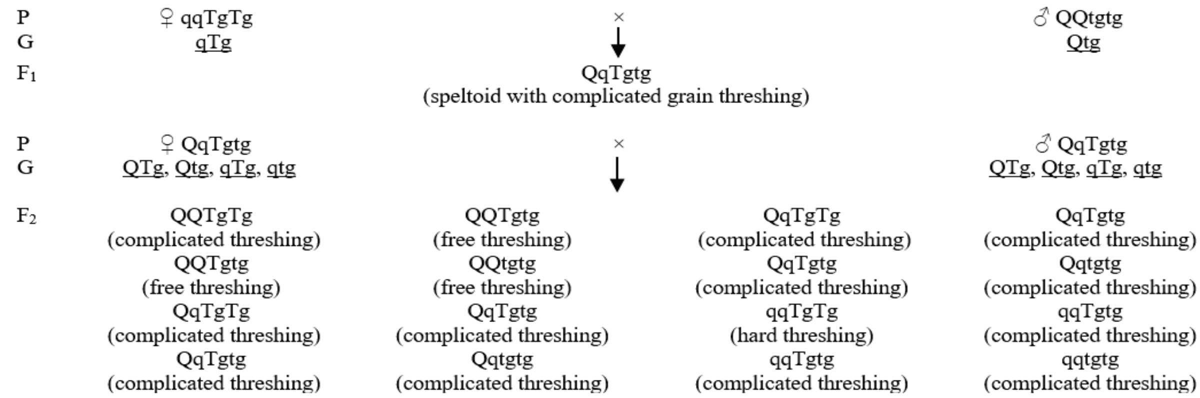

Fig. 3. Schematic of segregation by *Q/q* and *Tg/tg* genes of F_2 hybrids obtained by hybridization of *Triticum spelta* L. × *Triticum aestivum* L.

Table 2
Hybridological analysis of segregation of F_2 hybrids obtained by hybridization of *Triticum spelta* L. × *Triticum aestivum* L. by threshing quality (n = 4)

Number of plants in F_2	Complicated threshing	Free threshing	Hard threshing	Ratio	χ^2 actual	χ^2 theoretical
Expected	337	63	25	12 : 3 :1	–	5.992
Actual	319	80	26	12 : 3 :1	4.667	–

Note: * – the value of χ^2 is significant at the level P < 0.001.

Analysis of productivity and quality indicators. The next stage of the research was the analysis of productivity and grain quality indicators of the created samples. The analysis of the crop structure shows that in terms of grain mass from the main ear, samples 1817, 1559 and 1755 significantly exceeded the average group indicator (Table 3). The spike density in all studied samples was low (less than 16 spikelets per 10 cm of the spike rod), which was ensured by the presence of a long spike (within 12.6–18.0 cm). Samples 184, 202 (18.0 cm) and 1694 (17.8 cm) had the longest ear. In the conducted studies, the highest strength of flour was recorded in samples 13 (340 a. u.), 179 (340 a. u.), 1559 (330 a. u.), 1817 (345 a. u.) (Table 4).

Taking into account the classification by flour strength, all samples of spelt wheat were identified as satisfactory improvers, with the exception of samples 15 and 1674, which were classified as valuable wheats. The sign of hard grain/soft grain has an important technological significance in the bakery and confectionery industries. In the created materials, the grain hardness varied within 48.4–66.5 units. Taking into account the classification by grain hardness, samples 13, 179, 1559, 1786, and 202 are classified as hard-grained, samples 47, 66, 124, 1755, 1817, 93, and 184 are classified as semi-soft-grained, and the others as soft-grained.

The analysis of grain quality indicators made it possible to select short-stemmed samples 13 and 179, which are characterized by protein content, respectively, of 26.8% and 22.1%, gluten content of 48.1–55.8%, and grain glassiness in the range of 83–89%. It is worth noting sample 1559, which had a mass of 1000 grains of 62.1 g, a protein content of 20.8%, gluten – 42.9%, and a yield (on average 5.75 t/ha), significantly exceeded the group average in each of the years of research.

