Theoretical and Experimental Cryobiology

https://doi.org/10.15407/cryo35.02.149
UDC: 536.485:633.1

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STORAGE OF CEREAL SEEDS AT 4 °C

Seed longevity was studied for wheat (Triticum aestivum): var. erythrospermum, var. lutescens spring and winter bread; spring durum wheat (Triticum durum): var. hordeiforme, var. leucurum, var. melanopus, var. alexandrinum; winter rye (Secale cereale) subsp. cereale var. vulgare; spring barley (Hordeum vulgare): var. nutans, var. erectum, var. rikotense, var. nudum, var. pallidum; maize (Zea mays) subspecies: popcorn (subsp. everta), flint corn (subsp. indurata), dent corn (subsp. indentata), semident corn (subsp. semidentata), sweet (subsp. saccharata) when stored at a temperature 4 °C and seed moisture content of 6—7%. We assessed the germination dynamics of 41 samples of these genotypes during storage for up to 10 years. For most samples, no significant differences in germination were found as compared to the initial one. In some cases, an increase in seed germination was observed after 4—8 years of storage. Variations in seed germination depending on sample genotype were tracked. The paper analyses differences in seed longevity of different cultivars of studied species and discusses the effect of low temperatures on seed longevity and expression of genes, especially those that enhance abscisic acid catabolism.

Key words: *seeds, wheat, rye, barley, maize, low temperature, germination, longevity, abscisic acid.*

According to Ervart's classification, seeds of most cereal crops stored under natural conditions belong to mesobiotic seeds [14], *i. e.* seeds with a shelf life of 3 to 15 years under normal conditions.

At the current stage of scientific and industrial development, the need for seed storage is essential. There are special recommendations for optimising the grain crop seed storage for the industry of Ukraine. In particular, wheat, rye, barley and maize seeds should be stored at moisture content not more than 14% [3, 4, 6, 7].

For medium-term seed storage in gene banks, a temperature of 5—10 °C and relative humidity of 15 ± 3 % are recommended, and a temperature of −18 ± 3 °C and relative humidity of 15 ± 3 % for long-term one [9]. There is experience of seed storage under controlled and uncontrolled humidity, as well as under controlled positive and negative temperatures [21, 26, 23, 14, 25, 31, 32].

Storage of bread wheat seeds grown in the north-eastern forest-steppe of Ukraine allows, at seed moisture content of 6—7% in sealed containers, even in storage facilities with uncontrolled tempe-ratures, to maintain the initial seed germination rate above 90% for 9 years without significant changes [21]. Storage of durum wheat samples under controlled seed moisture conditions of 6—8% and initial germination of over 90%, even in a storage facility with uncontrolled temperature, ensured initial germination without changes for at least 10 years. No differences in seed longevity of different durum wheat varieties were observed [23].

When comparing the seed longevity of bread wheat (*Triticum aestivum* L.) and durum wheat (*T. durum* Desf.), it has been established that under model conditions at seed moisture content of 12–14 % and a temperature of 37 °C, the longervity of durum wheat seeds significantly exceeds that of

Reference: Zadorozhna OA, Shyianova TP. Storage of cereal seeds at 4 °C. *Probl Cryobiol Cryomed*. 2025; 35(3): 149—56. https://doi.org/10.15407/cryo35.02.149

bread wheat seeds. Under these model conditions, durum wheat had better germination rates in the early stages of ageing [20, 29].

Rye (*Secale cereale* L.) seed storage at low positive temperature and moisture content of 6—7% allows storing the samples for about 10 years with germination rate of at least 80% from an initial 90. Rye seed storage with moisture content of 5—7% in a storage facility at uncontrolled temperature in eastern forest-steppe zone of Ukraine for 42 months did not lead to a significant decrease of initial seed germination [22, 26, 27].

Barley (*Hordeum vulgare* L.) seed storage with moisture content of 5—8% in a storage facility with uncontrolled temperature also showed no significant changes in germination over 10 years, with an initial germination rate of at least 90% [24].

Similar results were observed for different varieties of maize (*Zea mays* L.). Low positive temperatures were used to extend the seed longevity during medium-term storage [25].

The aim of this study was to analyse the longevity of cereal seeds, such as wheat, rye, barley and maize, at storage temperature of 4 °C and to elucidate changes in seed germination under these storage conditions.

