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Research Article

Insights into oilseed rape seed deterioration: accelerated ageing effects on lipid composition and germination processes

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Abstract

Although high-quality naturally refined oil is rich in unsaturated fatty acids that give it exceptional biological value and a distinctive role within human nutrition, precisely because of its chemical composition oilseed rape seeds have limited longevity. This study addresses the complex dynamics of oilseed rape seed deterioration, shedding light on the impact of accelerated and natural aging on lipid composition and subsequent effects on germination and early seedling growth. Seeds from four oilseed rape varieties underwent 72 hours of accelerated aging at 41 °C and 100% relative humidity. Gas chromatography was employed for fatty acid (FA) composition analysis after converting FAs into volatile methyl esters (FAME). Tocopherols were quantified using high-performance liquid chromatography with fluorescence detection. Results revealed high initial germination across all genotypes, with a notable decline after one year of storage. Double-stress conditions intensified this decline, emphasizing the vulnerability of seeds to elevated temperature and humidity. Genotypic differences in germination underscore distinct mechanisms for preserving vigour under stress. Both natural and accelerated aging induced a significant reduction in unsaturated fatty acids, notably oleic and eicosenoic acids. The study highlights the crucial role of tocopherols in mitigating oxidative stress and preserving seed quality during aging. Altered lipid composition emerged as a factor influencing seed viability and seedling morphology, particularly under short-term storage and deterioration conditions. The findings contribute to a deeper understanding of oilseed rape seed resilience and offer insights into potential strategies for enhancing seed storage and maintaining seed quality in the face of environmental stressors.

Keywords: fatty acid composition; oilseed rape; seed ageing; tocopherols

Introduction

The seed is the fundamental and most dependable unit for plant propagation; therefore, the quality of seeds is crucial for achieving consistent and high yields. Consequently, germination performance, seedling establishment, seed vigour and speed and uniformity of germination are the main criteria when assessing the

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value of the seed lot (Fabrissin *et al*., 2021). Given that intensive physiological processes take place even in dry seeds, regardless of the storage condition, preserving the seed quality should be imperative for plant production. During the seed ageing, noticeable damage can occur and prevent its ability to repair itself, which can eventually cause a loss of vitality (Bewley *et al*., 2013). Deterioration of seed can be observed as the number of changes over time that affect its vital functions until the final loss of vitality.

After soybeans (*Glycine max* (L.) Merr.) and palm (*Elaeis guineensis* Jacq.), oilseed rape (*Brassica napus* L.) is the largest source of vegetable oil in the world (USDA, 2024), while in Europe it is considered the dominant oil species due to widespread adaptation to temperate climates (Sun *et al*., 2017). Nowadays, this plant species has a wide practical range and is produced for high-quality edible oil, fodder, and biofuel industries (Pokharel *et al*., 2020). Edible rapeseed oil is especially valued because it contains a desirable composition of fatty acids, primarily unsaturated fatty acids, with the simultaneous presence of a significant content of healthy bioactive compounds (Chew, 2020). The use-value of oilseed oil depends on the ratio of certain fatty acids. The nutritional and industrial properties of an oil, as well as its commercial value, are influenced by its fatty acid composition. The quality of the oil is determined by the presence of unsaturated fatty acids, such as oleic and linoleic acids, while certain fatty acids, like eruca, are considered less desirable or even undesirable. Special importance is placed on linoleic acid, essential for human nutrition, as it cannot be synthesized in the body and must be obtained through dietary intake. Although high-quality naturally refined oil is abundant in unsaturated fatty acids, providing exceptional biological value and holding a distinctive role in human nutrition, the limited longevity of oilseed rape seeds is attributed to their chemical composition. The polyunsaturated fatty acids in the seeds are highly sensitive to peroxidant degradation.

Changes observed during the ageing process in seeds include modifications such as lipid peroxidation (Oenel *et al*., 2017; Jovičić *et al*., 2017), protein carbonylation (Li *et al*., 2022), chromosomal aberration (Taghvaei *et al*., 2023), decreases in mRNA translation (Zhao *et al*., 2020) and DNA damage (Fu *et al*., 2015) and programmed cell death. Furthermore, the consequence of seed deterioration is a significant decrease in the rate of respiration due to a decrease in the amount of reserve carbohydrates, which may later result in insufficient nutrients necessary for germination or the inability to use them (Pichardo-González *et al*., 2010). However, among all the changes that occur during seed ageing, the main biochemical processes observed are fatty acid peroxidation and protein glycation (Nguyen *et al*., 2015) – a process known as autoxidation (Lopez-Fernandez *et al*., 2018). This activity occurs in two phases: during the first phase, spontaneous oxidation of unsaturated fatty acids is observed, while the second phase takes place in seeds that have lost the ability to germinate and includes oxidation of both saturated and unsaturated fatty acids (Shaban, 2013).

