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BIOLOGICAL PROPERTIES OF SPELT WHEAT AND PROSPECTS OF ITS USE IN BREEDING

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Spelt wheat (*Triticum aestivum* ssp. *spelta* (L.) Thell.) is a type of hulled wheat whose genome is the same as that of hexaploid common wheat (*T. aestivum* L.) and is characterized by many valuable properties, including plant resistance to pathogens, better adaptability to adverse environmental factors, increased protein content in the grain, and nutritional value of the grain. In recent years, the popularity and use of spelt in the world, and in Ukraine in particular, has been steadily growing, which is associated with the development of organic farming, as well as the need for high-quality food products provided by this crop. In this regard, the purpose of this review was to present the current state of research into the biological properties of spelt wheat, as well as the prospects for its use in breeding. The current hypotheses of the origin of this crop, its distribution in the world and Ukraine, as well as the biological characteristics of this cereal are briefly considered. The genetic features of spelt are highlighted in detail, in particular the genes of morphological traits, vernalization and photoperiod, the variability of waxy genes. The polymorphism in the genes of storage proteins and the prevalence of their alleles, which can be used as marker systems and a source of enriching the common wheat gene pool, are described. The modern data on the quality of spelt grain, including its physical properties, chemical composition, functional-technological and baking properties of flour are presented. The physiological effect of spelt consumption is highlighted. This cereal is considered as a source of useful genes for common wheat breeding. The information on modern strategies and new scientific directions of genetic improvement of this crop is presented.

Keywords: *Triticum spelta*, origin, distribution, biological properties, genetic features, grain quality, use in breeding.

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INTRODUCTION

Spelt wheat (*Triticum aestivum* ssp. *spelta* (L.) Thell.) is a type of hulled wheat, whose genome, AABBDD, is the same as that of the hexaploid common wheat (*T. aestivum* L.), has the forms of spring and winter type of development. The conducted analysis of spelt genotypes demonstrated its high rate of genetic diversity (Bertin et al., 2004); it is characterized by polymorphic distribution of repeated sequences in chromosomes (Gorieva-Duba et al., 2018); it has considerable differences in central zones (centAHG) of chromosomes 1A, 5B, and 7B, as compared to common wheat which demonstrates evolutionary chromosomal translocations and restructuring (Wang et al., 2024). Some researchers deem *T. spelta* to be the oldest hexaploid, from which other species originated, including common wheat (Lechterbeck, Kerig, 2024). The archeological data indicate the existence of spelt about 7000 BC in Iraq which corresponds to the Neolithic Age (Kohler-Schneider, Caneppele, 2009).

Spelt attracts the breeders' attention due to its valuable traits, which common wheat does not have, namely, plant resistance to pathogens, better adaptability to unfavorable environmental factors, increased protein content in kernel, nutritional value of kernel

(Chrpova et al., 2021; Diordiieva et al., 2024). It has such biological advantages as high tillering coefficient, easy cultivation conditions, high vitreousness of kernel which does not shatter and is not damaged by birds and insects, tolerance to excessive moisture, relatively early maturity, cold and winter resistance of plants (Zvedenyuk, 2013). Even the hull, closely covering the spelt kernel, plays a positive role in protecting grain from the accumulation of chemicals and mycotoxins, harmful for health (Salarov, Filipčhev, 2020). From the agronomical standpoint, spelt uses nutrients more efficiently than wheat thus requiring a smaller amount of pesticides, herbicides and fertilizers and does not need seed treatment prior to sowing due to the presence of hulls (Frakolaki et al., 2018). It is a natural wild wheat which reacts to climate change and deterioration of soil fertility less than modern wheat cultivars (Salarov, Filipčhev, 2020).

There are enough experimental data which demonstrate that nutritional characteristics of spelt kernel are better than those of modern cultivars of common wheat (Dinu et al., 2018). Spelt is notable for high protein content in kernel (8.0–10.0% more than in *Triticum aestivum* L., 3.0–8.0% more than in *T. sphaerococum* Persiv.), the availability of nutrients which are not present in products of animal origin (Geisslitz et al., 2019; Kraska et al., 2020; Huertas-Garcia et al., 2023; Porto et al., 2025). Spelt kernel contains more valuable lipids and minerals, including higher levels of Fe, Zn, Cu, Mg, and P, more vitamins and soluble dietary fiber (Rybalka et al., 2024; Valsalan et al., 2025). It has 8–10 times higher content of resistant starch (Escarnot et al., 2010), higher content of such antioxidants as folates, alkyl resorcinols, and phytosterols (Hammed, Simsek, 2014), has more selenium in kernel than modern wheat (Filipčev et al., 2013), contains less phytic acid which chelates minerals, and thus has not only high content of minerals but also is remarkable for their higher accessibility (Kohajdová, Karovičová, 2008; Longin et al., 2023). At the same time, spelt contains less carbohydrates and fiber than common wheat (Boukid et al., 2018, Rodríguez-Quijano et al., 2019). In addition, spelt grain flour has unique taste qualities, and baked bread has a long period of non-hardening (Tverdokhlib et al., 2013).

In recent years, the popularity and use of spelt in the world, and in Ukraine in particular, has been steadily growing, which is associated with the development of organic farming, as well as the need for high-quality food products provided by this crop (Huertas-Garcia et al., 2023; Rybalka et al., 2024). Spelt grain is used to produce flour, bran, cereal, pasta, bread, cookies, waffles, coffee, beer, pure alcohol, vodka. Another specificity of spelt is the possiblity to use grain in different ripening phases. “Green grain” — spelt grain, collected from the wax phase and after collection, dried and threshed, is used in soups, cutlets, sauces, puddings, yogurt additives, etc. (Kraska et al., 2020).

Despite high potential possibilities, spelt has not been widely adopted to industrial production yet. Its widespread adoption is hindered by low yields and a number of morphological characteristics that are disadvantageous for production, namely the difficulty of threshing the grain due to its tight enclosure by strong hull — the “filminess” and brittleness of the spike axis (Morgun et al., 2016). Other drawbacks include a relatively long growing season, poor drought tolerance, and susceptibility to powdery mildew, brown rust, yellow rust, and smut (Shelepov et al., 2013). Overall, in terms of yield and suitability for modern cultivation and processing technologies, spelt cannot currently compete with common and durum wheat varieties. However, through genetic improvement, enrichment of the gene pool, and increased efficiency of its breeding, it is possible to eliminate the shortcomings of this crop while preserving its valuable properties. Beneficial characteristics of this crop are the object of diverse scientific studies (Alvarez, 2021; Rybalka et al., 2024, Diordiieva et al., 2024; Wang et al., 2024; Morgun et al., 2025). Therefore, the purpose of this review was to present the current state of research into the biological properties of spelt wheat, as well as the prospects for its use in breeding.

Spelt origin. In terms of origin, spelt is divided into two subtypes: European spelt and Asian spelt (Alvarez, 2021). European spelt is subdivided into two ecological and morphological groups: western European (German) and Asturian (Spanish, Iberian). Winter forms prevail in the composition of the first group, and spring forms — in the second one (Alvarez, Guzmán, 2013). These groups differ in specific traits of the spike. Western European forms are mainly presented by awnless spikes, while Asturian forms always have awned spikes. Asian spelt is characterized by the presence of both winter and spring forms (Faris, 2014).

At present, the issue of spelt origin has not been elucidated completely yet. Some authors adhere to the hypothesis of the Asian origin (Zohary, Hopf, 2000), who distinguish Asian spelt as the foremother of common wheat. It is believed that Asian subtypes of this species could have been obtained due to spontaneous hydridization of *Triticum turgidum* ssp. *dicoccon* and *Aegilops tauschii* ssp. *strangulata*, which then gave rise to hexaploid species of hull-less species, including *Triticum aestivum* L. (Faris, 2014). The advocates of the hypothesis about the European origin of spelt believe that it was the product of hybridization of tetraploid wheat *T. dicoccum* (AABB) and *Ae. squarossa* (DD) (Dvorak et al., 2006). Modern molecular and genetic studies prove that the European *T. spelta* originated as a result of hybridization of hull-less wheat and hulled emmer (Dvorak et al., 2012; Sousa et al., 2021; Alvarez, 2021; Wang et al., 2024). Considering significant differences in the composition between the European and Asian subtypes of spelt, the absence of archaeological remains of spelt on the way from Asia to Europe, the opinion about independent origin of subtypes of this wheat is currently prevalent (Seabra et al., 2018; Peña-Chocarro et al., 2019; Lechterbeck, Kerig, 2024).

Blatter et al. (Blatter et al., 2004) analyzed the genes of highly molecular subunits of glutenins *Glu-B1-1* and *Glu-A1-2* in spelt subtypes and demonstrated that in both genes, the group of alleles was clustered in a separate, so called beta-subclade which confirms the independent origin of European and Asian spelt. It is assumed that European spelt obtained alleles of highly molecular subunits of glutenins from the initial tetraploid wheat. The research on the composition of subunits of glutenins of European spelt and related tetraploid and hexaploid species of *Triticum* genus confirms the hypothesis about the secondary origin of European spelt (Yan et al., 2003).

The use of artificial neural networks allowed confirming the division of European spelts into two groups — Spanish and European proper which includes the samples from the countries of western, central, and eastern Europe (Babenko et al., 2018). It is believed that central European spelt originated due to hybridization of free-threshing hexaploid wheat and hulled tetraploid einkorn (Dvorak et al., 2012). It explains why European spelt genetically differs from Asian spelt — it is not the immediate ancestor of common wheat, on the contrary, it is its later “relative”. In addition, a comprehensive molecular and genetic analysis demonstrates two independent pathways for the occurrence of central European and Iberian spelt (Abrouk et al., 2021). High incidence of allelic variant of vernalization gene *Vrn-D1s*, found in the Spanish spelt collection, and the rarity of this allele in other European samples confirm the hypothesis that Iberian spelt is a separate geographical group, which differs from the rest of European spelt (Curzon et al., 2021; Alvarez, 2021).

At present, the most probable hypothesis is the polyphyletic origin of spelt. It envisages that Asian spelt first appeared on the Caspian coast of Iran and became the ancestor for common wheat, and European spelt is the product of hybridization of hexaploid and tetraploid wheat (Lechterbeck, Kerig, 2024).

Spelt distribution. The archeological data indicate the existence of spelt in about 6000 BC in Iraq which corresponds to the Neolithic Age (Kislev, 1984). Pure spelt fields were found in Iran, some areas of Central Asia and Transcaucasia (Azerbaijan, Armenia, Tajikistan, Turkmenistan). As for European spelt, the data indicate its occurrence in central Europe in Early Bronze (Lechterbeck, Kerig, 2024). Its oldest findings are dated 2000 BC and are found in the territory of the Swiss and Italian Alps. Later, spelt plants were found in Germany, Czech Republic, Slovakia, and southern Italy. In Ukraine’s territory, spelt cultivation is associated with the population of the Bug-Dniester culture, dated about 5,000–6,000 BC (Shelepov et al., 2013).

For many centuries, spelt was a dominating species in Europe, grown in the regions with cold climate: Scandinavia, Germany, Switzerland, Poland. The area of its distribution is related to mountaineous districts, where spelt was spread in the regions of the north-western Alps. A special group of spelt remained in Asturia (Spain) (Alvarez, 2021). Till 1960-s, spelt was cultivated in the Ukrainian and Slovak Carpathians (Shelepov et al., 2013). At the beginning of the last century, spelt quickly transformed into the “island crop”, cultivated in the limited territory of the areas with traditional lifestyle. Spelt was ultimately pushed aside by modern cultivars of common wheat due to the fact that they had higher yields and allowed for saving resources, used for grain threshing.

Considerable volumes of spelt cultivation were resumed only at the end of the 20th century. It is related to the development of organic farming and the need for high nutritional value of kernel, ensured by this crop. At present, spelt is mostly cultivated at organic farms of western Europe, first of all, in German-speaking countries, and in Belgium, Italy, France, and since 1990-s — in Czech Republic, Poland, Hungary, and Slovakia. Now it is sown in mountaineous districts of Switzerland, Austria, Germany (the Alps), Spain, northern Caucasus, India, Ethiopia, and Morocco. It was transferred from the category of just low-spread botanic species into the rank of niche crops, and is ranked the third among wheats in terms of sown areas (Babenko et al., 2018). It is grown in Germany (100 thousand ha), Austria (13 thousand ha), Switzerland (5.5 thousand ha) (Alvarez, 2021). As of 2023, the Common Catalogue of Varieties of Agricultural Plant Species of the European Union was introduced 85 species of spelt wheat. However, at present, a small number of species is cultivated for production, and current genetic diversity of this crop is limited by landraces (Diordiieva et al., 2024; Wang et al., 2024).

In Ukraine's territory, spelt fields have been enlarged as well, and agricultural producers mainly cultivate it for export purposes. At first, spelt was brought to Ukraine from Switzerland over 25 years ago by yound farmers, who sowed it in the Vinnytsia and Ternopil regions. Now, this crop is also sown at farms of the Zhytomyr, Chernihiv, Khmelnytskyi, Kyiv, and Cherkasy regions, in the area of several thousand hectares. There aren't many major spelt grain producers in Ukraine; this sector is represented by Svarog Group based on Lotivka Organic LLC (Khmelnytsk region) and Grain Alliance (Kyiv region), LNZ GROUP (Cherkasy region) and Zhyva Nyva LLC (Zhytomyr region) have significant areas under this crop. As of February 2026, the State Register of Plant Varieties Suitable for Distribution in Ukraine lists seven spelt varieties: Zoria Ukrainy, Evropa, Bilberi, Vyshyvanka Bilotserkivska, Evrika, MV Martongold, and Paracelsus. The State Statistics Service does not collect data on spelt wheat cultivation, including it in the common wheat data instead. Overall, the area under cultivation for this crop in Ukraine can be estimated at a total of up to 10,000 hectares across all regions (Zaika, Karpuk, 2023).

Biological characteristics of spelt. Spelt is one of the few cereals that can be grown on stony soil and in harsh climatic conditions (Shelepov et al., 2013). It grows well at an altitude of 1,500 m above sea level, and the higher it is grown in the mountains, the better it performs compared to common wheat. This crop can be sown later than winter wheat, tolerate partial waterlogging, has higher resistance to adverse environmental factors than common wheat, and can be grown without any pesticides (Frakolaki et al., 2018). Moreover, spelt can grow in poorly drained and low-fertility soils, making it a suitable crop for organic farming.

