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Morphological diversity, productivity, and grain quality of wheat morphotypes obtained by *Triticum aestivum* × *Triticum spelta* hybridization

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Spike shape and morphology in wheat are key phenotypic traits determining the potential grain set per spike and influencing yield. Hybridization between common wheat and spelt generated a wide range of new forms differing in morphobiological traits, particularly in spike architecture. Determining productivity indicators of different wheat morphotypes based on spike shape remains an important approach for identifying genotypes that combine desirable morphological characteristics with high agronomic performance. In this context, the study of variation among morphotypes contributes to a better understanding of the relationship between spike architecture and yield formation. In this study, wheat samples were classified into distinct morphotypes according to spike morphology, and their productivity and grain quality parameters were comprehensively analyzed. Comparative evaluation of morphotypes revealed significant differences in yield components, grain weight per spike, protein content, and gluten content, allowing for the assessment of their breeding value and potential use in selection programs. Based on spike morphology, the obtained genetic diversity was classified into six morphotypes: spelts, speltoids, forms with a typical common wheat spike, squareheads, subcompactoids, and compactoids. It was established that common wheat and squareheads significantly outperformed other morphotypes: Their yield was on average 42–51% higher than that of speltoids and spelts and about 67% higher than that of subcompactoids and compactoids. A similar trend was observed for grain weight per spike, common wheat and squareheads outperformed speltoids by ~14%, spelts by ~19%, and subcompactoids and compactoids by ~34%. By contrast, the ranking by grain protein and gluten content was reversed: Spelts exhibited the highest values (around 19–20% protein and 42–44% gluten), followed by speltoids (about 16–17% and 35–38%), while common wheat and squareheads occupied an intermediate position (approximately 14.5–15.5% and 32–34%), and compactoids and subcompactoids showed the lowest levels (about 14–15% and 31–33%). The analysis of morphological diversity, productivity, and grain quality in wheat morphotypes derived from *Triticum aestivum* × *Triticum spelta* hybridization is important for breeding and genetic studies, enabling assessment of breeding value and identification of genotypes with optimal spike architecture and stable expression of economically valuable traits. This approach provides a basis for differentiating morphotypes according to yield components and grain quality parameters, including protein and gluten content. The revealed variability among morphotypes reflects the effectiveness of interspecific hybridization in generating genetically diverse material for further selection.

Keywords: spike morphology; sample; marker trait; ear density; ear length; productivity.

Introduction

Wheat is a strategically important crop, providing food security and serving as a raw material for various industries. Its breeding value largely depends on the genetic diversity of the parental material, which determines the potential for improving yield, grain quality, and stress resilience. Hybridization with spelt (*Triticum spelta* L.) offers a valuable opportunity to broaden the genetic base by introducing novel alleles for traits such as spike morphology, grain quality, and adaptability. Such crosses also result in a wide morphogenetic process in the progeny and segregation in spike morphology, manifested in significant variability in spike length, density, and shape. This allows the identification of different morphotypes with unique trait combinations that can be used for the targeted selection of promising genotypes in breeding programs. Genetic variability of wheat in terms of spike morphology is an important indicator of its genetic potential and breeding value. Spike shape, size, and other parameters directly influence crop productivity (Guo et al., 2018; Liu et al., 2024). Differences in inflorescence morphology are genetically determined and may be expressed through spike length, density, number of spikelets and grains, as well as the size and shape of glumes, etc. (Ji et al., 2025). Different wheat spike morphotypes can be considered independent genetic groups with clearly expressed specialization, enabling the development of source material in accordance with specific breeding objectives. The combination of morphotypes with contrasting levels of productivity and grain quality in the breeding process creates prerequisites for expanding genetic variability and increasing selection efficiency, particularly at the initial stages of breeding.