Table 3
Indicators of productivity of the wheat spelt samples obtained by hybridization of *Triticum spelta* L. × *Triticum aestivum* L., 2018–2020 (x ± SD, n = 4)

Origin ♀	Origin ♂	Sample	Mass of grain from the main ear, g	Ear length, cm	The number of grains in an ear, pcs.	Ear density, pcs./10 cm	Plant height, cm
Panna	Sample of spelt from Carpathian region	13	1.39 ± 0.10^{h}	13.8 ± 0.69^{g}	41 ± 2^{b}	15.5 ± 0.65^{a}	102 ± 6^{a}
Podolianka		15	1.87 ± 0.09^{d}	14.7 ± 0.56^{f}	43 ± 3^{a}	15.2 ± 0.62^{b}	75 ± 2^{e}
Krasnodarska 99		25	1.75 ± 0.08^{d}	15.2 ± 0.69^{d}	42 ± 3^{a}	15.3 ± 0.63^{a}	78 ± 3^{d}
Podolianka		47	1.52 ± 0.16^{f}	14.8 ± 0.69^{d}	43 ± 3^{a}	15.2 ± 0.62^{b}	92 ± 5^{c}
Panna		66	1.67 ± 0.16^{e}	14.5 ± 0.68^{e}	41 ± 2^{b}	14.7 ± 0.56^{bc}	95 ± 5^{c}
Yermak		124	1.82 ± 0.12^{d}	12.6 ± 0.43^{h}	43 ± 3^{a}	15.5 ± 0.65^{a}	94 ± 4^{c}
Podolianka		179	1.44 ± 0.09^{g}	13.4 ± 0.56^{g}	44 ± 3^{a}	15.4 ± 0.64^{a}	101 ± 5^{a}
Kryzhynka		1559	2.35 ± 0.13^{a}	15.7 ± 0.42^{c}	46 ± 3^{a}	15.5 ± 0.65^{a}	89 ± 4^{d}
Farandol'		1674	2.05 ± 0.13^{c}	14.1 ± 0.56^{f}	43 ± 3^{a}	15.2 ± 0.54^{b}	92 ± 5^{c}
Farandol'		1694	1.72 ± 0.12^{d}	17.8 ± 0.47^{a}	43 ± 3^{a}	14.4 ± 0.54^{c}	96 ± 3^{bc}
Panna		1755	2.28 ± 0.07^{b}	17.4 ± 0.50^{b}	44 ± 3^{a}	15.2 ± 0.69^{b}	96 ± 3^{bc}
Favorytka		1786	2.06 ± 0.09^{c}	15.2 ± 0.54^{d}	43 ± 3^{a}	15.7 ± 0.73^{a}	85 ± 2^{d}
Harus		1817	2.45 ± 0.10^{a}	16.2 ± 0.56^{c}	45 ± 3^{a}	14.9 ± 0.61^{b}	78 ± 4^{e}
Zoria Ukrainy	Podolianka	93	1.53 ± 0.10^{f}	16.8 ± 0.45^{b}	44 ± 3^{a}	14.8 ± 0.59^{b}	98 ± 4^{b}
Zoria Ukrainy		184	1.55 ± 0.07^{e}	18.0 ± 0.43^{a}	44 ± 3^{a}	14.2 ± 0.52^{cd}	100 ± 5^{ab}
Zoria Ukrainy	Panna	202	1.42 ± 0.09^{g}	18.0 ± 0.62^{a}	42 ± 4^{a}	13.8 ± 0.51^{d}	98 ± 3^{b}
		Average	1.80 ± 0.08^{d}	15.5 ± 0.62^{cd}	43 ± 4^{a}	15.0 ± 0.63^{b}	92 ± 7^{c}

Note: for Tables 3–5, different letters indicate values that are significantly different within one column according to results of the Tukey test ($P < 0.05$).