However, modern spelt cultivars intended for lowland cultivation have fairly high soil requirements, similar to those of common wheat, but with a lower nitrogen requirement. Therefore, spelt can be grown in water protection zones without any problems. It grows well on cultivated soils rich in humus and nutrients, as well as on soils with a pH close to neutral (Shelepov et al., 2013). Due to its well-developed root system, it can be used to combat soil erosion. Its tillering coefficient is 2–3 times higher than that of wheat. Spelt is a moisture- and light-loving crop, so its resistance to atmospheric and soil drought is low.

Spelt (120–180 cm) grows taller than common wheat and has long, narrow (15–20 cm) spikes. Spelt spikes are characterized by 3–4 flowers, from which two oblong kernels, tightly enclosed by hull, usually develop. Spelt genotypes have fewer kernels per spikelet compared to common wheat. A characteristic morphological feature of spelt is the separating layer, which forms at the upper end of the axis segment rather than the lower end, which is typically notable for other species with a brittle spike, due to which the segment fuses with the inner surface of the spike along its entire length (Longin et al., 2016). In addition, a characteristic feature of the spikelet hull is often a broad, rectangular upper end with a notch. In wheat morphology, the term "spelt-like" or "speltoid" hull form has even become established.

The hull content of spelt is both a disadvantage and an advantage of the crop. On the one hand, during sowing and germination, the hull protects the grain and then the seedlings from the effects of adverse environmental factors, which promotes the formation of healthy and robust seedlings (Riesen et al., 2008). Unthreshed kernel in hull is well-preserved due to the loose arrangement of the spikelets, which reduces grain overheating. The hull content also provides additional protection against damage by birds and insects (Tverdohlib et al., 2013). On the other hand, it complicates the use of mechanization means during cultivation and harvest processing. A negative trait of the crop is the brittleness of the spikelet as it ripens, which causes yield losses.

Asian and European spelt varieties differ in the morphological structure of the spikelet, which is determined by the genes, controlling it. European spelt varieties, genetically related to common wheat, have a more brittle spike axis (Dvorak et al., 2006). It was shown that in Iran, Tajikistan, Germany, Austria, and Switzerland, red-grained winter spelt varieties predominate, whereas white-grained varieties are much less common in both Asian and European countries. Awned spelt is not found in central European countries, whereas in southern Europe, western, and central Asia, awned spelt accounts for 100%.

It is known that spelt yields on low-nitrogen soils or under stress conditions are higher than those of common wheat, but are significantly lower under intensive cultivation (Sugar et al., 2019). For example, in Israel, the average spelt yield is 3.0–4.0 t/ha (Curzon et al., 2021), in Germany — 3.0–5.0 t/ha (Longin et al., 2023), whereas the average yield of common wheat in these countries reaches 7.0–8.0 t/ha. Spelt yields in Ukraine typically amount to 4–6 t/ha, which is approximately 70–80% of the yield of common wheat (Zaika, Karpuk, 2023). According to Wang et al. (2024), the differences in grain yield among spelt varieties in different environments may result from the activation of different sets of genes in each environment or from different responses of the same genes to changes in environmental conditions.

Genetic specifiticies of spelt. The genetics of spelt has been studied since the second half of the 19th century, as this crop serves as a source of genetic variation for a number of economically valuable traits in cereal breeding (Curzon et al., 2021; Huertas-Garcia et al., 2023). It has been established that several important genetic factors responsible for the differentiation and adaptation of spelt may have been inherited directly from tetraploid ancestors through hybridization, for example, the genes *TaQ-5A*, *TaCOP1-6A*, *TaHY5-like*, *TaPHYA-4B*, and *5A-CentAHG-H2* (Wang et al., 2024). These genes or genomic blocks underlie some key morphological and taxonomic differences between spelt and common wheat, including clingy hulls, grain threshing, and later flowering. They also provide specific resistance to stress factors and diseases, enabling spelt to adapt to harsh climatic conditions.

It was shown that the morphological traits of spelt plants, like those of common wheat, are determined by a small number of genes, and their inheritance is controlled by genes classified as "major morphological" genes, as they exert a significant influence on the plant phenotype. Key morphological characteristics of spelt, such as spike shape, filminess of the grain, and spike rachis brittleness, are controlled by a recessive allele of the *Q* gene with a pleiotropic effect, which belongs to the APETALA2 (AP2)-like transcription factors, and is located on the long arm of chromosome 5A (Greenwood et al., 2017; Curzon et al., 2021). Two key single-nucleotide substitutions distinguish the domesticated Q allele from the wild-type *q* allele: (1) a non-synonymous substitution of G for A in exon 8 near the AP2 domain region, resulting in an amino-acid change from valine to isoleucine (Simons et al., 2006) and (2) a neutral substitution of C for T at the miRNA172 binding site in exon 10 (Debernardi et al., 2017). The *q* allele confers on spelt a noticeably late heading and narrow, pyramidal spikelets with strong hull, which led to the formation of a taxonomically recognized subspecies (Wang et al., 2024). The manifestation of spelt traits depends largely on the interaction of *q* with genes controlling spikelet hull strength and rachis brittleness on other chromosomes. The non-brittle rachis (*Btr1*, *Btr2*) genes, located on the short arm of chromosome 3 in each wheat subgenome, determine the brittleness of the spike at maturity (Zhao et al., 2019). The recessive state of the *C* (Compactum) gene in spelt promotes spike elongation, in contrast to the dominant allele in dwarf wheat varieties,which shortens and compacts the spike (Johnson et al., 2008). In addition, the threshing characteristics of the grain are influenced by the type of kernel glumes, which in spelt is controlled by the dominant allele of the *Tg* (tenacious glumes) gene in a homozygous state, located on the short arm of chromosome 2 of each wheat subgenome (Alvarez, 2021). It is this gene, in combination with the *q* allele, that makes spelt "difficult to thresh." The first gene studied was *Tg-D1*, identified in populations derived from crosses between durum wheat and *Ae. tauschii*, and the non-threshing trait was attributed to the presence of the dominant *Tg-D1* allele (Simonetti et al., 1999). Later, orthologous genes were identified on chromosome 2BS (*Tg-B1*) and on chromosome 2AS (*Tg-A1*) (Dvorak et al., 2012). These data indicate that mutations in the *Tg-A1*, *Tg-B1*, and *Q* genes in common wheat determine the free-threshing trait (Faris, 2014). The presence of *qqTgTg* alleles in any modern breeding material is sufficient to classify it as spelt. This has led to the emergence of two distinct types of spelt: traditional/pure and modern/synthetic (Alvarez, 2021). The latter, derived from crossing common wheat with traditional spelt, has spikelets with a speltoid morphology. Unlike synthetic spelt, traditional spelt is obtained through breeding among its old varieties.

Allelic variations and prevalence of vernalization and photoperiod genes. The *VRN* gene system controls the response of plants to low temperatures, exposure to which is necessary for the induction of flowering (Hyles et al., 2020). The key gene determining the vernalization response in wheat is the MADS box transcription factor VERNALISATION1 (VRN1), which promotes the transition from vegetative to reproductive development (Yan et al., 2003). The presence of one or more dominant alleles of the *VRN* genes leads to the spring type of development, whereas the winter type is determined by their recessive alleles. The main gene controlling wheat sensitivity to day length is PHOTOPERIOD 1 (PPD1), whose loci are located on the short arms of chromosomes 2A, 2B, and 2D (Bentley et al., 2013). It has recently been established that the *TaCRY1a-2A* cryptochrome family gene plays a decisive role in controlling flowering time through photoperiodic regulation of the onset of flowering (Zhao et al., 2022). Most spelt samples also carry a late-flowering allele in the *Vrn1*, *Vrn2*, and *Ppd1* genes (Yan et al., 2003).

Muterko et al. (Muterko et al., 2015) identified a new spelt allele, *Vrn-D1s*, whose emergence is due to the insertion of a DNA transposon into the first intron. These authors found that the *Vrn-D1s* allele was present in three spelt samples from Spain and the United Kingdom. Further studies (Palomino, Cabrera, 2023) showed that the *Vrn-D1s* allele was dominant in the Spanish spelt collection. On the other hand, only one sample carrying this allele was identified in an assessment of a large collection of central European spelt, with the recessive allele *vrn-D1s* being the most frequently detected in the *VRN-D1* locus (Curzon et al., 2021). Spelt samples carrying the *Vrn-D1s* allele were classified as spring types (Muterko et al., 2015). This was indicated by the fact that all samples with this allele headed under long-day conditions without vernalization in both greenhouse and field experiments. Later, other allelic variants were identified in the *VRN1* genes, including a duplication of the *VRN-B1* locus, recently detected in some *T. spelta* samples (Muterko, Salina, 2019).

Palomino and Cabrera (Palomino, Cabrera, 2023) studied a collection of Spanish spelt samples (60 genotypes) using specific DNA markers to assess allelic variation in the *VRN-A1*, *VRN-B1*, *VRN-D1*, and *PPD-D1*, and the effect of their allelic combinations on heading dates. The highest frequency was recorded for the dominant allele *Vrn-D1s*, which was detected in 53 samples (88.3%). The second most common was the dominant allele *Vrn-A1b*, detected in 51 samples (85.0%), followed by the recessive allele *vrn-B1*, identified in 48 samples (80.0%). In the present study, the dominant allele *Vrn-A1a* was not detected in any of the samples examined, although it had previously been identified in spelt genotypes of various origin (Curzon et al., 2021). Only 9 (15.0%) samples carried the recessive allele *vrn-A1*. Regarding the *VRN-B1* gene, the results showed that the recessive allele *vrn-B1* was the most common, present in 80% of the samples studied, followed by the dominant allele *Vrn-B1a* (in 20% of the samples). However, the study did not identify genotypes carrying the *Vrn-B1b* and *Vrn-B1c* alleles.

Based on the maturity date of the samples, most spelt genotypes (91.7%) had a spring development pattern, and only five (8.3%) exhibited a winter development pattern (Palomino, Cabrera, 2023). PCR using specific markers detected the presence of at least one dominant allele of the *VRN1* gene in all spring genotypes, whereas samples carrying a triple recessive allele combination failed to produce spikes under both greenhouse and field conditions. Spelt samples carrying at least one dominant *VRN1* allele (*Vrn-A1b*) headed significantly later than those carrying two (*Vrn-A1b*, *Vrn-D1s*, or *Vrn-B1a*) or three (*Vrn-A1b*, *Vrn-B1a*, *Vrn-D1s*) dominant alleles in both greenhouse and field experiments. The spelt collection samples showed later heading compared to the local spring wheat variety Setenil, which had two dominant alleles, *Vrn-B1a* and *Vrn-D1a*, and the photoperiod-insensitive allele *Ppd-D1a*, whereas all spelt samples carried the photoperiod-sensitive *Ppd-D1b* allele. Screening of *PPD1* gene alleles in spelt germplasm, conducted by other authors (Curzon et al., 2021), also revealed a predominance of the *Ppd-D1b* allele in late-heading spelt genotypes. It has recently been established that the *TaCOP1-6A* gene may be responsible for the late heading date of spelt (Wang et al., 2024).

Polymorphism of storage proteins in *Triticum spelta* L. samples. Polymorphism of storage proteins (gliadins and glutenins) in spelt is a key tool for variety identification, study of genetic diversity, and breeding for grain quality. Among the alleles of gliadins and high-molecular weight glutenin subunits in spelt, both alleles identical to those in common wheat and specific alleles identified only in spelt have been detected (Blahodarova et al., 2023; Spetsov, Daskalova, 2024).

Caballero et al. (Caballero et al., 2004) identified variants of specific regions of the electrophoretic spectrum that may contain gliadins encoded by different loci in 403 Spanish spelt samples. The authors identified 61 spectrum types for ω-gliadins, 44 for γ-gliadins, 19 for β-gliadins, and 15 for α-gliadins. A total of 72 different bands were identified. These bands were grouped into spectral types within each of the four gel zones (ω-, γ-, β-, and α). For example, in the ω-gliadin zone, twenty-two bands were identified, forming 61 spectral types.

Ninieva et al. (Ninieva et al., 2013) analyzed 16 samples of spring and winter spelt of various origins based on grain quality indicators and electrophoretic spectra of storage proteins. Among the samples studied, 6 alleles were identified by the *Gli-B1* locus, 5 alleles by the *Gli-A1* locus, 4 alleles by the *Gli-A3* locus, and 2 each by the *Gli-D1* and *Gli-B5* loci. It was shown that three alleles predominate at the *Gli-A1* locus with approximately equal frequencies: *x*, *f*, and the provisionally designated allele *i+w3*, which has not been described in *T. aestivum*. By the *Gli-B1* locus, the *h* allele was predominant. By the *Gli-D1* locus, the *f* allele was present in almost all samples (93.8%); the other allele, *g*, was detected only in a sample from Tajikistan. Four alleles were detected by the minor *Gli-A3* locus, among which two alleles (designated as 1 and 2) predominated. It was shown that the presence of combinations of individual electrophoretic components of storage proteins is accompanied by the manifestation of grain quality traits: *Gli-A1x*, *Gli-B1h*, *Gli-B5b*, *Gli-B1p* type, and *Gli-B5a* — high protein and gluten content; *Gli-B1h*, *Gli-B5b*, and *Gli-A3-1* — large kernel size; *Glu-A1a*, *Glu-B1d*, and *Glu-D1a* — stable expression of the third group of gluten in terms of quality.

Blahodarova et al. (Blahodarova et al., 2023) conducted a study on eight *T. spelta* samples using the methods of storage protein electrophoresis in acidic PAGE and PCR with allele-specific primers. According to the PCR results, the *Gli-B1*.1 allele, with an amplification fragment length of 369 bp, was detected in *T. spelta* var. *album*, *T. spelta* var. *arduini* and *T. spelta* var. *vulpinum*. Five other varieties of spelt were found to have the *Gli-B1.2* allele with four different polymorphic fragments of amplification of 397–400 bp.

Six different allelic variants of gliadins were identified using the electrophoresis results. The varieties of *T. spelta* var. *album*, *T. spelta* var. *arduini* were found to have the *Gli-B1b* allele, *T. spelta* var. *vulpinum* — *Gli-B1n*. *T. spelta* var. *neglectum* had *Gli-B1f*, *T. spelta* var. *alefeldii* — *Gli-B1h*, *T. spelta* sbsp. *kuckuckianum* and *Tr. spelta* var. *duhamelianum* were found to have alleles, not present in the catalogue, which were designated 1 and 2 respectively.