Determining productivity indicators of wheat samples with different spike architecture is an effective approach for assessing genetic diversity and evaluating breeding value, as it enables the establishment of relationships between spike morphological traits and plant productivity and the identification of morphotypes with enhanced breeding value (Zhai et al., 2016; Halder et al., 2023). In a study of wheat cultivar collections for variation in spike morphological traits, Shen et al. (2025) found that spike shape and density are closely correlated with yield and thousand-kernel weight. Sun et al. (2023) reported that genetic variation in spike shape determines productivity potential and cultivar adaptability under different growing conditions. Ji et al. (2025) noted that spike length and grain set per spike are key traits for selecting promising genotypes and substantiated the need to analyze relationships between spike morphological parameters and productivity indicators to identify valuable genotypes. Guo et al. (2018) analyzed the relationship between spike morphological traits and wheat yield, establishing that the number of spikelets per spike, spike length, and density significantly affect yield. Based on spike morphological characteristics, approaches have been proposed for yield prediction and targeted genotype selection in breeding programs. Shen et al. (2025) demonstrated that spike shape and compactness are stable phenotypic traits suitable for classification and morphotyping of genotypes and for identifying breeding-valuable forms with optimal spike structure.

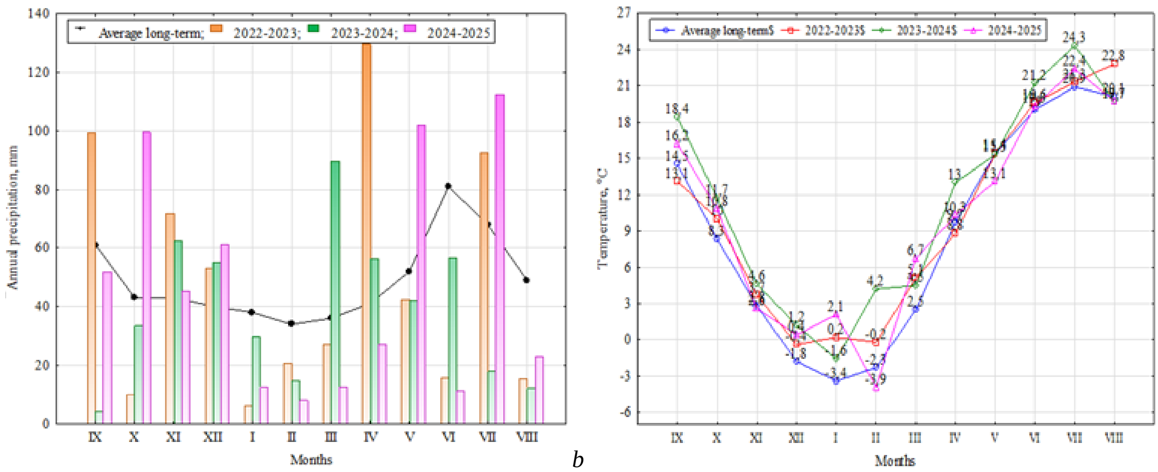
At Uman National University, hybridization of *Triticum aestivum* L. × *Triticum spelta* L. resulted in the development of a collection of wheat samples differing in the number of valuable breeding, agronomic, and marker traits, including spike morphology (Diordiieva et al., 2022). Along with typical inflorescence forms of common wheat and spelt, intermediate forms relative to the parental components were observed, as well as genotypes with different patterns of spike density, including compactness at the spike apex (squareheads), from the apex to the middle of the spike (subcompactoids), and along the entire spike (compactoids). Comparative analysis of different wheat morphotypes based on spike shape makes it possible to determine the target use of each morphotype in breeding and to identify promising genotypes. The objective of the study was to analyze productivity indicators of different wheat morphotypes based on spike shape and to determine their breeding value.

Materials and methods

Soil and weather conditions. 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 Oblast, the zone of the Right Bank Forest-Steppe of Ukraine during 2022–2025 (Fig. 1).