Low yield is a negative characteristic of spelt. It was expected that its hybridization with soft wheat would allow new forms to be obtained with improved productivity indicators. Sample 1817 stood out for yield (5.79 t/ha). It was characterized by high ecological plasticity (b_i = 1.23), but the quality of grain threshing was low (70%, Table 5).

Samples 1786 (5.15 t/ha), 1674 (5.21 t/ha) and 1755 (5.30 t/ha), which were characterized by average ecological plasticity (b_i = 0.96–1.06), were insignificantly inferior to the group index in yield. High threshing quality (80–84%) was observed in the samples 13 and 124.

Discussion

In the interspecific hybridization of spelt wheat and soft wheat, a wide form-forming process is observed according to a number of signs and indicators, in particular, according to the shape of the ear. A feature of the interaction of genes and cleavage in F_2 hybrids is the appearance of a square-headed spike, which was not present among the parental forms. In subsequent generations, there was also an increase in forms with a compactoid type of ear (short, super dense ear). The main importance in the formation of the speltoid form of the wheat ear is the gene *Q/q*, located in the long arm of chromosome 5A. The *q-5D* and *q-5B* genes are believed to be involved in the suppression of the speltoid trait (Sormacheva et al., 2015; Curzon et al., 2024). This does not exclude the importance of regulatory genes, only a single mutation in the sequence of which can lead to significant changes in the phenotype (Sichkar et al., 2016). The appearance among descendants of forms with a square-headed type of ear, which is not characteristic of the original forms, is explained by the interaction of recessive alleles of the *C/c* gene, which leads to a shortening of the length of the ear, spikelet scale and grain, and the extender genes *L1/l1*, *L2/l2*.

Table 4
Indicators of quality of the wheat spelt samples obtained by hybridization of *Triticum spelta* L. × *Triticum aestivum* L. (2018–2020, x ± SD, n = 4)

Origin ♀	Origin ♂	Sample	Vitrification, %	Content, % protein	Content, % gluten	Flour strength (W), a. u.	Grain hardness
Panna	Sample of spelt from Carpathian region	13	88 ± 2^{a}	26.8 ± 0.21^{a}	55.8 ± 0.47^{a}	340 ± 4^{a}	66.5 ± 1.05^{a}
Podolianka		15	85 ± 3^{b}	18.4 ± 0.35^{e}	38.7 ± 0.60^{e}	275 ± 9^{e}	48.4 ± 0.56^{h}
Krasnodarska 99		25	80 ± 3^{c}	18.1 ± 0.10^{f}	38.0 ± 0.25^{f}	288 ± 8^{d}	51.5 ± 0.54^{g}
Podolianka		47	85 ± 4^{b}	18.8 ± 0.40^{e}	38.7 ± 0.66^{e}	290 ± 5^{c}	56.8 ± 0.44^{e}
Panna		66	86 ± 4^{ab}	19.1 ± 0.54^{d}	39.5 ± 0.75^{d}	305 ± 4^{b}	58.7 ± 0.42^{d}
Yermak		124	76 ± 5^{d}	17.5 ± 0.43^{h}	38.2 ± 0.68^{f}	280 ± 3^{d}	55.1 ± 0.34^{f}
Podolianka		179	83 ± 4^{c}	22.1 ± 0.50^{b}	48.1 ± 0.72^{b}	340 ± 9^{a}	62.1 ± 0.54^{b}
Kryzhynka		1559	84 ± 3^{bc}	20.8 ± 0.52^{c}	42.9 ± 0.74^{c}	330 ± 5^{a}	60.8 ± 0.53^{bc}
Farandol'		1674	65 ± 3^{e}	16.4 ± 0.31^{i}	33.9 ± 0.62^{h}	254 ± 6^{f}	52.2 ± 1.10^{g}
Farandol'		1694	75 ± 2^{d}	17.8 ± 0.52^{g}	39.1 ± 0.78^{de}	285 ± 4^{d}	52.5 ± 0.43^{g}
Panna		1755	76 ± 2^{d}	18.5 ± 0.34^{e}	39.1 ± 0.65^{de}	284 ± 6^{d}	58.7 ± 0.43^{d}
Favorytka		1786	84 ± 3^{bc}	19.4 ± 0.26^{d}	40.8 ± 0.52^{d}	287 ± 6^{d}	62.1 ± 0.56^{b}
Harus		1817	85 ± 5^{b}	21.5 ± 0.50^{b}	43.6 ± 0.82^{c}	345 ± 7^{a}	58.7 ± 0.48^{c}
Zoria Ukrainy	Podolianka	93	85 ± 5^{b}	18.5 ± 0.31^{e}	37.2 ± 0.64^{g}	290 ± 7^{c}	56.4 ± 0.69^{ef}
Zoria Ukrainy		184	86 ± 3^{ab}	18.8 ± 0.49^{d}	38.2 ± 0.74^{f}	293 ± 7^{b}	57.1 ± 0.56^{e}
Zoria Ukrainy	Panna	202	88 ± 4^{a}	20.1 ± 0.24^{c}	41.8 ± 0.48^{cd}	330 ± 4^{a}	60.2 ± 0.45^{c}
		Average	82 ± 3^{c}	19.5 ± 0.38^{d}	40.8 ± 0.48^{d}	301 ± 9^{b}	57.4 ± 0.60^{e}