Kozub et al. (Kozub et al., 2014) analyzed a collection of *T. spelta* samples from the National Center for Plant Genetic Resources of Ukraine, most of which are European spelt varieties, using 8 storage protein loci. Seven alleles were identified in the *Gli-B1* locus, five — in *Gli-A1*, three — in *Gli-A3*, and two each — in the *Gli-D1* and *Gli-B5* loci. Only two alleles were found that had not previously been identified in common wheat: *Gli-B1hs**, *Gli-B1ps**. The *hs** allele is frequently present in spelt samples alongside the *Gli-B5b* allele, which encodes two remarkable ω-gliadins. The presence of the *Gli-B5b* allele is associated with the dark color of the spike hull, which is determined by the *Rg1* gene closely linked to it (with an average recombination rate of 0.6%).

In terms of the loci of high-molecular weight glutenin subunits in spelt, alleles that are also common in common wheat, predominate: *Glu-A1a*, *Glu-B1d*, *Glu-D1a* (Spetsov, Daskalova, 2024). The high-molecular weight and low-molecular weight subunits of glutenins in 270 European spelt, 15 Iranian, and 25 common wheat varieties were studied by An et al. (An et al., 2005). Twenty-two allelic variants were identified in European spelt samples in the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci, including eight new ones (*w*, *be*, *bf*, *bg*, *bh*, *bi*, *bj*, *bp*). In the *Glu-A1* locus, four alleles of high-molecular weight glutenins were identified, with alleles a and c present at frequencies of 84.48% and 12.59%, respectively. Five samples carried allele *b* at a frequency of 0.84%. Eleven alleles were identified in the *Glu-B1* locus, 6 of which were new. Two alleles, *Glu-B1f* (13+16) and *Glu-B1be* (6.1+22.1), were detected at frequencies of 41.48% and 33.7%, respectively. The *Glu-B1f* allele has a positive effect on baking quality and has the same rating as alleles 17+18 and 7+8 in the *Glu-B1* locus. The *Glu-B1f* allele is common in Spanish spelt samples, while the *Glu-B1be* allele, specific to the European spelt group, occurs with high frequency (Kozub et al., 2014). Seven alleles were identified in the *Glu-D1* locus, including the new *Glu-D1bp* (2.1+12). The

Glu-D1a allele (2+12), characterized by a low contribution to gluten quality, was the most common (90%) among the analyzed samples, while the *Glu-D1d* allele, which has the best effect on baking quality, was present in only seven samples (4.07%). The alleles *Glu-D1b*, *Glu-D1c*, and *Glu-D1e* were detected at low frequencies.

Subsequently, new alleles were identified in each of the three loci **(Table 1)**, and these alleles are being intensively studied for their contribution to spelt grain quality. For example, Cao et al. (Cao et al., 2022) identified two new subunits of high-molecular weight glutenins: 1Ax2.1* in *Glu-A1* and 1By19* in the *Glu-B1* locus in samples of European spelt.

Their structural similarities to high-quality x-type subunits have been identified, specifically the ones between 1Ax2.1* and 1Ax1 and 1Ax2*, as well as 1By19* and By16, By9, By8, and By18. The identified specific alleles of storage protein loci of spelt can be used to enrich the common wheat gene pool.

Currently, storage protein genes are used as markers for certain spelt traits. Gliadins, being the most im-

Table 1. The allelic composition of high-molecular weight glutenin loci in spelt samples

Locus	Allele	Subunit	Reference
Glu-A1	*a*	1	An et al., 2005
	b	2*	An et al., 2005
	c	null	An et al., 2005
	v	2.1*	Cao et al., 2022
	w	2.1	An et al., 2005
	y	2	Rodríguez-Quijano et al., 2019
Glu-B1	*a*	7	An et al., 2005
	b	7 + 8	An et al., 2005
	c	7 + 9	An et al., 2005
	d	6 + 8	An et al., 2005
	e	20; 20x + 20y	Spetsov, Daskalova, 2024
	f	13 + 16	An et al., 2005
	w	6* + 8*	Rodríguez-Quijano et al., 2019
	ba	13* + 16	McIntosh et al., 2013
	bb	6 + 18’	McIntosh et al., 2013
	be	6.1 + 22.1	An et al., 2005
	bf	6.1 + null	An et al., 2005
	bg	13* + 19*	An et al., 2005
	bh	13 + 22*	An et al., 2005
	bi	13 + 22.1	An et al., 2005
	bj	14* + 15*	An et al., 2005
	*hs**	hs*	Kozub et al, 2014
		1By19*	Cao et al., 2022
Glu-D1	*a*	2 + 12	An et al., 2005
	b	3 + 12	An et al., 2005
	c	4 + 12	An et al., 2005
	d	5 + 10	An et al., 2005
	e	2 + 10	An et al., 2005
	j	2 + 12*	Dai et al., 2020
	l	null + 12	Jang et al., 2020
	bp	2.1’ + 12	An et al., 2005
	r	2.3 + 12	McIntosh et al., 2013
	am	2 + 12’(12*)	Caballero et al., 2010
	ao	2.4 + 12	McIntosh et al., 2013
	ap	2.5 + 12	Alvarez, 2021

portant gluten proteins, directly influence such an agronomic trait as the quality indicators of grain processing products. It has been shown that certain types of γ- and ω-1,2-gliadins,, which are present in common wheat, are absent in spelt, which allows using these proteins as markers for detecting common wheat admixtures in spelt products (Koenig et al., 2015). Furthermore, these genes may not directly influence the expression of genes for agronomic traits but may mark them due to linked inheritance. Kozub et al. (Kozub et al., 2016) studied the genetic control of dark spikelet hull color in *T. spelta* using gliadins as genetic markers. They demonstrated that the *Gli-A1j** allele is linked to the dark-colored glume allele of the *Rg-A1* locus (*Rg-A1c* or *Rg-A1d*) and may serve as a marker for this trait.

Variability of waxy genes. The enzyme GBSS (Granule-Bound Starch Synthase) is a key enzyme in amylose biosynthesis, and its presence or absence, along with its functionality, determines the final composition and properties of starch (Guzmán, Alvarez, 2016). Reducing or blocking amylose synthesis decreases the share of this polysaccharide in starch granules. Consequently, their type, microstructure, size, thermal properties, and other characteristics change, as does their impact on the baking quality of flour. In the spelt genome, three homologous genes encode enzyme isoforms: *Wx-A1*, *Wx-B1*, and *Wx-D1*, located on the arms of chromosomes 7AS, 4AL, and 7DS, respectively. Mutations in these genes and the emergence of their null alleles lead to the appearance of a wax-like endosperm trait, known as waxy or partially waxy (Guzmán et al., 2022).

A study of spelt waxi genes conducted by Rodriguez-Quijano et al. (Rodriguez-Quijano et al., 1998) using 144 samples from Spain revealed variations in two of the three genes: two variants for *Wx-A1* and three for *Wx-B1*. A spelt collection of 420 samples was later studied, revealing variations in the three *Wx* genes (Guzmán et al., 2010). Three different alleles were identified in the *Wx-B1* locus: *Wx-B1a*, the null allele *Wx-B1b*, and *Wx-B1c'*. The latter two were less common (11.67% and 12.86%, respectively) than *Wx-B1a*. The samples studied showed homogeneity for the *Wx-D1* locus, where 99.52% contained the *Wx-D1a* allele. Two other alleles were also detected in this locus: the null allele *Wx-D1b*, which was present in only one sample, and the previously undescribed *Wx-D1g*. Subsequently, two alleles were detected in the *Wx-A1* locus: *Wx-A1a* and a new functional allele, *Wx-A1g* (Guzmán et al., 2012). The *Wx-A1g* allele, in combination with the null alleles of the *Wx-B1* and *Wx-D1* loci, makes it possible to obtain spelt varieties with an amylose content of more than 1% but less than 20% (Guzmán et al., 2012). The use of PCR analysis has increased the number of alleles identified in these loci (Guzmán, Alvarez, 2016). Currently, spelt samples can be divided into two types: type I and type II (Alvarez, 2021). Type I can be classified as the wild type, it covers numerous variants similar to those found in soft wheat (*Wx-A1a*, *Wx-B1a*, and *Wx-D1a*). In contrast, type II has some distinct differences from fype I, with 14 amino acid changes, nine of which are located within the mature protein (Guzmán et al., 2012).

The quality of spelt grain. Determining the composition, functional characteristics, and mechanisms underlying the formation of spelt grain quality is a critical task in the development of new cultivars of this crop, requiring a deeper understanding of all the components that determine this trait (Goriewa-Duba et al., 2018; Zaika, Karpuk, 2023). This is particularly relevant today due to the growing interest in plant-based proteins for human consumption. The grain quality of this crop is determined by a number of characteristics that can generally be classified into technological and physicochemical indicators. These indicators depend on two groups of factors: environmental and genetic (Tóth et al., 2022; Iqbal et al., 2026). Environmental factors include climatic conditions, soil characteristics, tillage methods, fertilizer application, and irrigation. Genetic factors are currently less studied; however, research into the genetic control and polymorphism of various enzymes and non-enzymatic proteins opens up new opportunities for breeding cultivars with optimal nutritional profiles.

Physical properties of spelt grain. A high 1,000-grain weight, density, and uniformity are characteristics of the grain, desirable for high-quality milling (Belcar et al., 2020). Grain size is an important parameter because it determines the distribution of nutrients across different parts of the grain. It is genetically determined, although it can vary significantly depending on climatic conditions, soil composition, and cultivation methods (Tóth et al., 2022; Iqbal et al., 2026). The average width of spelt grains (2.9 mm) is smaller, and the length is greater, than that of wheat varieties (Takac et al., 2021). Flour made from smaller grains may have a higher content of soluble fiber, minerals, and other components concentrated in the bran (Geisslitz et al., 2019). The primary determinant of yield and an indirect indicator of milling quality is the 1,000-grain weight, since a higher value is associated with greater flour extraction efficiency (Iqbal et al., 2026). Spelt is characterized by high variability in the 1000-grain weight, ranging from 27.7 to 59.4 g (Takac et al., 2021; Iqbal et al., 2026); however, the average values of this indicator for spelt (40.7 g) and wheat (40.2 g) do not differ significantly (Kandić et al., 2023). In addition, it has been shown that spelt genotypes have fewer grains per spike compared to wheat, which may provide more space for endosperm cells during the grain differentiation phase and lead to the formation of larger grains, as evidenced by the negative correlation between the total number of grains and the number of grains per spike, spikelets per spike, and fertile spikelets per spike (Takac et al., 2021).

Chemical composition of spelt grain. Compared to modern wheat varieties, spelt grain contains higher levels of both total and soluble protein, valuable lipids (especially Δ7-avenasterol), and minerals, as well as soluble dietary fiber; it also has a higher selenium content in the grain (Rybalka et al., 2024). The composition of spelt grain depends heavily on the genotype of the sample, its origin, and cultivation conditions (Kulathunga et al., 2021). The main components of spelt grain are carbohydrates, proteins, fats, and dietary fiber **(Table 2)**.

Similar to other *Triticum* species, carbohydrates are the most abundant components of spelt grain. The primary carbohydrate, as in other related species, is starch. Its content ranges from 61% to 68% of dry matter and is found predominantly in the endosperm (Kandić et al., 2023). The increase in starch content is largely responsible for the enlarged grain size (Shewry et al., 2013). Although the amount of this carbohydrate in spelt is similar to that in common wheat, it differs somewhat in quality. This is due to a higher proportion of type A starch compared to common wheat, which is less nutritious (Escarnot et al., 2012). Furthermore, the distribution of the side chains of spelt starch amylopectin indicates that it contains twice as many of the shortest type A chains as the amylopectin of common wheat. Another study (Lafiandra et al., 2014) found that spelt starch has a higher amylose content and a greater number of C-type starch granules compared to common wheat. In addition to starch, short-chain carbohydrates account for 2–3%, while other carbohydrate components (fiber) account for about 10%.

Protein content. The protein content in spelt grain is typically higher than in common wheat, but it varies significantly depending on such factors as genotype, cultivation location, cultivation methods, and climatic conditions (Porto et al., 2025). Its content can range from 11% to 25% (Rybalka et al., 2024). A study (Mikos, Podolska, 2012) found that this indicator is 30–47% higher in winter and spring spelt varieties compared to common wheat. The higher protein content in spelt is associated with an increased content of gliadins, which contribute to greater dough extensibility, one of the characteristic features of spelt (Takac et al., 2021). The composition of spelt protein and the relative proportions of each of its fractions show significant similarity to that of common wheat. The similarity between them lies in the fact that α-gliadins are dominant, followed by γ-gliadins, the amount of ω-gliadins is low, while the presence of high-molecular weight glutenin subunits in spelt is lower than in common wheat. The amount of albumins and globulins in whole-grain *T. spelta* flour is lower compared to wheat and ranges from 1.5 to 2.3 g/100 g (Podolska et al., 2020). It was shown (Geisslitz et al., 2019; Call et al., 2020) that the con-

Table 2. Chemical composition of spelt kernel

Components	%	Reference
Carbohydrates	60.9–67.6	Escarnot et al., 2012
Dietary fiber	7.7–18.5	Escarnot et al., 2012; Kulathunga et al., 2021
Protein	11.1–25.2	Escarnot et al., 2012; Wiwart et al., 2017; Podolska et al., 2020; Biel et al., 2021; Tóth et al., 2022; Rybalka et al., 2024; Morgun et al., 2025
Lipids	1.7–4.4	Escarnot et al., 2012; Wiwart et al., 2017; Kulathunga et al. 2021
Ash	1.4–2.2	Wiwart et al., 2017; Kulathunga et al., 2021

tent of gliadins in different genotypes ranged from 4.5 to 9.3 g/100 g, and that of glutenins — from 1.0 to 10.1 g/100 g. The smallest subfraction of gliadins was ω-gliadins, whose content ranged from 2.5% of total protein in spelt to 3.0% in wheat. The largest subfraction was α/β-gliadins, whose content ranged from 20.0% in spelt to 22.1% in common wheat (Podolska et al., 2020).

The gliadin-to-glutenin ratio (*Gli*/*Glu*) in spelt ranges from 2.8 to 4.0, whereas in wheat this value ranges from 1.5 to 3.1, which explains the higher extensibility of the dough and the lower volume of spelt bread (Geisslitz et al., 2019). These authors demonstrated that the mentioned ratios are influenced by the cultivation location, environmental conditions (temperature), and the amount and timing of fertilizer application. This also indicates that the protein composition of spelt and wheat overlaps significantly and depends on the measurement methods and the samples studied. It was shown that the variability in protein content and composition among spelt varieties is greater than that among harvest years (Call et al., 2020).