MATERIALS AND METHODS

The material for the research were seeds of bread wheat (*Triticum aestivum* L.) of different varieties: var. *erythrospermum* (Koern.) Mansf. spring — Rannia 93, winter — Albatros Odeskyi, Kuialnik; var. *lutescens* (Alef.) Mansf. spring — Yevdokia, Kharkivska 26, Voronezhskaia 6; winter — Inna, Bazhana; durum wheat (*Triticum durum* Desf.) different varieties: var. *hordeiforme* (Host) Koern. — Zhyzel, Omskaia Yantarnaia; var. *leucurum* (Alef.) Koern. — CD 57005, Leukurum 343H1; var. *melanopus* (Alef.) Koern. — CD 63891, CD 56177; var. *alexandrinum* (Host) Koern. — Tremis Preto. Winter rye (*Secale cereale* L.) subsp. *cereale* var. *vulgare* Koern. seeds: Grozynske, Abraksas, Somro, Dozor, Gazelle, Liniia 693 zs, Polikrosne 2, Kharkivska 55 were also studied; baley (*Hordeum vulgare* L.) different varieties: var. *nutans* Schubl. — Franu 123, Parnas, Eskort, Nutans 778; var. *erectum* — Rezibee, var. *rikotense Reg.* — Etyket, var. *nudum* L. — UA0803771, var. *pallidum* Ser. UA0802005. Maize (*Zea mays* L.) seeds were also used as research material. We investigated subspecies: popcorn *(subsp. everta* Sturt.*)* — UB0102622, R16AA; flint corn *(subsp. indurata* Sturt.*)* — C.50, UKh576; dent corn *(subsp. indentata* Sturt.*)* — DK6A, Mistseva HK9; semident corn *(subsp. semidentata* Kulesh.*)* — GR185, C.76; sweet (subsp. *saccharata* Koern.) — KS 224, Grosby early.

Experimental seeds were dried with an air stream at a temperature not exceeding 25 °C and a relative humidity of 25% up to the recommended moisture content of 6—7%. After drying, the seeds were placed in airtight containers: multilayer foil bags and stored at a temperature of 4 °C. To determine seed germination at the beginning and during storage, the appropriate methods [5] were used, which include germination between sheets of filter paper depending on crop at a temperature of 20—25 °C for 7—8 days. During the study, the germination of at least 100 seeds was analysed. One seed was considered as a unit of variation. The germination of samples was compared using the criterion of sample fractions [13] and Excel software (Microsoft, USA).

RESULTS AND DISCUSSION

The results of studies showed that after 8 years of storage of bread spring and winter wheat seeds (var. *erythrospermum* and var. *lutescens)* at a temperature of 4 °C, the germination of most samples was not significantly changed. In seed samples of var. *lutescens* (Yevdokia) and var. *erythrospermum* (Albatros Odeskyi), we observed a significant increase in germination ($p < 0.05$) by 10 and 13%, respectively. No dependence of bread wheat seed longevity on variety and type of development was found (Fig. 1).

After 8 years of storage at 4 °C and moisture content of 7%, the germination of durum wheat seeds of such varieties as var. *hordeiforme*, var. *leucurum,* var. *melanopus*, var. *alexandrinum* did not change significantly. However, after 6 years of storage, most samples showed a tendency towards increased germination. No advantages in longevity of durum wheat seeds of individual varieties were found (Fig. 2).

After rye seed storage for 9–10 years at 4 °C and moisture content of 7%, the germination rate of most samples did not change significantly. However, the germination rate of Somro seeds increased significantly by 17% after 4 years of storage ($p < 0.05$), and that of Kodor seeds did by 9% after 9 years of storage ($p < 0.05$) (Fig. 3).

Germination of most spring barley seed samples of var. *erectum*, var. *nutans*, var. *pallidum*, var.