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 ºC. Significant climatic variability was observed over the research years in its territory (Fig. 2). The most favorable weather conditions for winter wheat cultivation were recorded in 2022–2023, during which an optimal amount of precipitation (583.5 mm) with a uniform distribution was observed, along with an average air temperature of 9.9 °C. The greatest precipitation deficit (–96.3 mm relative to the norm) and the highest average annual temperature (11.8 °C) were recorded in the 2023–2024 agricultural years.

Fig. 1. Experimental breeding plots of *Triticum aestivum* × *Triticum spelta* hybridization



a *b*

Fig. 2. Weather conditions during the study (2022–2025) according to data from the Uman weather station: *a* – average monthly precipitation during the study period; *b* – average monthly air temperature

At Uman National University of Horticulture, the soils were classified as podzolized, heavy loam chernozems with low humus content. The arable layer contains a relatively low amount of humus (3.31%) and is characterized by a cloddy-dusty structure. In terms of the content of available (mobile) forms of phosphorus and potassium, the soil is classified as moderately supplied (80–130 mg/kg of soil). It has a neutral pH reaction (6.5–6.7) and is characterized by low capillary rise capacity. The soil is characterized by medium to increased availability of mobile forms of mineral nutrients: The content of mineral nitrogen (NO_3^- + NH_4^+) is 10–25 mg/kg of soil, mobile phosphorus (P_2O_5 according to Chirikov) accounts for 122 mg/kg, and exchangeable potassium (K_2O according to Chirikov) accounts for 135 mg/kg.

Plant material. The object of the study consisted of $F_{5–7}$ collection accessions of soft winter wheat with different spike morphology, developed at the Department of Genetics, Plant Breeding, and Biotechnology of Uman National University through reciprocal crosses between the high-yielding varieties of soft winter wheat (Favoritka, Smuhlianka, Zolotokolosa, Lehenda Myronivska, Panna, Bohdana, Lisova Pisnia) and the varieties of winter spelt wheat (Zoria Ukrainy and Europa). Hybridization was carried out by manually emasculating the flowers of the maternal plant and subsequently conducting forced pollination with the pollen of the parental form by the limited freedom method under a parchment covering. In the obtained progeny, starting from the second generation, a wide range of morphogenetic variation and segregation for a number of traits were observed. In F_5 generation, based on spike morphology, the genetic diversity was classified into six morphotypes: spelts, speltoids, samples with a typical common wheat spike, squareheads, subcompactoids, and compactoids (Diordiieva, 2022). Within each group, five of the best, stable, and uniform samples ($F_{5–7}$) were selected and analyzed for the expression level of economically valuable traits.

Research methods. In the studies, the generally accepted technology of growing winter wheat 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 a plant density of 4.5 million units per hectar. All phenological observations and analysis of parameters of crop structure 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) and *The Methodology for Conducting the Qualification Examination of Plant Varieties for Suitability for Distribution in Ukraine. Methods for Determining Crop Product Quality Indicators*. (2023). Plant biometrics (ear length, ear density, number of grains per ear) was determined in 50 plants, selected from each plot in two nonadjacent repetitions. Quality indicators (protein and gluten content) were determined by the infrared spectroscopy method using the Infratec™ Nova device (FOSS Analytical A/S, Hillerød, Denmark). The thousand-kernel weight was determined as the average of two samples of 500 seeds each, multiplied by two. After carrying out all the calculations and analyses, the grain was threshed and the yield was determined.

Statistical analysis of the research data was performed using Statistica 12 software (StatSoft, Inc., Tulsa, OK, USA, 2012). Results are expressed as the mean values of five replications and graphical visualization using boxplot analysis. The differences between samples were determined using Tukey's test, where the differences were considered significant at $P < 0.05$.

Results

Considering spike morphology, the entire developed genetic diversity of samples was classified into six morphotypes: spelts (Fig. 3a), speltoids (Fig. 3b), common wheat (Fig. 3c), squareheads (Fig. 3d), subcompactoids (Fig. 3e), and compactoids (Fig. 3f).