In addition, the protein fraction can be influenced by high temperatures, drought, and excess or deficiency of nutrients. Studies show that agronomic factors, such as nitrogen fertilizers and crop rotation, have a significant impact on the content of high- and low-molecular weight glutenins (Stepien, Wojtkowiak, 2013). Tóth et al. (Tóth et al., 2022) found that low nitrogen and phosphorus levels led to an increase in the gliadin fraction and a decrease in glutenins. Konopka et al. (Konopka et al., 2007) found that the concentration of γ-gliadins and glutenins decreased under water deficit conditions. Longin et al. (Longin et al., 2016) showed that spelt had a higher protein content than common wheat, although it received 35% less nitrogen fertilizers compared to common wheat, indicating that, despite limited nitrogen supply, spelt is capable of producing a high protein content.

There is no consensus regarding the aminoacid content of spelt grain protein. Studies demonstrated that spelt grain contains amounts of essential and non-essential aminoacids similar to those of common wheat (Żuk-Gołaszewska et al., 2022). Others claim that spelt has a higher content of essential aminoacids, particularly significantly higher levels of lysine and threonine (Drovacek et al., 2002). Studies (Waga et al., 2002) have shown that spelt grain contains higher levels of all aminoacids (except arginine) compared to common wheat, ranging from 20% to 60%. It was established that spelt wheat grain protein contains the highest levels of glutamic acid, proline, and leucine (Hospodarenko et al., 2016). Spelt proteins, like wheat proteins, are lysine- and threonine-limited **(Table 3)**. However, the aminoacid composition of these proteins is superior: lysine accounts for 58% and threonine for 86%, whereas in wheat, these figures are 52% and 70%, respectively (Drobot et al., 2014).

Table 3. The aminoacid composition of wheat and spelt proteins (Drobot et al., 2014)

Aminoacid	Whole-grain flour, content, mg/100 g	
	Wheat	Spelt
Threonine	372	588
Valine	621	1012
Methionine	216	266
Cysteine	261	389
Leucine	961	1212
Isoleucine	699	813
Tyrosine	361	496
Phenylalanine	652	771
Lysine	376	542
Aspartic acid	779	1026
Serine	588	844
Glutamic acid	3060	3545
Proline	1777	2348
Glycine	634	700
Alanine	464	614
Arginine	709	987
Histidine	378	537

Dietary fiber. Dietary fiber consists of cell wall polysaccharides found in the grain pericarp. There is a significant overlap in dietary fiber content between spelt and common wheat; however, the total fiber content in spelt is slightly lower than in common wheat, ranging from 7.7% to 14.9% (Escarnot et al., 2012), although studies (Kulathunga et al., 2021) have found that this amount can reach 18.5%. The dietary fiber in spelt consists mainly of arabinoxylan, β-glucan, fructan, arabinogalactan, cellulose, lignin, and resistant starch. Soluble dietary fiber fractions predominate in the grain (Escarnot et al., 2012). Escarnot et al. (Escarnot et al., 2015) attempted to evaluate the dietary fiber components of spelt compared to common wheat. Higher values of total arabinoxylan content were found in wheat (6.1%–7.9%), whereas in spelt, the range was 4.7%–6.8%. Despite this quantitative difference, the ratio of arabinose to xylose (total arabinoxylan) was found to be nearly identical for both varieties.

Lipid content. Comparative studies demonstrated that the total lipid content in spelt is low but slightly higher than in common wheat, ranging from 1.7% to 4.4% (Wiwart et al., 2017; Kulathunga et al., 2021). In hulled wheat varieties, including spelt, the content of saturated fatty acids (e.g., palmitic acid) and polyunsaturated fatty acids (e.g., linoleic and linolenic acids) is typically lower compared to common wheat, but there is a higher content of monounsaturated fatty acids (e.g., oleic acid) (Kulathunga et al., 2021). A study of the fatty acid composition of wheat and spelt oils revealed that spelt lipids are represented by a greater variety of fatty acids **(Table 4)**.

Table 4. The fatty acid composition of spelt and common wheat flour (Drobot et al., 2014)

Fatty acids	Mass fraction of fatty acids in oils, %	
	Wheat	Spelt
Saturated	27.819	13.951
C10:0 (capric)	—	0.045
C12:0 (lauric)	—	0.317
C14:0 (myristic)	0.011	0.09
C16:0 (palmitic)	16.612	8.733
C18:0 (stearic)	9.852	3.978
C19:0 (nanodecanoic)	—	0.645
C20:0 (arachic)	0.381	—
C22:0 (behenic)	—	0.143
C24:0 (lignoceric)	0.963	—
Monounsaturates	18.416	29.494
C16:1 (palmitoleic)	0.545	0.067
C18:1 (oleic)	15.122	29.395
C20:1 (gadoleic)	2.01	0.032
C22:1 (erucic)	0.739	—
Polyunsaturates	66.4	62.5
C18:2 (linoleic)	62.4	59.5
C18:3 (linolenic)	3.8	2.9
C20:2 (eicosadienoic)	0.2	0.1

Of particular importance is the content of unsaturated fatty acids, which is significantly higher in spelt grain than in common wheat. The application of nitrogen at a rate of 50 kg/ha increased the fat content in spelt grain (Andruszczak, 2018).

The mineral and vitamin composition of spelt grain is similar to that of common wheat, but there are significant differences in some elements. A study (Suchowilska et al., 2012) found that spelt has significantly higher levels of phosphorus, iron, manganese, cobalt, copper, potassium, and zinc than common wheat. It contains significant amounts of silicon, which the plant obtains from minerals. It was established that the ash, macro-, and micronutrient content was higher in spelt samples, both in fine and coarse-ground bran (Rybalka et al., 2024). Although the phosphorus content in spelt was higher than in wheat, the phytic acid content showed the opposite trend and was 40% lower compared to wheat, which may indicate that it has higher endogenous phytase activity (Longin et al., 2023; Rybalka et al., 2024). Gomez-Becerra et al. (Gomez-Becerra et al., 2010) demonstrated that the Ca/Fe ratio, in combination with the oleate/palmitate ratio, serves as a tool to distinguish spelt from wheat and address the growing problem of spelt flour falsification.

Experimental studies indicate higher levels of vitamins A, E, and D in spelt grain (Biel et al., 2021). Compared to wheat, whole-grain spelt flour contains slightly less vitamin B1 (0.39 mg/100 g and 0.43 mg/100 g, respectively) and vitamin B2 (0.13 mg/100 g and 0.16 mg/100 g, respectively), but significantly more vitamin PP (6.5 mg/100 g and 4.9 mg/100 g, respectively); B5 (0.96 mg/100 g and 0.49 mg/100 g, respectively); Bc (42 μg/100 g and 39 μg/100 g, respectively); vitamin E (2.86 mg/100 g and 2.71 mg/100 g, respectively); vitamin K (3.71 μg/100 g and 1.92 μg/100 g, respectively) (Drobot et al., 2014). The richer vitamin and mineral composition of spelt can be explained by its specific ability — to absorb nutrients from the soil better than common wheat (Kohajdová Z, Karovičová, 2008).

Technological quality of spelt grain. Grain quality indicators, such as moisture content, appearance, grain weight and hardness, are particularly important for the food industry, as they determine storage potential, yield, shelf life, and bread crumb structure. These traits are genetically regulated and inherited and are the focus of breeding programs aimed at their improvement (Safdar et al., 2023). The technological quality indicators of spelt grain are characterized by moisture content, typically up to 14.5%; high protein content (11–25%); and high crude gluten content (up to 60%), although it is often “weak” in terms of physical properties, requiring special dough mixing techniques. Due to its glume, the specific weight (grain volume weight) of unhulled spelt is quite low, but after hull removal, it approaches that of high-quality wheat and ranges from 704–770 g/l. Spelt typically has a high vitreous index (70–90%), indicating a high protein content and a dense grain structure. Three main components of spelt grain have been identified that are associated with its technological quality: starch, gluten, and purindolines (Alvarez, 2021).

Starch is the main component of the grain, consisting of two primary D-glucose homopolymers: amylose — a linear polysaccharide that forms a colloidal dispersion in hot water, and amylopectin — a branched polysaccharide that is completely insoluble. The proportions of amylose and amylopectin in starch have a significant impact on flour processing quality, and starches with a high amylose content are better suited for developing healthy products because they are digested more slowly in the human gastrointestinal tract (Rybalka et al., 2024). The typical amylose/amylopectin ratio for spelt starch is approximately 1:3 (Lafiandra et al., 2014). The interaction between the two polymers can influence the physical and chemical properties of starch (gelatinization, binding, and gel formation), and consequently, the quality of the final products (Guzmán et al., 2022). Starch is associated not only with food quality but also with shelf life and nutritional value of food products: a higher amylose content conditions a higher content of resistant starch (Guzmán et al., 2022). Spelt starch can contain 2% to 21% more amylose than winter wheat (Wilson et al., 2008). In addition, it is a key factor determining the dynamic properties of dough, especially during heating (Zamaratskaia et al., 2021).

Gluten is a continuous viscoelastic protein network that forms when flour is mechanically mixed with water. It is calculated as wet or dry and is an important parameter determining the quality of baked goods, as it affects water absorption capacity, cohesiveness, viscosity, and elasticity of dough. Spelt varieties have been found to have a higher gluten content compared to wheat, but its quality is lower, which is associated with a higher content of gliadins (Takač et al., 2021). It has been shown that gliadins predominate in spelt gluten, whereas glutenins predominate in common wheat gluten.

Puroindolines (puroindoline *a* and puroindoline *b*) determine the grain texture, which influences its milling properties and water absorption properties of the flour. The variations in puroindoline in spelt have been little studied, probably because spelt generally has a soft texture (Takač et al., 2021). To date, no spelt sample has been reported to contain alleles different from the wild-type (*Pina-D1a* and *Pinb-D1a*).

Functional and technological properties of spelt flour. Spelt flour has a nutty flavor, it is more easily digestible, contains more nutrients, and absorbs more water (by 3.5%) compared to wheat flour. The protein content is significantly higher in whole-grain spelt flour compared to whole-grain wheat flour (Frakolaki et al., 2018; Takac et al., 2021; Kandić et al., 2023). For example, the total protein content in spelt flour samples ranged from 16.6% to 20.2% of dry matter, whereas in wheat flour it ranged from 11.4% to 13.7% (Kandić et al., 2023).

Although gluten content is high, it is less elastic and more brittle than in common wheat and is often rated as “weak” or “satisfactorily weak” by the deformation index (Kandić et al., 2023). This means that the dough holds its shape less well and may “spread out.” Raw gluten, as an indicator, is associated with the baking quality of flour, as it acts as a binding agent that holds the flour and other ingredients together and ultimately creates the dough structure. The gluten content in spelt flour ranged from 42.2% to 66.0% of dry matter, while in common wheat it ranged from 19.5% to 35.5% (Kandić et al., 2023). The studies have found that spelt has a significantly higher crude gluten content than wheat (Belcar et al., 2020; Rachon et al., 2020; Takac et al., 2021).

Although the protein and gluten content in spelt were high, the associated quality characteristics showed low values (Tóth et al., 2022). The average gluten expansion rate was 7.8 mm/h, whereas for the wheat varieties Glenly and Ukrainka, it was 2.5 and 1.1 mm/h, respectively. The glycemic index was 59.2, whereas for the wheat varieties Glenly and Ukrainka, it was 97.3 and 99.7, respectively. The sedimentation index characterizes the viscoelastic properties and quality of proteins and indicates the potential for fermentation in dough. It was found that the sedimentation index in spelt was lower than in common wheat (Podolska et al., 2020; Tóth et al., 2022). The average value for spelt samples was 34.7 ml, while for the common wheat varieties Glenly and Ukrainka, it was 48.0 ml and 45.6 ml, respectively (Tóth et al., 2022). Significantly higher values were found in the common wheat variety Bamberka (41.1 ml) than in the spelt variety Rokosz (29.7 ml) (Podolska et al., 2020).

The average starch content was significantly higher in wheat (66.4% of dry matter) than in spelt flour (62.5% of dry matter) (Tóth et al., 2022). Similar results (66.4% and 64.2% of dry matter) were obtained in the study (Frakolaki et al., 2018). A study (Kandić et al., 2023) confirmed that spelt genotypes with lower starch content had higher protein content in the grain. The average amylose content in spelt flour (17% of dry matter) and wheat flour (17.1%) showed no significant difference (Kandić et al., 2023). As for amylopectin content in flour, there were no significant differences between the two varieties: in spelt, it averaged 83% of dry matter, while in wheat it had an average content of 82.8%.

Significant differences were observed between the two varieties regarding the content of insoluble fiber (NDF) and hemicellulose (Kandić et al., 2023). The NDF content in spelt flour genotypes averaged 62.6% of dry matter, whereas in wheat flour it was 69.6%. The hemicellulose content in spelt flour ranged from 48.0% to 59.9% of dry matter, while in wheat it ranged from 60.9% to 66.9%. Escarnot et al. also reported lower NDF and hemicellulose contents in spelt genotypes compared to wheat (Escarnot et al., 2010, 2012).

The ADF (acid-detergent fiber) index is a specific parameter characterizing the content of the least digestible substances, and as it increases, feed/food digestibility decreases. Spelt genotypes had higher mean ADF values (7.87% dry utilization (DU)) compared to wheat (6.70% DU), indicating that wheat is superior in terms of digestibility (Kandić et al., 2023). The lignin (4.75% DU) and cellulose (3.12% DU) contents in spelt samples were higher compared to wheat genotypes (4.53%, 2.21% DU, respectively) (Kandić et al., 2023). However, Escarnot et al. (Escarnot et al., 2010) reported that lignin content was similar in spelt and wheat genotypes. A lower dietary fiber content in spelt flour compared to wheat was found in a study (Suchowilska et al., 2020). The total sugar content in spelt flour ranged from 0.72 to 3.12 mg g^{-1} of dry matter, whereas in common wheat genotypes, it ranged from 1.92 to 3.0 mg g^{-1} (Kandić et al., 2023). A comparison of the results obtained by different authors indicates that these traits were strongly influenced by environmental factors.