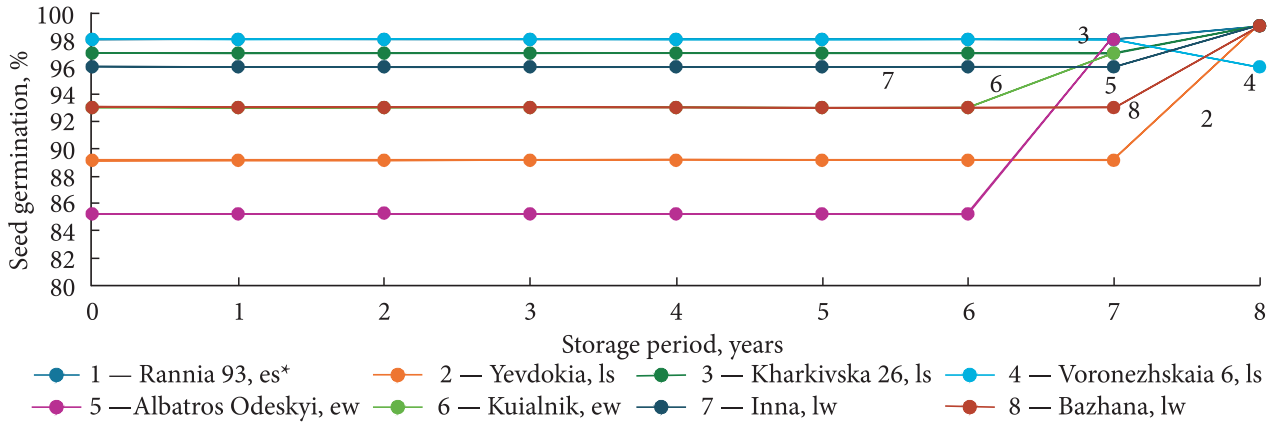

Fig. 1. Germination of bread wheat seeds stored at 4 °C; *es — var. *erythrospermum*, spring; ls — var. *lutescens*, spring; ew — var. *erythrospermum*, winter; lw — var. *lutescens*, winter. In samples 2 — Yevdokiia and 5 — Albatros Odeskyi, germination differs significantly from initial germination after 7—8 years of storage ($p < 0.05$)

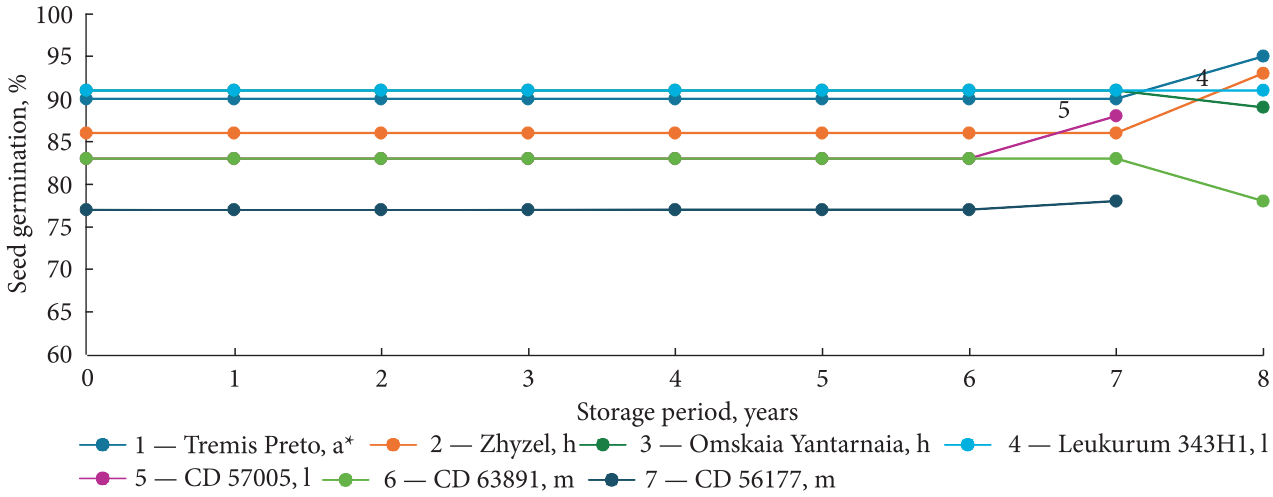

Fig. 2. Germination of durum wheat seeds stored at 4 °C: * a — var. *alexandrinum*, h — var. *hordeiforme*, l — var. *leucurum*, m — var. *melanopus*

nudum, and var. *rikotense* did not change significantly after 7—8 years of storage at 4 °C and 6% moisture content. However, after 7 years of storage, seed germination of samples UA0803771 and UA0802005 increased significantly by 17 and 23%, respectively ($p < 0.05$). Significant increase in germination rate by 15% ($p < 0.05$) was observed for Franu 123 after 8 years of storage. No advantages in the longevity of spring barley seeds of individual varieties were found (Fig. 4).