Note: see Table 3.

Table 5
The yield of the wheat spelt samples obtained by hybridization of *Triticum spelta* L. × *Triticum aestivum* L. (2018–2020, x ± SD, n = 4)

Origin ♀	Origin ♂	Sample	Yield, t/ha 2018	Yield, t/ha 2019	Yield, t/ha 2020	Yield, t/ha average	b_i^*	Threshing quality, %
Panna	Sample of spelt from Carpathian region	13	4.42 ± 0.52 [f]	4.02 ± 0.42 [e]	3.41 ± 0.31 [e]	3.95 ± 0.41 [e]	0.87	80 ± 4 [ab]
Podolianka		15	5.14 ± 0.48 [d]	4.85 ± 0.42 [c]	4.21 ± 0.26 [c]	4.73 ± 0.38 [c]	0.81	75 ± 2 [c]
Krasnodarska 99		25	4.98 ± 0.56 [d]	4.54 ± 0.48 [c]	3.87 ± 0.33 [c]	4.46 ± 0.45 [c]	0.96	76 ± 4 [c]
Podolianka		47	4.68 ± 0.58 [e]	4.18 ± 0.49 [d]	3.52 ± 0.35 [d]	4.13 ± 0.47 [d]	1.00	70 ± 3 [d]
Panna		66	4.85 ± 0.65 [e]	4.35 ± 0.55 [d]	3.53 ± 0.43 [d]	4.24 ± 0.54 [d]	1.14	74 ± 3 [c]
Yermak		124	5.05 ± 0.58 [cd]	4.56 ± 0.55 [c]	3.78 ± 0.44 [c]	4.46 ± 0.52 [c]	1.10	84 ± 3 [a]
Podolianka		179	4.56 ± 0.53 [e]	4.14 ± 0.46 [d]	3.48 ± 0.33 [d]	4.06 ± 0.44 [d]	0.94	78 ± 4 [b]
Kryzhynka		1559	6.27 ± 0.61 [a]	5.87 ± 0.51 [a]	5.11 ± 0.33 [a]	5.75 ± 0.48 [a]	1.01	72 ± 3 [d]
Farandol’		1674	5.74 ± 0.54 [c]	5.24 ± 0.46 [b]	4.64 ± 0.32 [b]	5.21 ± 0.45 [b]	0.95	75 ± 2 [c]
Farandol’		1694	5.12 ± 0.58 [d]	4.65 ± 0.46 [c]	4.01 ± 0.28 [c]	4.59 ± 0.45 [c]	0.96	77 ± 3 [b]
Panna		1755	5.87 ± 0.47 [b]	5.28 ± 0.47 [b]	4.74 ± 0.39 [b]	5.30 ± 0.46 [b]	0.96	78 ± 5 [b]
Favorytka		1786	5.78 ± 0.61 [bc]	5.12 ± 0.52 [b]	4.54 ± 0.39 [b]	5.15 ± 0.50 [bc]	1.06	75 ± 3 [c]
Harus		1817	6.47 ± 0.65 [a]	5.87 ± 0.59 [a]	5.04 ± 0.51 [a]	5.79 ± 0.58 [a]	1.23	70 ± 3 [d]
Zoria Ukrainy	Podolianka	93	4.58 ± 0.54 [e]	4.20 ± 0.45 [d]	3.52 ± 0.32 [d]	4.10 ± 0.43 [d]	1.11	72 ± 4 [d]
Zoria Ukrainy		184	4.62 ± 0.58 [e]	4.58 ± 0.51 [d]	3.58 ± 0.35 [d]	4.26 ± 0.48 [d]	1.05	75 ± 4 [c]
Zoria Ukrainy	Panna	202	4.43 ± 0.52 [e]	4.08 ± 0.44 [d]	3.45 ± 0.29 [d]	4.20 ± 0.41 [d]	1.07	74 ± 3 [c]
		Average	5.16 ± 0.55 [d]	4.72 ± 0.52 [c]	4.02 ± 0,42 [c]	4.64 ± 0.49 [c]	–	76 ± 4 [c]