The SRC (Solvent Retention Capacity) method is a technique for determining the ability of flour to retain a solvent, based on centrifuging the sample after incubation with various solvents (water, lactic acid, sodium carbonate, sucrose). It allows for the measurement of moisture-absorbing capacity, as well as the functionality of flour components such as pentosans and glutenin, which helps assess their impact on dough quality. Significant differences were observed between spelt and wheat in terms of the SRC of water and sodium carbonate (Kandić et al., 2023). For spelt genotypes, the water SRC values ranged from 60.5% to 67.1%, while for wheat genotypes — from 72.6% to 78.0%. The SRC value for sodium carbonate, which is related to the content of damaged starch in flour, ranged from 79.9% to 88.7% in wheat flour, while in spelt flour, it ranged from 66.4% to 76.7%. The SRC value for sucrose, which is related to the arabinoxylan content in flour, was slightly higher on average (96.9%) in wheat genotypes compared to spelt genotypes (92.8%), indicating a slightly higher arabinoxylan content in common wheat (Kandić et al., 2023). A study (Aghagholizadeh et al., 2019) reports that the SRC of lactic acid can be used to determine the quantity and quality of glutenin fractions present in flour. Lactic acid SRC in wheat flour ranged from 68.0% to 81.3%, and in spelt it ranged from 64.7% to 68.9%.

Glutinous properties. The glutinous properties of flour depend on various chemical components of the grain, as well as their interactions. Starch granules do not dissolve in water at room temperature, but they become disorganized during heat treatment. Glutinocity curves indicate the ability of starch to retain water and swell when the suspension is heated from 25 to 95°C, and their shape depends on the ratio of amylose to amylopectin, as well as protein and fat compounds. Peak viscosity (Vpeak) indicates the maximum consistency obtained when heating flour with excess water, and spelt genotypes showed significantly higher values compared to common wheat (Kandić et al., 2023). Peak viscosities were observed in the range of 25 to 27 minutes, and Vpeak for spelt genotypes ranged from 370 to 970 Brabender units (BU), whereas for wheat genotypes these values ranged from 170 to 560 BU. The highest peak temperature (92.3°C) was observed in spelt, and the lowest (84.7°C) — in wheat genotypes. The final viscosity for spelt genotypes ranged from 460 to 1,200 BU, and for wheat, from 230 to 850 BU. In another study (Tóth et al., 2022), the average peak viscosity in spelt was 3706 cP (centipoise), ranging from 1751 cP to 3824 cP. The average starch gelatinization temperature was higher for spelt (63.5°C) than for wheat samples (61.3°C); the average gelatinization time was 9.0 min, and the average starch damage index (12.7) was lower in spelt than in wheat (17.3 and 18.8 for the Glenly and Ukrainka varieties, respectively).

A correlation analysis of these characteristics conducted by Toth (Toth et al., 2022) showed that the viscous properties of starch (peak, minimum, final, and reverse viscosity) negatively correlated with protein and gluten content, but positively correlated with quality-determining characteristics (glycemic index, Zeleny sedimentation index, dough stability). Water absorption positively correlated with starch damage, but negatively correlated with viscosity parameters and starch gelatinization temperature. The starch gelatinization temperature also correlated positively with the glycemic index, Zeleny sedimentation index, and dough stability.

Baking properties of spelt. Dough made from spelt flour is characterized by lower stability and elasticity and higher extensibility; it forms 2.5–3.5 times slower than dough made from wheat flour (Sobczyk et al., 2017). In spelt, it is softer and stickier after mixing, making it more difficult to work with, and the loaf volume is generally smaller than that of modern wheat varieties (Takač et al., 2021). The farinograph parameters showed lower average values compared to wheat: gluten expansion ranging from 1.0 to 20.5 mm, Zeleny sedimentation index ranging from 16.0 to 73.0 ml, dough softening — up to 306.0 farinograph units, and water absorption ranging from 51.3% to 63.3% (Tóth et al., 2022). The flour yield after milling was highly variable for spelt, ranging from 31.8% to 75.1% and averaging 58.2%.

Spelt bread typically has a denser structure and a lower specific volume (by 10–20%) than wheat bread (Schober et al., 2002). The products have a characteristic golden or yellowish hue, a rich nutty aroma, and a sweet aftertaste. Due to its high fiber content and protein characteristics, spelt bread stays soft longer. Spelt carbohydrates are digested more slowly, which positively affects nutritional value. Due to the delicate structure of gluten, it is important to avoid intensive kneading so that the dough does not lose its ability to retain gas. Spelt often requires less liquid than specified in standard wheat recipes, or requires a different hydration regime (Arendt, Zannini, 2013).

Frakolaki et al. (Frakolaki et al., 2020) investigated the potential use of spelt flour for bread baking in mixtures of spelt and wheat flour (with spelt content ranging from 0% to 100% in 10% increments). It was found that a spelt flour content of up to 20% yields bread quality and organoleptic characteristics similar to those of wheat bread, whereas a content exceeding 70% leads to a deterioration in the bread quality characteristics. Callejo et al. (Callejo et al., 2015) found that spelt bread has high crumb elasticity but low crumb uniformity compared to wheat bread. Rodríguez-Quijano et al. (Rodríguez-Quijano et al., 2019) demonstrated that spelt dough exhibits low strength and viscosity and higher degradation as indicated by SDS measurements, alveograph, and consistograph readings, suggesting weaker gluten in spelt.

The Hagberg falling number provides an indication of alpha-amylase activity in the grain and the baking quality of the flour (Safdar et al., 2023). Podolska et al. (Podolska et al., 2020) found that *Triticum spelta* had the highest falling number compared to common wheat. Literature data indicate significant differences in this parameter among spelt varieties. According to (Rachon et al., 2016), the falling number ranged from 228 s (Ceralio variety) to 354 s (Holstenkorn variety), and according to (Tóth et al., 2022), it ranged from 103 s to 613 s across different spelt genotypes.

The rheological characteristics of dough depend on the properties of the flour components and their interaction, which arises as a result of hydration and the input of energy during mixing. In the study by Podolska et al. (2020), soft wheat was characterized by a flour strength "W" value (312×10^{-4} J), while spelt had a lower value (146×10^{-4} J), indicating a lower quality of its gluten complex and its suitability for production, for example, of waffles. These results are confirmed by Sobczyk et al. (Sobczyk et al., 2017). The dough energy of spelt is lower compared to common wheat and varies significantly — from 24 cm^2 to 71 cm^2.

The P parameter of the Chopin Alveograph is an indicator of dough elasticity and depends on the degree of flour absorbency. Common wheat has higher dough elasticity compared to spelt (Sobczyk et al., 2017; Podolska et al., 2020). In spelt, this parameter is highly variable and ranges from 54 mm to 218 mm. The dough extensibility (L) in *Triticum spelta* (88 mm) was slightly higher compared to common wheat (79 mm) (Sobczyk et al., 2017). The P/L index for the common wheat variety Bamberka was 1.53, and for the spelt variety Rokosz — 0.71 (Podolska et al., 2020). Wheat suitable for confectionery products should have a P/L ratio below 0.50 (Sobczyk et al., 2017).

The amount of high-molecular weight (HMW-GS) and low-molecular weight (LMW-GS) glutenin subunits positively correlates with dough energy and bread volume, whereas gliadin content and a higher gliadin-to-glutenin ratio have a negative effect on these parameters. Podolska et al. (Podolska et al., 2020) found that the HMW-GS to LMW-GS ratio ranged from 0.38 (common wheat) to 0.40 (spelt). The higher gliadin:glutenin ratio in spelt compared to wheat is likely the main reason for the lower baking quality of dough made from this grain.

The physiological (nutritional) effect of spelt consumption. Spelt was first cultivated as a bread grain in the 8th century BC and is currently regaining well-deserved attention (Frakolaki et al., 2018). Growing awareness of the close link between diet and human health is currently significantly changing people's dietary preferences worldwide, driving increased consumption of foods with high nutritional value. One reason for the interest in spelt is its presumed beneficial nutritional effects and higher content of health-promoting components (e.g., higher levels of protein, unsaturated fatty acids, minerals, vitamins, and phytochemicals). For example, the silicon oxide found in the grains of this cereal is important for skin, hair, and nails, and also enhances brain function. The zinc found in spelt is a well-known therapeutic agent for intestinal disorders. Valuable aminoacids (phenylalanine, tyrosine, and isoleucine) are essential for the proper functioning of the nervous system. Dietary fiber is recommended for the prevention of gastrointestinal disorders, as it likely helps prevent the development of type 2 diabetes, obesity, gallstone disease, and colorectal cancer (Sztupecki et al., 2023). Hemicellulose can bind heavy metals, which makes it an important component of dietary fiber in grains and improves food quality (Koenig et al., 2015). Due to its high content, dietary fiber can swell and absorb water in the human digestive tract, leading to positive physiological effects (Singh et al., 2018).

Today, the higher nutritional value of whole grains compared to refined grains is widely recognized (Dinu et al., 2018; Valli et al., 2018), as the beneficial components are primarily located in their outer layers. In addition to their excellent nutritional properties, pleasant taste, and aroma, spelt flour and baked goods are becoming increasingly popular due to their high digestibility, as well as their suitability for consumers with gluten sensitivity (Koenig et al., 2015). A significant number of patients who do not have celiac disease but suffer from wheat-related health issues can tolerate products made from certain spelt varieties (Dinu et al., 2018). Thorup et al. (Thorup et al., 2014) sought to demonstrate the physiological effects of consuming spelt in type 2 diabetes and found that it causes a lower acute glycemic response compared to common wheat.

Celiac disease is a chronic autoimmune disorder in which the consumption of gluten proteins from wheat, spelt, rye, and barley in genetically susceptible individuals causes damage to the lining of the small intestine. In celiac disease, the most toxic peptide segments (epitopes) are present in gluten proteins, but other proteins also contribute to the development/induction of the disease. The cytotoxicity of spelt was found to be similar to that of common wheat, and despite their different origins, both genomes contain regions encoding toxic celiac disease epitopes (Chhuneja, Arora, 2020). Although clinical tests showed sensitivity to spelt proteins, the level of which was associated with the severity of celiac disease symptoms, the frequency of positive symptoms was significantly lower in spelt than in wheat. A comprehensive study of the reactivity of 195 wheat samples and 240 spelt samples to the monoclonal antibodies A1 and G12 showed a slightly higher average reactivity for spelt than for wheat, but varieties with low reactivity were identified (Escarnot et al., 2018).

Irritable bowel syndrome (IBS) is a general term for gastrointestinal disorders partially associated with the consumption of carbohydrates known as FODMAPs (fermentable oligo-, di-, and monosaccharides and polyols). According to the available literature, the FODMAP content in spelt is similar to that in common wheat — 1.1–2.1 g/100 g, with fructan, which is considered a component of dietary fiber, accounting for the largest share (Longin et al., 2020). The positive effect of spelt consumption may be more closely linked to its processing conditions, such as extended fermentation periods or the absence of additives (Guerrini et al., 2019).

Spelt as a source of beneficial genes for common wheat breeding. Spelt has a significant potential as a genetic resource for improving a wide range of agronomic traits in common wheat, from yield and its components to resistance to diseases and abiotic stresses (Xie et al., 2015; Rapp et al., 2017; Geisslitz et al., 2019; Morgun et al., 2025). In both domestic and global practice, there are many examples of the successful use of various spelt ecotypes in breeding and subsequent hybridization with naked wheat to improve the latter (Diordiieva et al., 2024; Morgun et al., 2025).

Spelt has been successfully used as a source of genes of resistance to certain wheat diseases. The first studies were conducted on resistance to rust, mainly to yellow wheat rust (*Puccinia striiformis* West.), and several interesting genes (*Yr5* and *Yr10*) were identified, which were transferred to common wheat. Genes of resistance against leaf rust (*P. recondita* f. sp. *tritici*), such as *Lr44*, *Lr65*, or *Lr71*, and against stem rust (*P. graminis* f. sp. *tritici*) have also been identified in spelt samples (Dinkar et al., 2020). Genes of resistance to powdery mildew (*Erysiphe graminis* f. sp. *tritici*) have also been found in spelt (Goriewa-Duba et al., 2020). However, the presence of traits considered undesirable, primarily, plant height, brittle rachis, and grain hull, limits its use for breeding of other agronomic traits (Alvarez, 2021).

Concerns about the nutritional quality of modern foods have sparked interest in developing materials with higher levels of micronutrients necessary for proper nutrition. These traits can be transferred from spelt to common wheat through crossing with donor lines of this cereal (Srinivasa et al., 2014), allowing for the development of biofortified wheat with good technological qualities.

Research by Ukrainian and foreign scientists has demonstrated the positive effects of crossing common wheat and spelt, in particular, a significant expansion of the existing genetic diversity of both common wheat and spelt, and the creation of new forms that combine the high protein and gluten content of spelt with the high yield potential of common wheat (Diordiieva et al., 2024; Morgun et al., 2025).

New research directions in the genetic improvement of spelt. Two directions in the breeding work with spelt have been identified: its revival as a standalone crop and its use as a source of economically valuable traits in breeding programs for common wheat (Alvarez, 2021). Breeding efforts are aimed at improving overall spelt productivity while simultaneously reducing undesirable traits, such as low spike yield or susceptibility to lodging (Takač et al., 2021). Since the 1990s, a fundamentally new trend has emerged in the breeding of wheat and other cereal crops — the creation of varieties with colored (purple, blue, black) grains, which is now gaining significant momentum in many countries around the world (Rybalka et al., 2024). The dark pigmentation of the grain is caused by anthocyanin pigments, which exhibit high antioxidant and anti-inflammatory activity, protect cells from the destructive effects of free radicals, and have a wide range of positive effects on the human body, including protection against metabolic syndromes such as obesity, diabetes mellitus, hypertension, dyslipidemia, cancer, and cardiovascular diseases (Lin et al., 2017). They slow down aging, have a neuroprotective effect, and wheat varieties with colored grains and high anthocyanin content have high functional food status (Rybalka et al., 2024).

Among existing spelt varieties, there were no genotypes with colored grains. The Bilberi spelt variety, featuring dark purple grains and improved nutritional value, was developed and registered in Ukraine for the first time in the world (Rybalka et al., 2024). The grain color of the Bilberi variety is significantly darker than the purple grain of the Chornobrova variety (the Bilberi variety was obtained by crossing Schwabenkorn spelt and Chornobrova wheat). Thus, under the same growing conditions, the anthocyanin content in the Chornobrova variety is ~60 mg/kg, while in spelt it is nearly 80 mg/kg. Bilberi spelt has a high protein content in the grain (16.8%) and gluten content (45%) (Rybalka et al., 2024). Whole-grain flour from the Bilberi variety is used to bake bread using a special technology, as well as biscuit products such as cookies and crackers.