Storage of maize seeds of various subspecies: pop, flint, dent, semi-dent and sweet for 9 years at a temperature 4 °C and an average moisture content of 7.7% either did not change germination or caused its slight increase (Fig. 5). For example, the storage of sweet corn seeds under the specified conditions did not affect the germination of sample UB0102622, but increased it by 5% in sample R16AA ($p < 0.05$). Germination rate of both samples (C.50, UKh576) of flint corn remained unchanged. Storage of dent corn seeds did not change the germination rate of Mistseva NK, but improved it by 7% for DK6A ($p < 0.05$). Semi-dent maize seed storage did not affect the germination of sample GR185, but increased it by 8% for C.76 ($p < 0.05$). In sweet maize seeds after 7 years of storage at 4 °C, the germination of KS 224 augmented by 23% ($p < < 0.05$), while the germination of Grosby early remained unchanged (Fig. 5).

Thus, for maize stored at 4 °C and seed moisture content of 7.7%, there is a variation in longevity depending on sample genotype, with the general trend for all subspecies, *i. e.* maintenance of seed germination at the initial level or its improvement.

Effects of low positive temperatures on plants have been studied both at vegetative stage and at

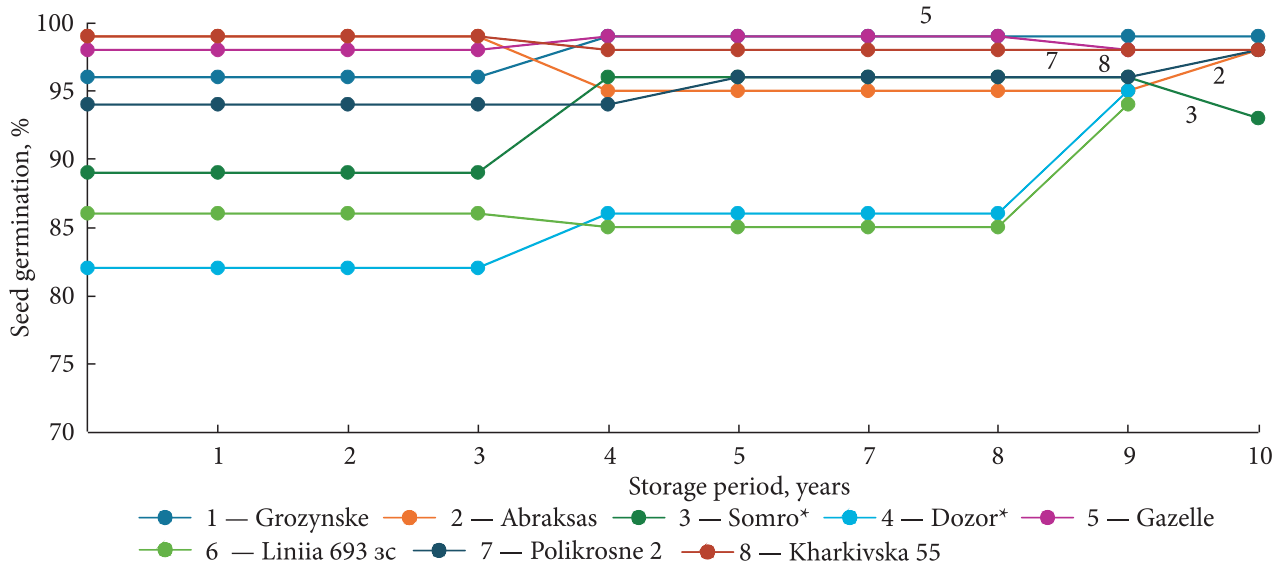

Fig. 3. Germination of rye seeds stored at 4 °C: * 3 — Somro, 4 — Dozor, significant difference from initial germination after 4 years of storage ($p < 0.05$)