Note: see Table 3; b_i – regression coefficient.

A sign of squarehead can have a different genetic nature. The cause of its occurrence can be polysomy, aberrations or gene mutations. The latter can have a monogenic recessive or dominant character or dominant with the manifestation of recessive epistasis (Johnson et al., 2008). The shape of the ear, in particular the density, is also affected by gene *C/c*, the recessive state of which causes a shortening of the length of the ear, scales and grain, and the lengthening genes *L1/l1*, *L2/l2*. In the presence of recessive alleles of all these genes in hexaploid wheat, a short, dense mace-shaped ear of the "squarehead" type develops. In the absence of spike extender genes, common wheat forms a short and dense spike and becomes squareheaded or club-shaped (Gospodarenko et al., 2016; Sichkar et al., 2016).

Currently, more than 20 specific genes (*Rht1–Rht20*) have been identified in the genetic plasma of the genus *Triticum* L., which provide a significant diversity of wheat in terms of plant height (Yakymchuk, 2018). Scientists also point to the effect of modifier genes (Berry & Berry, 2015). There are no reports on genetic control of plant height in spelt wheat in the scientific literature. According to scientists, hybrid forms obtained by crossing different types of wheat occupy an intermediate position between the original forms in terms of plant height (Acquaah, 2007; Tverdohlib & Boguslavskii, 2010). However, the facts of dominance and superdominance of the high-stemmed form are described in the scientific literature (Gulkanian, 1971; Sichkar et al., 2016). Scientists also record selective (additive interaction of genes) and hybrid (complementary interaction of genes) dwarfism in the offspring (Grant et al., 2018). When hybridizing spelt with common wheat varieties carrying dominant or recessive genes for dwarfism, various types of gene interaction (complementary, epistatic, polymeric) and the formation of offspring with a wide range of variability in plant height are observed.

Despite the fact that the demand for spelt is now growing among agricultural producers, scientific research and breeding programs are being revived, it still remains a rare, little-studied species that needs breeding and genetic improvement. Among the sources of scientific literature, a small amount of data was found on the genetic control of plant height, the patterns of its inheritance, and the relationship with other economic and valuable indicators. In the process of research, it was established that the decrease in the height of spelt wheat plants has a positive effect on its yield and the mass of grain from the ear. The introgression of the genetic material of short-growing common wheat varieties into the genome of spelt wheat made it possible to distinguish among the offspring highly productive short-growing genotypes 1817 and 1559.