The Institute of Plant Physiology and Genetics of the National Academy of Sciences of Ukraine has launched a program aimed at creating spelt genetic material with the target trait "black grain," which combines a blue color in the grain hull and a purple color in the aleurone layer of the endosperm and has the highest anthocyanin content and the highest antioxidant activity in the grain and its processed products. For the first time in Ukraine, the black-grain spelt variety Dobra Novyna has been created and submitted for the State variety testing in 2023.

CONCLUSION

Over the past few decades, spelt has been gaining increasing attention as a food product due to its image as a "healthier, more natural, and less 'bred' grain" than common wheat. Initiatives to preserve biodiversity and efforts to improve nutritional needs have contributed to the current growth in interest in its production (Rakszegi et al., 2025). Significant progress has been made in spelt breeding and genetic improvement (Curzon et al., 2021).

Spelt variety breeding is primarily carried out by Swiss and German companies; it is their varieties that are currently grown in Europe and Ukraine, where winter varieties dominate in the production. The following varieties are common in Europe: Franckenkorn, Ceralio, Schwabenkorn, Ostro, Oberkulmer Rothkorn, Schwabenspelz, Holstenkorn, and the most widespread is Baulander Spelz, which has very good technological properties. Most of these varieties are characterized by tall stalks (up to 140 cm), so they often lodge when sown on fertile soils or after legume predecessors. The Institute of Plant Production named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, where breeding work on spelt has been underway for 20 years. A number of lines with easy threshing ability have been developed, whose yields are comparable to those of common wheat. Extensive research and variety development for this crop are also being conducted at the Uman National University of Horticulture of the Ministry of Education and Science of Ukraine. In particular, the first winter spelt varieties in Ukraine, Zoria Ukrainy and Evropa, have been developed. The work on the genetic improvement of spelt has also begun at the Institute of Plant Physiology and Genetics of the National Academy of Sciences of Ukraine, where a collection of spring and winter forms of this crop has been established (Morgun et al., 2025).

To obtain new spelt varieties with agronomic characteristics better suited to modern agricultural technologies, hybridization with semi-dwarf common wheat is used. This process, which is generally time-consuming, can be shortened using rapid breeding methods (Watson et al., 2018). Alternatively, the anther culture for producing double haploids can be used for the same purpose (Lantos, Pauk, 2021). In fact, new varieties are being developed using both doubled haploids and self-pollination followed by breeding through rapid propagation. These new varieties have short plant height, which allows for mechanization and helps prevent the usual lodging. European varieties such as Alkor, Badengold, Ceralio, and Cosmos have already been developed (Alvarez, 2021). The studies conducted with these new spelt varieties have shown that, although their grain yield is significantly higher than that of traditional spelt, they are more sensitive to environmental stressors (Rachon et al., 2020; Biel et al., 2021).

Despite growing market demand and agricultural areas, there is a lack of systematic evaluation of genotypic performance across different environments and years, and the genetic diversity present in modern spelt germplasm collections remains understudied (Iqbal et al., 2026). Limited information is available on the genotypic adaptability of spelt, particularly regarding its suitability for cultivation and use under European conditions. Furthermore, most current studies evaluate qualitative or agronomic traits separately (Dolijanović et al., 2022; Takač et al., 2021), which does not allow for a comprehensive assessment of genotype characteristics.

Thus, spelt has recently attracted significant attention, as evidenced by the increasing number of studies on its various forms and genotypes based on quantitative and qualitative traits. However, most of these studies were conducted with a limited number of samples, which could have led to biased results. For this reason, the evaluation of large spelt collections helps identify new genotypes with valuable traits that can be used to develop better-adapted spelt varieties and enhance the genetic diversity of common wheat.

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REFERENCES

Abrouk M, Athiyannan N, Müller T, Pailles Y, Stritt C, Roulin AC, Chu C, Liu S, Morita T, Handa H, Poland J, Keller B, Krattinger SG (2021) Population genomics and haplotype analysis in spelt and bread wheat identifies a gene regulating glume color. *Commun Biol, 4*:375. https://doi.org/10.1038/s42003-021-01908-6

Aghagholizadeh R, Kadivar M, Nazari M, Ahmadi H, Azizi MH (2019) Capability of solvent retention capacity to quality of flat bread in three wheat cultivars. *Journal of Food Science and Technology, 56*(2):775–82. https://doi.org/10.1007/s13197-018-3537-8

Alvarez JB (2021) Spanish Spelt Wheat: From an Endangered Genetic Resource to a Trendy Crop. *Plants, 10*(12):2748. https://doi.org/10.3390/plants10122748

Alvarez JB, Guzman C (2013) Spanish ancient wheat: a genetic resource for wheat quality breeding. *Adv Crop Sci Tech, 1*:e101. https://doi.org/10.4172/2329-8863.1000101

An X, Li Q, Yan Y, Xiao Y, Hsam SLK, Zeller FJ (2005) Genetic diversity of European spelt wheat (*Triticum aestivum* ssp. *spelta* L. em Thell.) revealed by glutenin subunit variations at the *Glu-1* and *Glu-3* loci. *Euphytica, 146*:193–201. https://doi.org/10.1007/s10681-005-9002-6

Andruszczak S (2018) Spelt wheat grain yield and nutritional value response to sowing rate and nitrogen fertilization. *J. Anim. Plant Sci, 28*(5):1476–84.

Arendt EK, Zannini E (2013) Wheat and other *Triticum* grains. In: Arendt EK, Zannini E (eds) Cereal Grains for the Food and Beverage Industries. Woodhead Publishing Series in Food Science, Technology and Nutrition, pp. 34–42. https://doi.org/10.1533/9780857098924.1

Babenko LM, Hospodarenko HM., Rozhkov RV, Pariy YF, Pariy MF, Babenko AV, Kosakivska IV (2018) *Triticum spelta*: Origin, biological characteristics and perspectives for use in breeding and agriculture. *Regul. Mech. Biosyst, 9*(2):250–7. https://doi.org/10.15421/021837

Belcar J, Sobczyk A, Sobolewska M, Stankowski S, Gorzelany J (2020) Characteristics of technological properties of grain and flour from ancient varieties of wheat (einkorn, emmer and spelt). *Acta Universitatis Cibiniensis Series E: Food Technology, 269*(24):269–78. https://doi.org/10.2478/aucft-2020-0024

Bentley A, Horsnell R, Werner CP, Turner AS, Rose GA, Bedard C, Howell P, Wilhelm EP, Mackay IJ, Howells RM, et al (2013) Short, natural, and extended photoperiod response in BC2F4 lines of bread wheat with different Photoperiod-1 (Ppd-1) alleles. *J. Exp. Bot, 64*(7):1783–93. https://doi.org/10.1093/jxb/ert038

Bertin P, Gregoire D, Massart S, de Froidmont D (2004) High level of genetic diversity among spelt germplasm revealed by microsatellite markers. *Genome, 47*:1043–52. https://doi.org/10.1139/g04-065

Biel W, Jaroszewska A, Stankowski S, Sobolewska M, Kepi´nska-Pacelik J (2021) Comparison of yield, chemical composition and farinograph properties of common and ancient wheat grains. *Eur. Food Res. Technol, 247*:1525–38. https://doi.org/10.1007/s00217-021-03729-7

Blahodarova OM, Ruzhitskaya OM, Sechnyak OL, Tkachenko FP (2023) Aprobation of common wheat molecular markers for the determination of the allelic composition of gliadins of *Triticum spelta* L. *Factors of experimental evolution of organisms, 33*:13–7. https://doi.org/10.7124/FEEO.v33.1592

Blatter RHE, Jacomet S, Schlumbaum A (2004) About the origin of European spelt (*Triticum spelta* L.): allelic differentiation of the HMW Glutenin B1-1 and A1-2 subunit genes. *Theor. Appl. Genet, 108*:360–7. https://doi.org/10.1007/s00122-003-1441-7

Boukid F, Folloni S, Sforza S, Vittadini E, Prandi B (2018) Current Trends in Ancient Grains-Based Foodstuffs: Insights into Nutritional Aspects and Technological Applications. *Comprehensive Reviews in Food Science and Food Safety, 17*(1):123–36. https://doi.org/10.1111/1541-4337.12315

Caballero L, Martin LM, Alvarez JB (2004) Variation and genetic diversity for gliadins in Spanish spelt wheat accessions. *Genet Resour Crop Ev, 51*:679–86. https://doi.org/10.1023/B:GRES.0000034575.97497.6e

Caballero L, Peña RJ, Martín LM, Alvarez JB (2010) Characterization of Mexican Creole wheat landraces in relation to morphological characteristics and HMW glutenin subunit composition. *Genet Resour Crop Evol, 57*:657–65. https://doi.org/10.1007/s10722-009-9501-8

Call L, Kapeller M, Grausgruber H, Reiter E, Schoenlechner R, D'Amico S (2020) Effects of species and breeding on wheat protein composition. *Journal of Cereal Science, 93*:102974. https://doi.org/10.1016/j.jcs.2020.102974

Callejo MJ, Vargas-Kostiuk ME, Rodríguez-Quijano M (2015) Selection, training and validation process of a sensory panel for bread analysis: Influence of cultivar on the quality of breads made from common wheat and spelt wheat. *J. Cereal Sci, 61*:55–62. https://doi.org/10.1016/j.jcs.2014.09.008

Cao Y, Zhang J, Wang R, Sun H, Yan Y (2022) Molecular characterization and SNP-based molecular marker development of two novel high molecular weight glutenin genes from *Triticum spelta* L. *Int. J. Mol.Sci, 23*(19):11104. https://doi.org/10.3390/ijms231911104

Chhuneja P, Arora JK (2020) Exploring genetic variability for developing celiac disease safe wheat (eds) Wheat and Barley Grain Biofortification, Woodhead, Publishing, Punjab, India, pp 183–202. https://doi.org/10.1016/B978-0-12-818444-8.00007-9

Chrpova J, Grausgruber H, Weyermann V, Buerstmayr M, Palicova J, Kozova J, Travnıckova M, Nguyen QT, Amores JEM, Buerstmayr H, Janovska D (2021) Resistance of winter spelt wheat [*Triticum aestivum* subsp. *spelta* (L.) Thell.] to fusarium head blight. *Frontiers* *in Plant Science, 12*:661484. https://doi.org/10.3389/fpls.2021.661484

Common catalogue of varieties of agricultural plant species — Consolidated version 27.01.2023.

Curzon AY, Kottakota C, Nashef K, Abbo S, Bonfil DJ, Reifen R, Bar-El S, Rabinovich O, Avneri A, Ben-David R (2021) Assessing adaptive requirements and breeding potential of spelt under Mediterranean environment. *Sci. Rep, 11*:7208. https://doi.org/10.1038/s41598-021-86276-1

Dai S, Xu D, Yan Y, Wen Z, Zhang J, Chen H, et al (2020) Characterization of high- and low-molecular-weight glutenin subunits from Chinese Xinjiang wheat landraces and historical varieties. *J Food Sci Technol, 57*:3823–35. https://doi.org/10.1007/s13197-020-04414-5

Debernardi JM, Lin H, Chuck G, Faris JD, Dubcovsky J (2017) MicroRNA172 plays a crucial role in wheat spike morphogenesis and grain threshability. *Development, 144*:1966–75. https://doi.org/10.1242/dev.146399

Dinkar V, Jha SK, Mallick N, Niranjana M, Agarwal P, Sharma JB (2020) Molecular mapping of a new recessive wheat leaf rust resistance gene originating from *Triticum spelta*. *Sci Rep, 10*:22113. https://doi.org/10.1038/s41598-020-78679-3

Dinu M, Whittaker A, Pagliai G, Benedettelli S, Sofi F (2018) Ancient wheat species and human health: Biochemical and clinical implications. *J. Nutr. Biochem, 52*:1–9. https://doi.org/10.1016/j.jnutbio.2017.09.001

Diordiieva IP, Riabovol IS, Riabovol LO, Babii MM, Fedorenko SV, Serzhuk OP, Maslovata SA, Liubchenko AI, Novak ZM, Liubchenko IO (2024) Breeding and genetic improvement of spelt wheat (*Triticum spelta*) by interspecific hybridization. *Regulatory Mechanisms in Biosystems, 15*(3):463–8. https://doi.org/10.15421/022465

Dolijanović Ž, Nikolić SR, Subić J, Jovović Z, Oljača J, Bačić J (2022) Organic spelt production systems: Productive and financial performance in three orographic regions. *Italian Journal of Agronomy, 17*:2025. https://doi.org/10.4081/IJA.2022.2025

Drobot VI, Semenova AB, Mykhonik LA (2014) Comparative characteristics of the chemical composition and technological properties of whole-milled wheat flour and spelt flour. *Grain storage and processing, 4*:1–6.

Drovacek V, Curn V, Moudry J (2002) Evaluation of amino acid content and composition in spelt wheat varieties. *Cereal Research Communications, 30*(1):187–93. https://doi.org/10.1007/BF03543407

Dvorak J, Akhunov ED, Akhunov AR, Deal KR, Luo MC (2006) Molecular characterization of a diagnostic DNA marker for domesticated tetraploid wheat provides evidence for gene flow from wild tetraploid wheat to hexaploid wheat. *Mol. Biol. Evol, 23*(7):1386–96. https://doi.org/10.1093/molbev/msl004

Dvorak J, Deal KR, Luo MC, You FM, von Bortel K, Dehghani H (2012) The origin of spelt and free-threshing hexaploid wheat. *J. Heredity, 103*(3):426–41. https://doi.org/10.1093/jhered/esr152

Escarnot E, Jacquemin JM, Agneessens R, Paquot M (2012) Comparative study of the content and profiles of macronutrients in spelt and wheat, a review. *Biotechnology, Agronomy and Society and Environment, 16*(2):243–56.