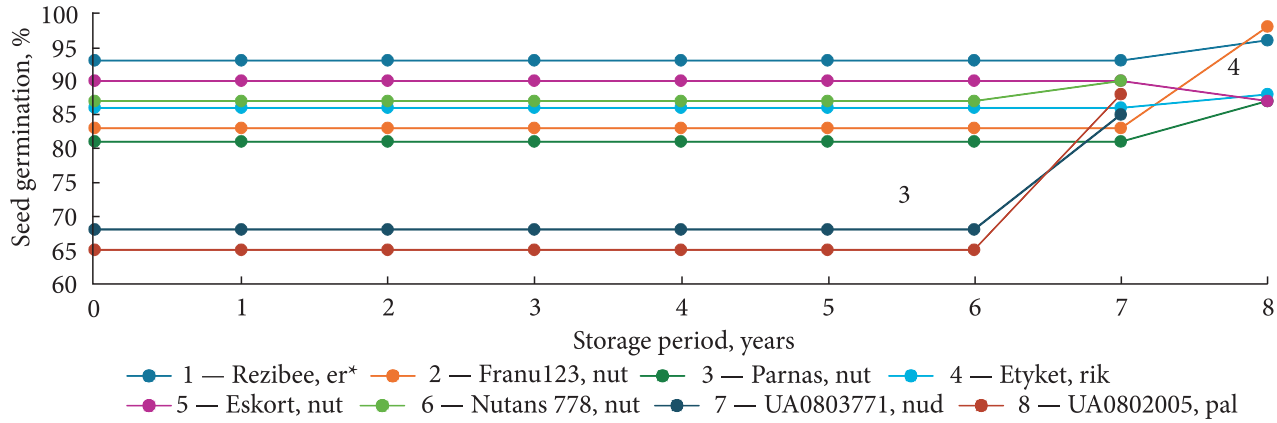

Fig. 4. Germination of barley seeds stored at 4 °C:* er — var. *erectum*, nut — var. *nutans*, pal — var. *pallidum*, rik — var. *rikotense*. In samples 2-Fran 123, 7-UA0803771, 8-UA0802005, germination differs significantly from the initial one after 7 years of storage ($p < 0.05$)

seed stage. Membrane stability is crucial for cold resistance, as cold-resistant plants are characterised by higher levels of lipid unsaturation, which ensures membrane fluidity and maintains normal metabolism. Low temperatures disrupt the exchange of reactive oxygen species, which can cause oxidative damage, that is mitigated by antioxidant protection. Additional adaptation to cold is also supported by hormonal regulation involving abscisic acid (ABA), auxin, gibberellins and other phytohormones [32].

Plant responses to low temperatures were analysed in terms of phenotype, hormonal status and signalling pathways in work of M. Yu [19]. Complex mechanisms have been identified by which plants respond to low-temperature stress, including numerous transcriptional and regulatory factors that influence the corresponding signalling pathways and play a decisive role in plant resistance.

Genes responsible for resistance to low temperatures have been identified in the model organism *Arabidopsis thaliana*. Thus, there is a wide range of ways in which plants overcome cold stress. The main ones are CBF (C-repeat binding factor), ABA-dependent photoregulation, and others. CBF genes are activated and expressed at low temperatures by specifically binding to the conserved structural domain of the COR (COLD-REGULATED) gene promoter, which leads to the accumulation of protective substances: osmoregulatory and cryoprotective proteins and increases tolerance to cold or freezing [24].