Fig. 3. Wheat morphotypes based on spike shape:
a – spelts; *b* – speltoids; *c* – forms with a typical common wheat spike; *d* – squareheads; *e* – subcompactoids; *f* – compactoids

The classification of the developed wheat samples into morphotypes was based on the traits "spike length" and "spike density" (Table 1).

Table 1
Characteristics of wheat collection sample morphotypes based on spike shape

Morphotype	Characteristic
Spelts	long (>15 cm), loose (<16 spikelets/10 cm) spike with coarse glumes and difficult threshing of grain
Speltoids	elongated (12–15 cm), loose to medium-density spike with low grain threshing quality
Forms with a typical common wheat spike	spike medium density (17–22 spikelets/10 cm) and lenght (8–12 cm) with typical glumes and free threshing grain
Squareheads	spike with a compacted upper part. Spike lenght 8–12 cm, density 17–22, 23–28 spikelets/10 cm. Grain is free-threshing
Subcompactoids	shortebed spike (6–8 cm) with a compacted upper and middle part
Compactoids	short (< 6 cm), very dense (> 28 spikelets/10 cm) spike

Comparative analysis of different wheat morphotypes based on spike shape revealed that the longest spikes (14.8–16.1 cm) were observed in spelt morphotype samples. Samples of the common wheat morphotype were significantly shorter than spelt, with the spike length ranging 10.0–11.2 cm. Speltoids, occupying an intermediate position between spelts and common wheat, had the spike length of 13.5–14.9 cm. They were significantly longer than common wheat morphotype samples but considerably shorter than the spelt spikes. In squareheads, the spike length ranged from 10.5 to 11.5 cm, which was comparable to common wheat. The shortest spikes were recorded in subcompactoids (6.2–8.2 cm) and compactoids (5.0–6.5 cm), significantly shorter than all other morphotypes.

Regarding spike density, the analyzed morphotypes ranged from loose (14.5–15.9 spikelets/10 cm of spike rachis) in spelt samples to very dense (31.5–38.2 spikelets/10 cm) in compactoids (Fig. 4a). Spike density in samples with a typical common wheat spike (21.6–23.4 spikelets/10 cm) and squareheads (21.7–23.8 spikelets/10 cm) did not differ significantly. Speltoid forms were significantly less dense (16.3–18.3 spikelets/10 cm) but considerably denser than spelt samples.

The highest grain set per spike was recorded in common wheat morphotype samples (45–50 grains) and squareheads (45–48 grains) (Fig. 4b). Other morphotypes had significantly fewer grains per spike. Compactoid samples showed a notably lower grain weight per spike (0.92–1.05 g) and thousand-kernel weight (37.5–39.5 g) compared with other samples. The highest grain weight per spike was observed in common wheat (1.30–1.46 g) and squarehead (1.31–1.43 g) morphotypes (Fig. 4c). Speltoids (1.18–1.28 g), spelts (1.08–1.22 g), and subcompactoids (1.03–1.21 g) had significantly lower grain weight per spike. Subcompactoids and compactoids were the lowest for this trait.