Escarnot E, Agneessens R, Wathelet B, Paquot M (2010) Quantitative and qualitative study of spelt and wheat fibres in varying milling fractions. *Food Chemistry, 122*(3):857–63. https://doi.org/10.1016/j.foodchem.2010.02.047

Escarnot E, Dornez E, Verspreet J, Agneessens R, Courtin CM (2015) Quantification and visualization of dietary fibre components in spelt and wheat kernels. *J. Cereal Sci, 62*:124–33. https://doi.org/10.1016/j.jcs.2015.01.003

Escarnot E, Gofflot S, Sinnaeve G, Dubois B, Bertin P, Mingeot D (2018) Reactivity of gluten proteins from spelt and bread wheat accessions towards A1 and G12 antibodies in the framework of celiac disease. *Food Chem, 268*:522–32. https://doi.org/10.1016/j.foodchem.2018.06.094

Faris J (2014) Wheat domestication: key to agricultural revolutions pasts and future. In: Tuberosa R, Graner A, Frison E (eds) Genomics of Plant Genetic Resources, Dordrecht: Springer, pp. 439–464. https://doi.org/10.1007/978-94-007-7572-5_18

Filipčev B, Šimurina O, Bodroža-Solarov M, Obreht D (2013) Comparison of the bread-making performance of spelt varieties grown under organic conditions in the environment of northern Serbia and their responses to dough strengthening improvers. *Hemijska Industrija, 67*(3):443–53. https://doi/org/10.2298/HEMIND 120606083F

Frakolaki G, Giannou V, Topakas E, Tzia C (2018) Chemical characterization and breadmaking potential of spelt versus wheat flour. *Journal of Cereal Science, 79*:50–6. https://doi.org/10.1016/j.jcs.2017.08.023

Frakolaki G, Giannou V, Tzia C (2020) The properties and breadmaking potential of freshly baked and frozen bakery products during partial replacement of wheat flour with spelt flour. *Food Sci. Technol. Int, 26*:485–92. https://doi.org/10.1177/1082013220905379

Geisslitz S, Longin CFH, Scherf K, Koehler P (2019) Comparative study on gluten protein composition of ancient (einkorn, emmer and spelt) and modern wheat species (durum and common wheat). *Foods, 8*(9):409. https://doi.org/10.3390/foods8090409

Gomez-Becerra HF, Erdem H, Yazici A, Tutus Y, Torun B, Ozturk L, Cakmak I (2010) Grain concentrations of protein and mineral nutrients in a large collection of spelt wheat grown under different environments.

J. Cereal Sci, 52(3):342–49. https://doi.org/10.1016/j.jcs.2010.05.003

Goriewa-Duba K, Duba A, Suchowilska E, Wiwart M (2020) An analysis of the genetic diversity of bread wheat x spelt breeding lines in terms of their resistance to powdery mildew and leaf rust. *Agronomy, 10*(5):658. https://doi.org/10.3390/agronomy10050658

Goriewa-Duba K, Duba A, Kwiatek M, Wiśniewska H, Wachowska U, Wiwart M (2018) Chromosomal distribution of pTa-535, pTa-86, pTa-713, 35S rDNA repetitive sequences in interspecific hexaploid hybrids of common wheat (*Triticum aestivum* L.) and spelt (*Triticum spelta* L.). *PLOS ONE, 13*(8):e0203162. https://doi.org/10.1371/journal.pone.0203162

Goriewa-Duba K, Duba A, Wachowska U, Wiwart M (2018) An evaluation of the variation in the morphometric parameters of grain of six *Triticum* species with the use of digital image analysis. *Agronomy, 8*(12):296. https://doi.org/10.3390/agronomy8120296

Hospodarenko GM, Liubych VV, Polianetska IO (2016) The amino acid content of spelt wheat protein depending on the origin of variety and strain. *Bulletin of the Uman national university of horticulture, 2*: 44–8.

Greenwood JR, Finnegan EJ, Watanabe N, Trevaskis B, Swain SM (2017) New alleles of the wheat domestication gene *Q* reveal multiple roles in growth and reproductive development. *Development, 144*(11):1959–65. https://doi.org/10.1242/dev.146407

Guerrini L, Parenti O, Angeloni G, Zanoni B (2019) The bread making process of ancient wheat: a semi-structured interview to bakers. *Journal of Cereal Science, 87*:9–17. https://doi.org/10.1016/j.jcs.2019.02.006

Guzmán C, Alvarez JB (2016) Wheat waxy proteins: Polymorphism, molecular characterization and effects on starch properties. *Theor. Appl. Genet, 129*:1–16. https://doi.org/10.1007/s00122-015-2595-9

Guzmán C, Caballero L, Moral A, Alvarez JB (2010) Genetic variation for waxy proteins and amylose content in Spanish spelt wheat (*Triticum spelta* L.). *Genet Resour Crop Evol, 57*:721–5. https://doi.org/10.1007/s10722-009-9507-2

Guzmán C, Caballero L, Yamamori M, Alvarez JB (2012) Molecular characterization of a new waxy allele with partial expression in spelt wheat. *Planta, 235*:1331–39. https://doi.org/10.1007/s00425-011-1577-7

Guzmán C, Ibba MI, Álvarez JB, Sissons M, Morris C (2022) Wheat quality. In: Reynolds MP, Braun HJ (eds) Wheat Improvement. Springer, Cham, Switzerland, pp. 177–193. http://dx.doi.org/10.1007/978-3-030-90673-3_11

Hammed AM, Simsek S (2014) Hulled wheats: a review of nutritional properties and processing methods. *Cereal Chemistry, 91*(2):97–104. https://doi.org/10.1094/CCHEM-09-13-0179-RW

Huertas-Garcia A, Tabbita F, Alvarez J, Sillero JC, Ibba M, Rakszegi M, Guzman C (2023) Genetic variability for grain components related to nutritio l quality in spelt and common wheat. *Journal of Agricultural and Food Chemistry, 71*(28):10598–606. https://doi.org/10.1021/acs.jafc.3c02365

Hyles J, Bloomfield MT, Hunt JR, Trethowan RM, Trevaskis B (2020) Phenology and related traits for wheat adaptation. *Heredity, 125*:417–30. https://doi.org/10.1038/s41437-020-0320-1

Iqbal A, Ahmad N, Roman M, HlisnikovskýL, Jiří H, Hejcman G (2026) Performance assessment of diverse spelt wheat (*Triticum spelta* L.) genotypes across three years seasons in Central Europe. *Int. Journal of Plant Production, 20*:28 https://doi.org/10.1007/s42106-026-00412-3

Jang YR, Cho K, Kim SW, Altenbach SB, Lim SH, Sim JR, et al (2020) Development of an optimized MALDI-TOF-MS method for high-throughput identification of high-molecular-weight glutenin subunits in wheat. *Molecules, 25*(18):4347. https://doi.org/10.3390/molecules25184347

Johnson ER, Nalam VJ, Zemetra RS, Riera-Lizarazu O (2008) Mapping the compactum locus in wheat (*Triticum aestivum* L.) and its relationship to other spike morphology genes of the Triticeae. *Euphytica, 163*(2):193–201. https://doi.org/10.1007/s10681-007-9628-7

Kandić V, Nikolić V, Simić M, Žilić S, Stevanović M, Mandić D, Dodig D (2023) Spelt wheat (*Triticum spelta*) and common bread wheat compared for nutritional contents and functional-technological properties. *Chil. J. Agric. Res, 83*(2). http://dx.doi.org/10.4067/s0718-58392023000200146

Kislev M (1984) Emergence of wheat agriculture. *Paléorient, 10*(2):61–70.

Koenig A, Konitzer K, Wieser H, Koehler P (2015) Classification of spelt cultivars based on differences in storage protein compositions from wheat. *Food Chemistry, 168*:176–82. https://doi.org/10.1016/j.foodchem.2014.07.040

Kohajdová Z, Karovičová J (2008) Nutritional value and baking applications of spelt wheat. *Acta Scientiarium Polonorum, Technologia Alimentaria, 7*(3): 5–14.

Kohler-Schneider M, Caneppele A (2009) Late neolithic agriculture in eastern Austria: archaeobotanical results from sites of the Baden and Jevišovice cultures (3600–2800 bc). *Veget Hist Archaeobot, 18*:61–74. https://doi.org/10.1007/s00334-007-0129-3

Konopka I, Tańska M, Pszczółkowska A, Fordoński G, Kozirok W, Olszewski J (2007) The effect of water stress on wheat kernel size, color and protein composition. *Pol J. Nat. Sci, 22*(2):157–71. https://doi.org/2478/v10020-007-0016-5

Kozub NA, Boguslavskii RL, Sozinov IA, Tverdokhleb YeV, Xynias IN, Blume YaB, Sozinov AA (2014) Alleles at storage protein loci in *Triticum spelta* L. accessions and their occurrence in related wheats. *Cytology and Genetics, 48*(1):33–41. https://doi.org/10.3103/S0095452714010046

Kozub NA, Sozinov IA, Niniyeva AK, Tverdokhleb YeV, Blume YaB, Boguslavskii RL (2016) Genetic marking of glume color in *Triticum spelta* L. var. *caeruleum* using gliadins. *Cytology and Genetics, 50*(3):168–72. https://doi.org/10.3103/S0095452716030075

Kraska P, Andruszczak S, Gawlik-Dziki U, Dziki D, Kwiecinska-Poppe E (2020) Wholemeal spelt bread enriched with green spelt as a source of valuable nutrients. *Processes, 8*(4):389. https://doi.org/10.3390/pr8040389

Kulathunga J, Reuhs BL, Zwinger S, Simsek S (2021) Comparative study on kernel quality and chemical composition of ancient and modern wheat species: Einkorn, emmer, spelt and hard red spring wheat. *Foods, 10*(4):761. https://doi.org/10.3390/foods10040761

Lafiandra D, Riccardi GM, Shewry PR (2014) Improving cereal grain quality for diet and health. *Journal of Cereal Science, 59*(3):312–26. https://doi.org/10.1016/j.jcs.2014.01.001

Lantos C, Pauk J (2021) In vitro anther culture for doubled haploid plant production in spelt wheat. In: Segui-Simarro JM (eds) Doubled haploid technology. Methods in molecular biology, Humana, New York 2287:257–266. https://doi.org/10.1007/978-1-0716-1315-3_13

Lechterbeck J, Kerig T (2024) Inventions, innovations and the origins of spelt wheat. *Vegetation History and Archaeobotany, 33*:547–557. https://doi.org/10.1007/s00334-023-00978-2

Lin BW, Gong CC, Song HF, Cui YY (2017) Effects of anthocyanins on the prevention and treatment of cancer. *Br J Pharmacol, 174*(11):1226–43. https://doi.org/10.1111/bph.13627

Longin CFH, Afzal M, Pfannstiel J, Bertsche U, Melzer T, Ruf A, Heger C, Pfaff T, Schollenberger M, Rodehutscord M (2023) Mineral and phytic acid content as well as phytase activity in flours and breads made from different wheat species. *International Journal of Molecular Science, 24*(3):2770. https://doi.org/10.3390/ijms24032770

Longin CFH, Beck H, Gütler A, Gütler H, Heilig W, Zimmermann J, Bischoff SC, Würschum T (2020) Influence of wheat variety and dough preparation on FODMAP content in yeast-leavened wheat breads. *Journal of Cereal Science, 95*:103021. https://doi.org/10.1016/j.jcs.2020.103021

Longin CFH, Ziegler J, Schweiggert R, Koehler P, Carle R, Würschum T (2016) Comparative study of hulled (einkorn, emmer, and spelt) and naked wheats (durum and bread wheat): agronomic performance and quality traits. *Crop Sci, 56*:302–11. https://doi.org/10.2135/cropsci2015.04.0242

McIntosh RA, Yamazaki Y, Dubuvsky J, Roger J, Morris C, Appels R, Xia XC. Catalogue of gene symbols for wheat. 12th International Wheat Genetics Symposium; Yokohama, Japan; 8–13 September 2013.

Mikos M, Podolska G. (2012) Bread-making quality of old common bread (*Triticum aestivum* ssp. *vulgare* L.) and spelt (*Triticum aestivum* ssp. *spelta* L.) wheat cultivars. *Journal of Food, Agriculture and Environment, 10*(3–4): 221–4.

Morgun VV, Radchenko OM, Dubrovna, OV (2025) Spelt wheat: biological properties and economic significance. *Fìzìol. rosl. genet, 57*(2):117–36. https://doi.org/10.15407/frg2025.02.117

Morgun VV, Sichkar SM, Pochunok VM, Ninieva AK, Chuhunkova TV (2016) Characterization of spelt wheat (*Triticum spelta* L.) collection accessions by performance elements and bread-making quality. *Fiziol. rosl. genet, 48*(2):112–9.https://doi.org/10.15407/frg2016.02.112

Muterko A, Balashova I, Cockram J, Kalendar R, Sivolap Y (2015) The new wheat vernalization response allele *Vrn-D1s* is caused by DNA transposon insertion in the first intron. *Plant Mol. Biol. Repor, 33*:294–303. https://doi.org/10.1007/s11105-014-0750-0

Muterko A, Salina E (2019) *VRN1*-ratio test for polyploid wheat. *Planta, 250*:1955–65. https://doi.org/10.1007/s00425-019-03279-z

Ninieva AK, Kozub NO, Sozinov IO, Leonov OYu, Rybalka OI, Tverdokhleb EV, Boguslavsky R (2013) Characterization of *Triticum spelta* L. accessions for grain quality and electrophoretic spectra of storage proteins. *The Bulletin of Vavilov Society of Geneticists and Breeders of Ukraine, 11*(1):96–105.