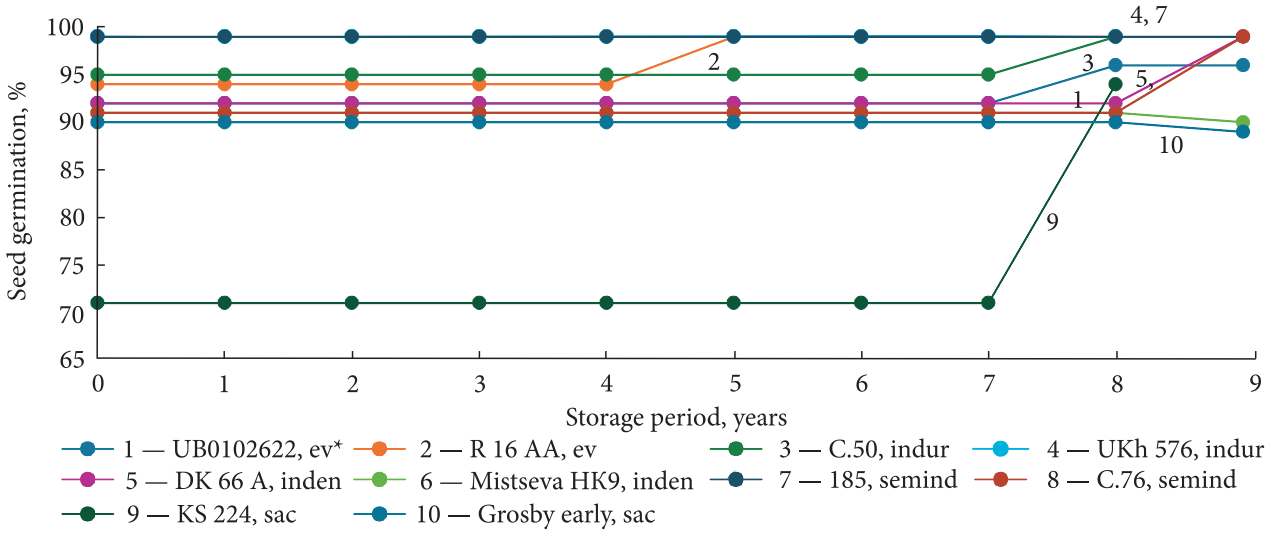

Fig. 5. Germination of maize seeds stored at 4 °C:* ev — popcorn (subsp. *everta*), indur — flint (subsp. *indurata*), inden — dent (subsp. *indentata*), semind — semi-dent (subsp. *semidentata*), sac — sweet (subsp. *saccharata*). In samples 2-R 16 AA, 5-DK 66 A, 8-C.76 and 9-KS 224, there was a significant difference from the initial germination rate after 5—9 years of storage ($p < 0.05$)

When plants are subjected to cold stress, complex biochemical and molecular adaptation mechanisms are activated and regulated by transcriptional and translational modifications of genes. These mechanisms are divided into ABA-dependent and ABA-independent pathways associated with the expression of relevant genes through the action of various transcription factors. In addition, transcriptional and post-translational modifications modulate gene expression in signalling cascade at different levels, ultimately leading to the acclimatisation of plants to low-temperature stress [2].

The state of dormancy and seed germination is regulated by many phytohormones. Ethylene, auxin and brassinosteroids promote seed germination in a state of dormancy, but it is believed that the leading regulators of this process are ABA and gibberellic acid (GA). Balanced ratio of ABA/GA, regulated by the dynamics of their synthesis and catabolism, determines the condition of seeds depending on their sensitivity to environmental factors [15]. For rice seeds, it has been established that low temperatures can affect gene expression enhancing that of genes involved in ABA catabolism (OsCYP707A family) and GA biosynthesis (OsGA20ox and OsGA3ox families).

To further understand the molecular mechanisms of rice seed embryo dormancy, additional research in needed, in particular comparative analysis of sequences and expression of genes that determine embryonic dormancy, and the design of gene regulation networks covering all stages of dormancy and germination [15].

The endogenous level of ABA is controlled by a complex of regulatory mechanisms, including biosynthesis, catabolism, transport, and signalling pathways. This complex regulatory network acts at levels of transcription, translation, and post-translational modifications. Most of the genes involved in ABA biosynthesis, catabolism and transport have been described, and the mechanisms regulating its metabolism have been identified. ABA perception by cell receptors and signalling pathways that respond to external conditions are known. Local ABA concentration is critical for triggering ABA-mediated signalling during plant development and in response to environmental changes [2].

This process is inhibited at high temperatures during germination, (thermoinhibition), involving ABA, GA and ethylene. The genes encoding 9-cis-epoxycarotenoid dioxygenase (NCEDs) are key to the induction of germination at high temperatures. Genes responsible for the biosynthesis of GA and ethylene are suppressed under these conditions, which limits germination. When the temperature decreases, the effect of ABA on germination inhibition weakens [8, 18].

Seed structure and properties depends on plant genes expression during seed maturation. Detected phenotypic variation made it possible to identify quantitative trait loci (QTL) that control seed

development in interaction with environmental factors (QTL × E) [10].

There are two critical phases in the life cycle of plants: seed germination and flowering which are regulated by genetic and environmental factors. The model plant *Arabidopsis thaliana* has been found to contain the DELAY OF GERMINATION1 (DOG1) gene, which is involved in regulating seed dormancy in response to temperature and is genetically linked to the control of flowering time in different ecotypes [12].

Current research into the genetic basis of seed viability variation involves genomics and transcriptomics use to identify candidate genes that influence seed germination and germination rate. It is believed that secondary and relative seed dormancy can be weakened over time under favourable conditions of light, temperature, post-harvest ripening and cooling [16].