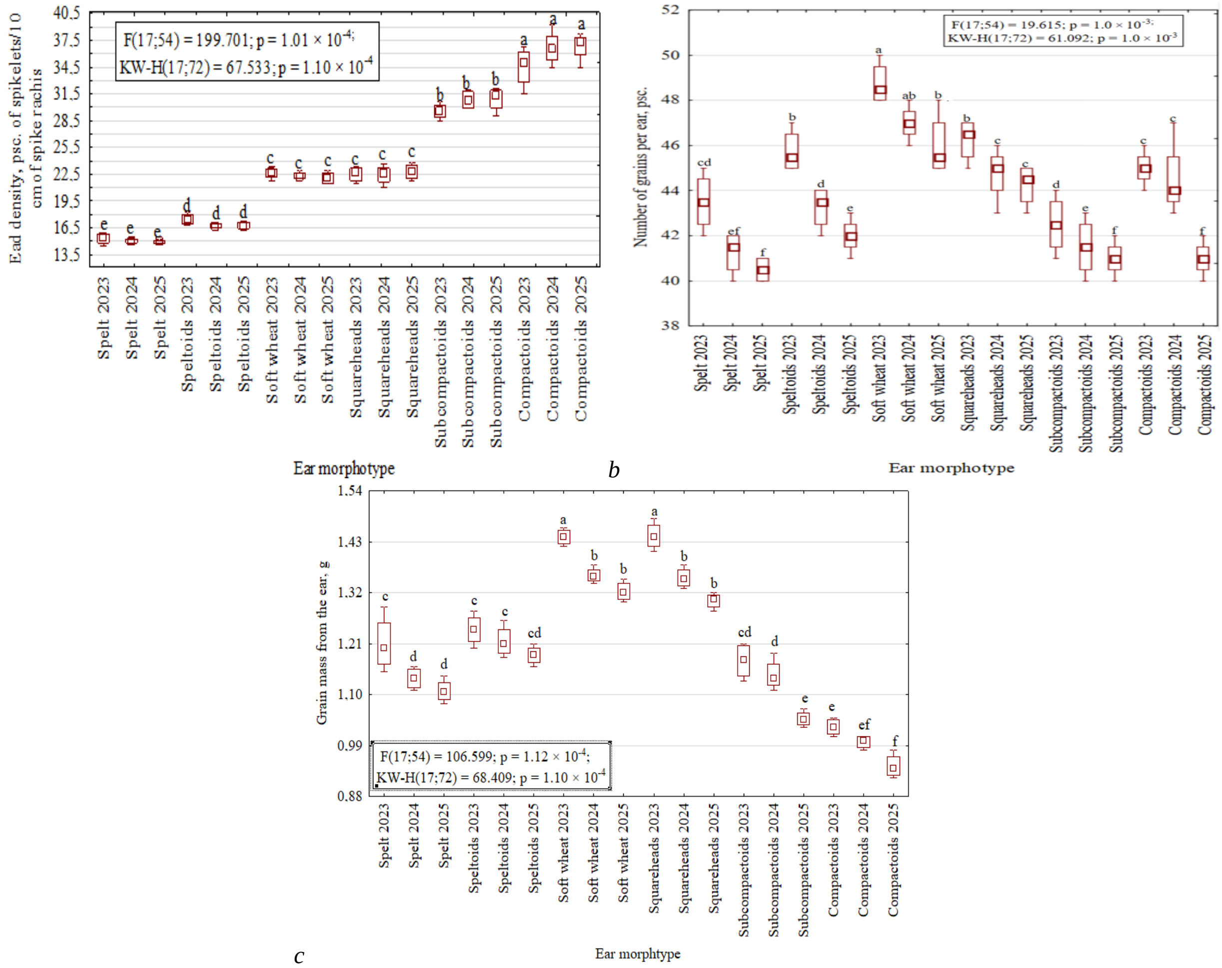


Fig. 4. Spike parameters of different wheat morphotypes, 2023–2025: *a* – spike density, spikelets/10 cm of spike rachis; *b* – number of grains per spike; *c* – grain weight per spike, g; different letters above boxes indicate statistically significant differences among means according to Tukey's HSD test ($P < 0.05$); small square – median value; upper and lower boundaries of the box – 25th and 75th percentiles; vertical lines (whiskers) – range of non-outlier values; n = 5

Spelts exceeded all studied morphotypes in grain gluten content (42.8–44.2%) (Fig. 5a). Speltoids were characterized by the grain gluten content of 35.3–37.8%, which was significantly lower than that of spelts but significantly higher than that of the other morphotypes. Samples of common wheat (31.8–33.2%), squareheads (31.6–34.1%), subcompactoids (31.5–32.8%), and compactoids (31.8–33.1%) did not differ significantly in grain gluten content. A similar trend was observed for grain protein content, which was highest in spelt (19.1–20.1%) and speltoid (15.9–17.2%) morphotypes (Fig. 4b). Samples of common wheat (47.0–48.5 g), squareheads (46.5–47.8 g), spelts (46.5–48.6 g), and speltoids (46.2–47.8 g) did not differ significantly in thousand-kernel weight (Fig. 5c).