Palomino C, Cabrera A (2023) Evaluation of the allelic variations in vernalisation (*VRN1*) and photoperiod (*PPD1*) genes and genetic diversity in a spanish spelt wheat collection. *Int. J. Mol. Sci, 24*(22):16041. https://doi.org/10.3390/ijms242216041

Peña-Chocarro L, Pérez-Jordà G, Alonso N, Antolin F, Teira-Brion A, Teresa JP, Moya EMM, Reyes DL (2019) Roman and medieval crops in the Iberian Peninsula: a first overview of seeds and fruits from archaeological sites. *Quat Int., 499*:49–66. https://doi.org/10.1016/j.quaint.2017.09.037

Podolska G, Aleksandrowicz E, Szafrańska A (2020) Bread making potential of *Triticum aestivum* and *Triticum spelta* species. *Open Life Sciences, 15*(1):30–40. https://doi.org/10.1515/biol-2020-0004

Porto AL, Ingraffia R, Amato G, Frenda AS, Gargano G, Guarino S, Ruisi P, Viola E, Settanni L, Giambalvo D (2025) Evaluation of einkorn, emmer and spelt genotypes through an integrated approach: Agronomic performance, chemical composition, aromatic profile, bread characteristics and consumers' perception. *Journal of Cereal Science, 126*:104303. https://doi.org/10.1016/j.jcs.2025.104303

Rachon L, Bobryk-Mamczarz A, Kiełtyka-Dadasiewicz A (2020) Hulled wheat productivity and quality in modern agriculture against conventional wheat species. *Agriculture, 10*(7):275. https://doi.org/10.3390/agriculture10070275

Rachoń L, Szumiło G, Szafrańska A, Kotyrba D (2016) Bread-making potential of selected spring wheat species depending on crop year and production technology intensity. *Zemdirbyste-Agriculture, 103*(4):369–76. https://doi.org/10.13080/z-a.2016.103.047

Rapp M, Beck H, Gütler H, Heilig W, Starck N, Römer P, Cuendet C, Uhlig F, Kurz H, Würschum T, Longin CFH (2017) Spelt: Agronomy, quality, and flavor of its breads from 30 varieties tested across multiple environments. *Crop Science, 57*(2):739–47. https://doi.org/10.2135/cropsci2016.05.0331

Rakszegi M, Tóth V, Tömösközi S, Jaksics E, Cseh A, Karsai I, Mikó P (2025) Inter-and intraspecific study on compositional quality traits of diverse sets of spelt and common wheat. *Journal of Cereal Science, 123*(4):104162. https://doi.org/10.1016/j.jcs.2025.104162

Riesen T, Winzeler H, Ruegger A, Fried M (2008) The Effect of Glumes on Fungal Infection of Germinating Seed of Spelt (*Triticum spelta* L.) in Comparison to Wheat (*Triticum aestivum* L.) *Journal of Phytopathology, 115*(4):318–24 DOI: 10.1111/j.1439-0434.1986.tb04344.x

Rodriguez-Quijano M, Nieto-Taladriz MT, Carrillo JM (1998) Polymorphism of waxy proteins in Iberian hexaploid wheats. *Plant Breed, 117*(4):341–4. https://doi.org/10.1111/j.1439-0523.1998.tb01951.x

Rodríguez-Quijano M, Vargas-Kostiuk ME, Ribeiro M, Callejo MJ (2019) *Triticum aestivum* ssp. vulgare and ssp. spelta cultivars. 1. Functional evaluation. *Eur Food Res Technol, 245*:1561–70. https://doi.org/10.1007/s00217-019-03263-7

Rybalka OI, Polyshchuk SS, Chervonys MV, Morgun VV, Morgun BV (2024) Unique spelt wheat (*Triticum aestivum* ssp. *spelta* L.) with dark-purple grain color. *Fiziol. rosl. genet., 56*(5):419–30. https://doi.org/10.15407/frg2024.05.419

Safdar LB, Dugina K, Saeidan A, Yoshicawa GV, Caporaso N, Gapare B, Umer MJ, Bhosale RA, Searle IR, Foulkes MJ, Boden SA, Fisk ID (2023) Reviving grain quality in wheat through non-destructive phenotyping techniques like hyperspectral imaging. *Food Energy Secur, 12*(5):e498. https://doi.org/10.1002/fes3.498

Salarov M, Filipčhev B (2020) Spelt vs common wheat: potential advances and benefits. *Acta Innovations, 35*:57–64. https://doi.org/10.32933/ActaInnovations.35.4

Seabra L, Tereso J, Bettencourt AMS, Dinis A (2018) Crop diversity and storage structures in the settlement of Crastoeiro (Northwest Iberia): new approaches. *Trab De Prehist, 75*(2):361–78. https://doi.org/10.3989/tp.2018.12221

Shelepov VV, Gavrilyuk NN, Vergunov VA (2013) Wheat: biology, morphology, selection, seed production (ed) Kyiv: Logos.

Shewry PR, Hawkesford MJ, Piironen V, Lampi AM, Gebruers K, Boros D, Andersson AAM, Aman P, Rakszegi M, Bedo Z, Wardi JL (2013) Natural variation in grain composition of wheat and related cereals. *Journal of Agricultural and Food Chemistry, 61*(35):8295–303 https://doi.org/10.1021/jf3054092

Schober TJ, Clarke CI, Kuhn M (2002) Characterization of functional properties of gluten proteins in spelt cultivars using rheological and quality factor measurements. *Cereal Chemistry, 79*(3):408–17. http://dx.doi.org/10.1094/CCHEM.2002.79.3.408

Simonetti MC, Bellomo MP, Laghetti G, Perrino P, Simeone R, Blanco A (1999) Quantitative trait loci influencing free-threshing habit in tetraploid wheats. *Genet. Resour Crop. Evol, 46*:267–71. https://doi.org/10.1023/A:1008602009133

Simons KJ, Fellers JP, Trick HN, Zhang Z, Tai YS, Gill BS, Faris JD (2006) Molecular characterization of the major wheat domestication gene *Q*. *Genetics, 172*(1):547–55. https://doi.org/10.1534/genetics.105.044727

Singh A, Kaur V, Kaler R.S.S (2018). A review on dietary fiber in cereals and its characterization. *J. of Applied and Natural Science, 10*(4):1216–25. https://doi.org/10.31018/jans.v10i4.1894

Sobczyk A, Pycia K, Stankowski S, Jaworska G, Kuzniar P (2017) Evaluation of the rheological properties of dough and quality of bread made with the flour obtained from old cultivars and modern breeding lines of spelt (*Triticum aestivum* ssp. *spelta*). *J Cereal Sci, 77*:35–41. https://doi.org/10.1016/j.jcs.2017.07.013

Sousa T, Ribeire M, Sabenca C, Igrejas G (2021) The 10,000-year success story of wheat. *Foods, 10*(9):2124. https://doi.org/10.3390/foods10092124

Spetsov P, Daskalova N (2024) Allelic variation of high-molecular-weight glutenin genes in *Triticum* species and triticale (× *Triticosecale* Wittmack). *OBM Genetics, 8*(2). http://dx.doi.org/10.21926/obm.genet.2402225

Srinivasa J, Arun B, Mishra VK, Chand R, Sharma D, Bhardwaj SC, Joshi AK (2014) Accessing spelt gene pool to develop well-adapted zinc- and iron-rich bread wheat. *Crop. Sci, 54*:2000–10. https://doi.org/10.2135/cropsci2013.12.0801

Stepien A, Wojtkowiak K (2013) Composition of gluten proteins in spring and winter wheat grains cultivated under conditions of varied fertilization. *Acta Agric Scand, Section B-Soil & Plant Science, 63*(7):588–94. https://doi.org/10.1080/09064710.2013.829866

Sztupecki W, Rhazi L, Depeint F, Aussenac T (2023) Functional and nutritional characteristics of natural or modified wheat bran non-starch polysaccharides: A literature review. *Foods, 12*(14):2693. https://doi.org/10.3390/foods12142693

Suchowilska E, Wiwart M, Kandler W, Krska R (2012) A comparison of macro- and microelement concentrations in the whole grain of four *Triticum* species. *Plant Soil Environ, 58*(3):141–47. https://doi.org/10.17221/688/2011-PSE

Suchowilska E, Wiwart M, Krska R, Kandler W (2020) Do *Triticum aestivum* L. and *Triticum spelta* L. hybrids constitute a promising source material for quality breeding of new wheat varieties? *Agronomy, 10*(1):43 https://doi.org/10.3390/agronomy10010043

Sugar E, Fodor N, Sandor R, Bonis P, Vida G, Arendas T (2019) Spelt wheat: An alternative for sustainable plant production at low N-levels. *Sustainability, 11*:6726. https://doi.org/10.3390/su11236726

Takac V, Tóth V, Rakszegi M, Mikić S, Mirosavljević M, Kondić-Špika A (2021) Differences in processing quality traits, protein content and composition between spelt and bread wheat genotypes grown under conventional and organic production. *Foods, 10*(1):156. https://doi.org/10.3390/foods10010156

Thorup AC, Gregersen S, Jeppesen PB (2014) Ancient wheat diet delays diabetes development in a type 2 diabetes animal model. *Rev Diabet Stud, 11*(3):245–57. https://doi.org/10.1900/rds.2014.11.245

Tóth V, Láng L, Vida G, Mikó P, Rakszegi M (2022) Characterization of the protein and carbohydrate related quality traits of a large set of spelt wheat genotypes. *Foods, 11*:2061. https://doi.org/10.3390/.foods11142061

Tverdokhlib OV, Holik OV, Niniyeva AK, Bohuslavs’kyy RL (2013) Spelt in organic farming. Handbook of the Ukrainian farmer. 154–155.

Valli V, Taccari A, Di Nunzio M, Danesi F, Bordoni A (2018) Health benefits of ancient grains. Comparison among bread made with ancient, heritage and modern grain flours in human cultured cells. *Food Research International, 107*: 206–15. https://doi.org/10.1016/j.foodres.2018.02.032

Valsalan A, Hucl P, Malalgoda M (2025) Evaluating the breadmaking potential of wholemeal flours from einkorn, emmer, and spelt grown in the Canadian prairies. *Cereal Chemistry, 102*(3):506–19. https://doi.org/10.1002/cche.10865

Waga J, Węgrzyn S, Boros D, Cygankiewicz A (2002) Utilization of spelt wheat (*Triticum aestivum* ssp. *spelta*) for improving the nutritional qualities of common wheat (*Triticum aestivum* ssp. *vulgare*). *Biuletyn instytutu hodowli i aklimatyzacji roślin, 221*:3–16. https://doi.org/10.37317/biul-2002-0083

Wang Y, Wang Z, Chen Y, Lan T, Wang X, Liu G, Xin M, Hu Z, Yao Y, Ni Z, Sun Q, Guo W, Peng H (2024) Genomic insights into the origin and evolution of spelt (*Triticum spelta* L.) as a valuable gene pool for modern wheat breeding. *Plant Comm, 5*(5):100883. https://doi.org/10.1016/j.xplc.2024.100883

Watson A, Ghosh S, Williams MJ, Cuddy WS, Simmonds J, Rey M, Hatta M, Hinchliffe A, Steed A, Reynolds T, Adamski N, Breakspear A, Korolev A, Rayner T, Dixon L, Riaz A, Martin W, Ryan M, Edwards D, Batley J, Raman H, Carter J, Rogers C, Domoney C, Hickey LT (2018) Speed breeding is a powerful tool to accelerate crop research and breeding. *Nature Plants, 4*:23–9. https://doi.org/10.1038/s41477-017-0083-8

Wilson JD, Bechtel DB, Wilson GWT, Seib PA (2008) Bread quality of spelt wheat and its starch. *Cereal Chemistry, 85*(5):629–38. https://doi.org/10.1094/CCHEM-85-5-0629

Wiwart M, Szafrańska A, Wachowska U, Suchowilska E (2017) Quality parameters and rheological dough properties of 15 spelt (*Triticum spelta* L.) varieties cultivated today. *Cereal Chemistry, 94*(6):1037–44. https://doi.org/10.1094/CCHEM-05-17-0097-R

Xie Q, Mayes S, Sparkes DL (2015) Spelt as a genetic resource for yield component improvement in bread wheat. *Plant Genetic Resources, 55*(6): 2753–65 https://doi.org/10.2135/cropsci2014.12.0842

Yan L, Loukoianov A, Tranquilli G, Helguera M, Fahima T, Dubcovsky J (2003) Positional cloning of the wheat vernalization gene *VRN1*. *Proc. Natl. Acad. Sci, 100*(10):6263–8. https://doi.org/10.1073/pnas.0937399100

Zaika N, Karpuk L (2023) Yield and quality of spelta grain (*Tríticum spélta* L.) in the conditions of the Forest Steppe of Ukraine. *Agrobiology, (1)*:114–22. https://doi.org/10.33245/2310-9270-2023-179-1-114-122

Zamaratskaia G, Gerhardt K, Wendin K (2021) Biochemical characteristics and potential applications of ancient cereals — An underexploited opportunity for sustainable production and consumption. *Trends in Food Science & Technology, 107*:114–23. https://doi.org/10.1016/j.tifs.2020.12.006

Zhao Y, Xie P, Guan P, Wang Y, L, Y, Yu K, Xin M, Hu Z, Yao Y, Ni Z (2019) Btr1-A induces grain shattering and affects spike morphology and yield-related traits in wheat. *Plant and Cell Physiology, 60*(6):1342–53. https://doi.org/10.1093/pcp/pcz050

Zhao Z, Dent C, Liang H, Lv J, Shang G, Liu Y, Liu H, Feng F, Wang F, Pang J, Li X, Ma L, Li B, Sureshkumar S, Wang JW, Balasubramanian S, Liu H (2022) CRY2 interacts with CIS1 to regulate thermosensory flowering via FLM alternative splicing. *Nature communications, 13*(1):7045. https://doi.org/10.1038/s41467-022-34886-2

Zohary D, Hopf M (2000) Domestication of plants in the old world, 3rd edn. New York, Oxford

Zvedenyuk T. Spelt is a cereal from the Stone Age (2013) *Grain, 7*:82–90.

Żuk-Gołaszewska K, Majewska K, Tyburski J, Gołaszewski J (2022) Nutritional properties of organic spelt wheats in different growth stages and the resulting flours. *J. Elem, 27*(3): 645–62. https://doi.org/10.5601/jelem.2022.27.1.2267

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БІОЛОГІЧНІ ВЛАСТИВОСТІ ПШЕНИЦІ СПЕЛЬТИ ТА ПЕРСПЕКТИВИ ЇЇ ВИКОРИСТАННЯ У СЕЛЕКЦІЇ

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Пшениця спельта (*Triticum aestivum* ssp. *spelta* (L.) Thell.) – різновид плівчастої пшениці, геном якої такий самий, як у гексаплоїдної м’якої пшениці (*T. aestivum* L.) та характеризується багатьма цінними властивостями, серед яких стійкість рослин до патогенів, краща адаптивність до несприятливих чинників довкілля, підвищений вміст білка в зерні, харчові цінності зерна. В останні роки популярність і використання спельти у світі, й Україні зокрема, невпинно зростає, що пов’язано із розвитком органічного землеробства, а також з потребою у високій якості продуктів харчування, яку забезпечує дана культура. У зв’язку з цим метою даного огляду було представити сучасний стан досліджень біологічних властивостей пшениці спельти, а також перспективи її використання у селекції. Коротко розглянуто сучасні гіпотези походження даної культури, її поширення у світі та Україні, а також біологічні характеристики цього злаку. Детально висвітлено генетичні особливості спельти, зокрема гени морфологічних ознак, яровизації та фотоперіоду, варіабельність генів ваксі. Описаний поліморфізм за генами запасних білків та поширеність їх алелів, які можуть бути використані як маркерні системи та джерело збагачення генофонду м’якої пшениці. Представлено сучасні дані про якість зерна спельти, зокрема його фізичні властивості, хімічний склад, функціонально-технологічні та хлібопекарські властивості борошна. Висвітлено фізіологічний ефект споживання спельти. Розглянуто цей злак як джерело корисних генів для селекції м’якої пшениці. Представлено відомості про сучасні стратегії та нові наукові напрями генетичного поліпшення даної культури.

Ключові слова: *Triticum spelta*, походження, поширення, біологічні властивості, генетичні особливості, якість зерна, використання в селекції.