The emergence from dormancy during cold storage of *Lilium pumilum* bulbs is accompanied by ultrastructural changes. Comparison of gene expression levels between samples during storage showed that regulatory pathways of carbohydrate metabolism and phytohormone signalling were activated. Some differentially expressed genes associated with antioxidant activity, epigenetic modifications, and transcription factors are induced in response to low temperatures, controlling the complex mechanisms of dormancy break [1].

For agricultural crops, seed germination at the level of phytohormone metabolism and gene expression under different environmental conditions has been studied insufficiently. For wheat seeds, the low storage temperatures were found to change the metabolism of carbohydrates, fatty acids, nucleotides, and amino acids, thereby ensuring the stability of cell structures and delaying oxidative processes [28].

Studies of maize seed storage model conditions at temperatures of 15, 20, and 35 °C and humidity of up to 15% [31] showed changes in metabolism of amino acids, glycerolipids, glycerophospholipids, starch, and sucrose during storage.

An increase in germination rate of maize and other cereal seeds can be explained by changes in gene expression, in particular the ABA signalling pathway, during exposure to low temperatures and seed emergence from dormancy [1, 2, 10, 20].

For dwarf turk's cap lily (*Lilium pumilum* DC.), the transcriptomic profiles of seeds stored at 20 and 4 °C were created based on RNA sequencing results. Principal component analysis showed the gene expression in lotus seeds to be more stable at 4 °C than at 20 °C. The expression levels of genes in the ABA signalling pathway were significantly suppressed at low temperatures [17].

Under model conditions for rye seeds at 4, −20 °C in the eastern forest-steppe zone of Ukraine, a correlation was found between the activity of ABA in seeds, storage temperature and seed mois-ture content. The lowest ABA activity was recorded at the lowest temperature ($r \geq 0.69$) and seed mois-ture content of 5%. So, we can expect that seeds will germinate the most rapidly under conditions of low temperature and low moisture content [28].

CONCLUSIONS

Thus, seeds of the studied samples of bread wheat (spring and winter), durum wheat, winter rye, com-mon barley and maize with moisture content of 6—7% at 4 °C were stored for up to 10 years without any change in germination or with its increase. In some cases, seed germination improved by 5—23% after 4—8 years of storage. Seed germination varied depending on sample genotype. No stable differences in seed longevity of different varieties of the studied species were found.

Based on our previous findings and those of other researchers, this increase in seed germination can be explained by changes in the expression of genes that control ABA metabolism during long-term seed exposure to low positive temperatures. Additional analysis of specific gene expression using orthological approach is required to provide a more detailed explanation of increased seed germination in the studied cereals.

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Received 31.03.2025
Accepted for publication 11.09.2025

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ЗБЕРІГАННЯ НАСІННЯ ЗЕРНОВИХ КУЛЬТУР ЗА 4 °С

Досліджено довговічність насіння зразків пшениці м'якої (*Triticum aestivum*): var. *erythrospermum*, var. *lutescens* ярої та озимої; пшениці твердої ярої (*Triticum durum*): var. *hordeiforme*, var. *leucurum*, var. *melanopus*, var. *alexandrinum*; жита посівного озимого (*Secale cereale*) *subsp. cereale* var. *vulgare*; ячменю звичайного (*Hordeum vulgare*): var. *nutans*, var. *erectum*, var. *rikotense*, var. *nudum*, var. *pallidum*; кукурудзи (*Zea mays*) підвидів: розлусна (*subsp. everta*), кремениста (*subsp. indurata*), зубувата (*subsp. indentata*), напівзубувата (*subsp. semidentata*), цукрова (*subsp. saccharata*) при зберіганні за температури 4 °С та вологості насіння 6—7 %. Оцінено динаміку схожості насіння 41 зразка зазначених генотипів протягом зберігання до 10 років. Для більшості зразків не виявлено істотних відмін схожості порівняно з вихідною. В окремих випадках спостерігали підвищення схожості насіння після 4—8 років зберігання. Відстежено варіювання схожості насіння залежно від генотипу зразка. У роботі аналізується наявність відмін за довговічністю насіння різних різновидів досліджених видів і обговорюється вплив низької температури на довговічність насіння та експресію генів, особливо посилюючих катаболізм абсцизової кислоти.

***Ключові слова*:** насіння, пшениця, жито, ячмінь, кукурудза, низька температура, схожість, довговічність, абсцизова кислота.