On average, over 2023–2025, the highest yields were recorded in common wheat and squarehead morphotypes, measuring 6.21 and 6.19 t/ha, respectively, significantly exceeding spelt yields by 2.09–2.11 t/ha, speltoids by 1.84–1.85 t/ha, subcompactoids by 2.19–2.21 t/ha, and compactoids by 2.72–2.73 t/ha (Fig. 4d). No significant differences in yield were found between spelt (3.92–4.35 t/ha) and speltoid (4.15–4.60 t/ha) morphotypes, nor between subcompactoids (3.80–4.15 t/ha) and compactoids (3.30–3.61 t/ha).

Summarizing the obtained research results, wheat morphotypes classified by spike shape are arranged in the following order according to yield and grain weight per spike: common wheat (5.94–6.51 t/ha, 1.30–1.46 g) ≈ squareheads (5.95–6.42 t/ha, 1.28–1.48 g) > speltoids (4.15–4.60 t/ha, 1.16–1.28 g) > spelt (3.92–4.35 t/ha, 1.11–1.22 g) > subcompactoids (3.80–4.15 t/ha, 1.03–1.15 g) > compacttoids (3.30–3.84 t/ha, 0.92–1.05 g). The arrangement of wheat morphotypes according to grain protein and gluten content is as follows: spelt (19.1–20.0%, 42.1–44.0%) > speltoids (15.9–17.2%, 35.3–37.8%) > common wheat (14.5–15.1%, 31.8–33.2%) ≈ squareheads (14.4–15.5%, 31.6–34.1%) > compactoids (14.5–15.0%, 31.8–33.0%) > subcompactoids (14.3–14.8%, 31.5–32.6%).

Discussion

It is well known that among all wheat species, spelt is distinguished by the longest spikes (Liu et al., 2018; Biel et al., 2021). Hybridization of spelt with other species, particularly common wheat, results in progeny with considerable variability in spike length and density, which is associated with the interaction of different genetic systems controlling these traits in the parental species (Hospodarenko et al., 2016; Diordiieva et al., 2024). The formation of spike architecture is the result of the interaction between genetic factors and environmental conditions, including temperature regime, photoperiod, and the level of mineral nutrition. Changes in spike structure can significantly affect such parameters as the number of grains per spike and grain weight, and consequently, overall yield (Wolde & Schnurbusch, 2019; Luo et al, 2023; Ji et al, 2025).

The main factor in the formation of the speltoid type of wheat spike is the Q/q gene, located on the long arm of chromosome 5A. The q-5D and q-5B genes are believed to play a role in suppressing the speltoid trait (Simons et al, 2006; Sormacheva et al., 2015; Curzon et al., 2024). This does not diminish the importance of regulatory genes, as a single mutation in their sequence can lead to significant phenotypic changes (Sichkar et al., 2016). The appearance of squareheaded spike forms among descendants is explained by the interaction of recessive alleles of the C/c gene, causing shortening of the spike, spikelet glumes, and grains, along with the influence of the spike-extender genes L1/l1 and L2/l2. The squarehead trait can have different genetic bases, including polysomy, chromosomal aberrations, or gene mutations. These mutations may be monogenic and recessive, dominant, or dominant with recessive epistasis (Johnson et al., 2008). Squarehead wheat forms have high breeding value due to the combination of optimal spike density and high grain set, which ensures stable yield formation even under varying growing conditions. These forms often exhibit increased adaptability to abiotic stresses, making them promising for use in breeding programs aimed at enhancing productivity and improving plant architecture.