A negative characteristic of spelt is also the low quality of grain threshing, which is associated with the fragility of the ear shaft and the presence of coarse ear scales. The formation of the ear of wheat with free threshing of the grain is controlled by the *Q/q* gene with pleiotropic effect, which is located in the long arm of chromosome 5A. It is an APETALA-2 transcription factor that controls flower development in plants (Faris et al., 2003). A mutation in just one pair of nucleotides in the alleles of the *Q/q* gene was crucial in the process of wheat domestication, because it led to the emergence of an ear with a flexible shaft and free threshing (recessive allele) instead of an ear with a brittle shaft and coarse ear scales of the ear, which makes threshing difficult (dominant allele) (Faris et al., 2006; Gil-Humanes et al., 2009). The importance of regulatory genes is not excluded, only a single mutation in the sequence of which can lead to significant changes in the phenotype (Kato et al., 1998; Kosuge et al., 2012). In addition, the nature of threshing is influenced by the type of spikelet scale, which in hexaploid wheat species is controlled by the recessive allele *tg* of the *Tg/tg* gene in the homozygous state. Different combinations of alleles of the *Q/q* and *Tg/tg* genes were found in the offspring of crossing common wheat with spelt. In this regard, significant variability in the nature of grain threshing was recorded. It is likely that samples 124 and 13 have the *QQtgtg* genotype, which leads to the formation of a phenotype with light grain threshing (80–84%). Scientists point out that as the height of spelt plants decreases, the features of their morphological and anatomical structure change, which significantly affects the development of other features (Lyfenko et al., 2014; Berry & Berry, 2015). Therefore, it is possible to observe incomplete realization of the yield potential of the genotype.

The productivity of spelt in areas of low agricultural productivity or under stress conditions is higher than that of common wheat, so it is traditionally grown as a sustainable alternative to common wheat in marginal wheat growing areas with limited yield potential (Sugár et al.., 2019). However, with intensive farming, the productivity of spelt is significantly inferior to common wheat. Thus, in Israel the average yield of spelt is 3.0–4.0 t/ha (Curzon et al., 2024), in Germany 3.0–5.0 t/ha (Longin et al., 2022), while the average yield of common wheat in these countries reaches 7.0–8.0 t/ha. Spelt has many undesirable genes that control agronomically valuable indicators and prevent its cultivation in modern agricultural systems, in particular, alleles *Rht-B1a*, *Rht-D1a* and *q*, which control the formation of tall stems and threshing quality (Wang et al., 2024). If they are present in the genotype of the variety, an increase in laying, a decrease in productivity, and the complication of mechanical harvesting and further processing are recorded. Therefore, breeders conduct targeted hybridization of spelt and common wheat to introduce valuable genes into the spelt genome and improve its agrobiological characteristics (Diordiieva et al., 2022). In our research, low-growing spelt samples 1559 (5.75 t/ha), 1755 (5.30 t/ha) and 1674 (5.21 t/ha) were identified, which were characterized by high productivity. These samples are promising starting material for further breeding and genetic improvement of common wheat and spelt.

It is known that when a parental form of wheat with a high content of protein and gluten is crossed with a form in which the value of these indicators is low, the offspring inherit the characteristics of the worst parent (Nemeth et al., 2015; Rybalka et al., 2018). Therefore, when hybridizing spelt with common wheat, it is important to preserve the high content of protein and gluten in the seeds of the offspring. In order to create new forms of spelt, strong and valuable initial forms of grain quality should be involved in the hybridization system. In the conducted studies, the highest grain quality indicators were recorded in sample 13, which was created with the participation of the high-quality grain of the mild winter wheat variety Panna.

Conclusions

By hybridization of *Triticum spelta* L. × *Triticum aestivum* L. a new sample of spelt wheat with a broad genetic basis was obtained and valuable forms with a high level of manifestation of economic and valuable traits were isolated. By interspecific hybridization, new genetic sources of traits deficient for breeding have been identified. They have a great practical importance for further breeding and genetic improvement of spelt, as they can enrich the existing gene pool of the crop. Hybridization of spelt wheat with soft wheat helps to solve the current problematic issues of breeding of spelt, in particular, reducing of plant height, creation of forms with free grain threshing from the ear and select constant, short-stem genotypes with high yield and grain quality.

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