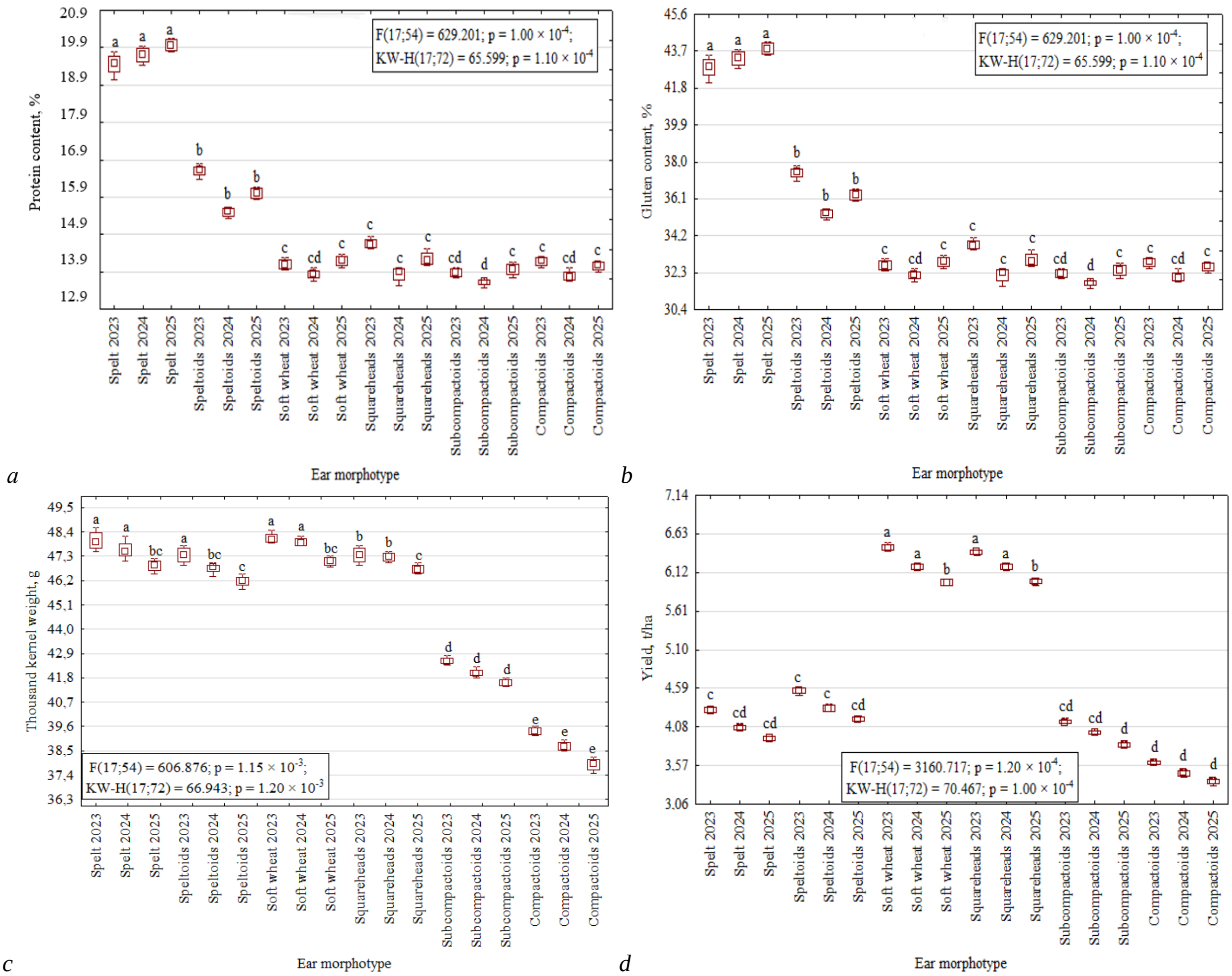


Fig. 5. Grain yield and quality of different wheat morphotypes based on spike shape, 2023–2025: *a* – grain protein content, %; *b* – grain gluten content, %; *c* – thousand-kernel weight, g; *d* – yield, t/ha; see Figure 4

The increased spike density in wheat samples with compactoid and subcompactoid spike forms is due to shortened internodes of the spike rachis, resulting from genetically determined changes in growth processes. This leads to a more compact arrangement of spikelets without significantly reducing their number (Zhou et al., 2021; Ji et al., 2025). Spike morphology, particularly density, is influenced by the C/c gene, where its recessive state reduces spike, glume, and grain length. The spike-extender genes L1/l1 and L2/l2 promote elongation. In hexaploid wheat, the presence of recessive alleles for all these genes produces a short, dense, mace-shaped spike of the squarehead type. In the absence of spike-extender genes, common wheat forms a short, dense spike, and develops a square-headed or club-shaped spike (Hospodarenko et al., 2016; Sichkar et al., 2016). Such forms of wheat have breeding value for improving plant architecture and increasing spike productivity. Higher spike density results in a greater concentration of spikelets and grains per unit length of the spike rachis, creating conditions for increased grain weight per spike and realization of high productivity potential.

Spike compactness is often accompanied by shorter stems, an important factor in lodging resistance (Liu et al., 2022; Ji et al., 2025). In addition, compactoid forms exhibit enhanced adaptability to adverse abiotic factors, which contributes to yield stability (Frantova et al., 2022; Wang et al., 2023). The clear phenotypic expression and stability of spike density allow it to be used as a morphological marker in breeding programs for analyzing hybrid progeny. Although compactoid samples had high grain set per spike, the increased number of grains per unit length of the spike rachis led to spatial restricttions in grain development, resulting in small and deformed seeds.

The predominance of common wheat and squarehead morphotypes in terms of yield is due to an optimal combination of yield structure elements, namely, optimal spike density and high spikelet fertility. Speltoids combine medium spike density with moderate grain weight per spike. Spelts, with low spike density and grain set, do not exhibit high productivity. Subcompactoids show increased spike density, which is accompanied by reduced grain weight per spike due to spatial constraints on grain development and lower filling efficiency. Compactoids, with excessive spike density, produce small and deformed grains, resulting in low yield.

High grain protein content in spelt and speltoid morphotypes is genetically determined, as progeny from spelt × common wheat crosses typically inherit high-quality grain traits from spelt (Takac et al., 2021; Wiwart et al., 2023). This is consistent with the evolutionary status of spelt as a hulled wheat, in which selection pressure was historically directed less toward yield maximization and more toward grain composition, resulting in relatively higher protein concentration (Hospodarenko et al, 2016; Żuk-Gołaszewska et al, 2022). Common wheat and squarehead morphotypes demonstrate elevated contents of grain protein and gluten, along with high yield, which underlines their breeding and agronomic value. Compactoids do not significantly lag behind common wheat and squareheads in grain quality, and when combined with high spike density and potential productivity, this supports their suitability for inclusion in breeding programs. Their inclusion in hybridization schemes may facilitate the development of new genotypes that effectively combine high productivity with improved grain quality, particularly under conditions where both traits are critically important (Konopatskaia et al, 2017).

Conclusions

Hybridization of *Triticum aestivum* L. × *Triticum spelta* L. resulted in a collection of wheat samples representing different morphotypes, which differ in a range of valuable agronomic and marker traits. The morphotypes were ranked based on spike morphology and productivity traits. The study confirmed the usefulness of morphotyping by spike shape for a comprehensive assessment of the breeding value of wheat samples, as different morphotypes significantly differ in productivity parameters. It was established that common wheat and squarehead morphotypes combine high yield with elevated contents of grain protein and gluten, while spelt and speltoid morphotypes are characterized by high grain quality and can serve as valuable breeding material. Compactoid and subcompactoid morphotypes can be utilized to improve plant architecture and increase spike productivity.

Further research in this direction will help refine the criteria for selecting promising wheat morphotypes and using them as parental material for developing high-yielding cultivars.

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The authors declare no conflict of interest.

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