This study aimed to contribute a better understanding of the mechanisms of oilseed rape seed deterioration, analysing and comparing changes in the lipid composition during the conditions of natural and accelerated ageing of the seed and its influence on the process of seed germination and early seedling growth. The insight gained from these mechanisms is essential for the development of effective storage and preservation techniques, ensuring the maintenance of seed quality and viability over extended periods.

Materials and Methods

Germination assay

Seeds from four varieties of oilseed rape ('Jovana', 'Zorica', 'Zlatna', 'Anna'), cultivated at the Institute of Field and Vegetable Crops in Novi Sad, Serbia, were utilized in this study. Prior to the experiment, the seeds underwent a sterilization process using a 5% sodium hypochlorite solution for five minutes, followed by thorough rinsing with distilled water. The standard germination test was conducted following the ISTA Rules (2019). This involved four replications of 100 seeds each, which were sown on filter paper in Petri dishes. The final count was performed seven days after sowing, distinguishing between normal and abnormal seedlings.

This included measuring the shoot and root lengths, as well as the fresh weights of both shoot and root. The germination percentage was calculated based on seedlings that demonstrated typical growth characteristics, including a well-developed hypocotyl and root. Seedlings exhibiting any degree of damage to essential structures were categorized as abnormal.

To accelerate seed ageing, seeds were exposed to high relative humidity at 41 °C for 72 hours. Following this accelerated ageing process, a standard germination test and seedling growth performance measurement were carried out in the same manner as for the unaged seeds.

Determination of fatty acid composition

Oil samples were extracted from seeds using a hydraulic press. The fatty acid (FA) composition was analysed via gas chromatography (Konik HRGC 4000) coupled with a flame ionizing detector, after the fatty acids were chemically converted to volatile methyl esters (FAME). This conversion was achieved by subjecting 10 µl of oil samples to transesterification with 190 µl of a methanolic trimethylsulfonium hydroxide solution (0.2 mol/dm^3). Peak identification was carried out by comparing the relative retention times with those of a commercial standard mixture of FAME. The fatty acid contents were expressed as weight percentages of total FAME.

Quantification of tocopherols was performed using high-performance liquid chromatography (HPLC) on a Nucleosil 100-5 NH_2 column with fluorescence detection (λex=280 nm, λem=340 nm). The mobile phase consisted of n-hexane and ethyl acetate (70/30, v/v) with a flow rate of 1 ml/min. The relative retention values and maximum absorption values at specific retention times were used to identify and confirm the presence of tocopherols in a 20 µl injection volume of the solution samples. These samples were prepared by diluting 300 µl of oil in 2 ml of n-hexane.

The oil content was measured using nuclear magnetic resonance (NMR) spectroscopy. Glucosinolate content was inferred from the sulfur content, which was analysed using a CHNS elemental analyser (VarioEL, Analysensystem GmbH).

After the initial testing, the seeds were stored under uncontrolled warehouse conditions for 12 months. Following this storage period, all analyses were repeated, including those after accelerated ageing.

Statistical analyses

The data were analysed for normality before statistical analysis, and they were normal in all studied traits. Statistical analyses were performed using a combination of two-way analysis of variance and Duncan's multiple-range test, facilitated by Statistica StatSoft software. Correlation coefficients were calculated, and significant correlations were reported at the $P < 0.05$ threshold.

Results

Germination performance during natural and accelerated ageing oilseed rape seed

The effect of natural and accelerated seed ageing on germination parameters and early growth of oilseed rape genotypes is illustrated in Table 1. Germination percentage, atypical seedlings and shoot fresh weight after natural and germination percentage and shoot length after accelerated ageing were the only parameters that were significantly affected by the two considered factors and their interaction.

Table 1. Two-way ANOVA for the germination and growth parameters

Factor	Traits						
	Germination percentage	Atypical seedlings	Non-germinated seeds	Shoot length	Root length	Shoot fresh weight	Root fresh weight
	Control						
Storage duration (S)	***	***	*	***	NS	***	NS
Genotype (G)	*	*	NS	NS	NS	*	NS
S × G	*	**	*	NS	NS	*	NS
	Accelerate Ageing						
Storage duration (S)	***	*	NS	*	**	NS	NS
Genotype (G)	*	NS	**	*	NS	**	NS
S × G	*	NS	*	*	*	NS	NS

Values with asterisk *, **, ***, are statistically different at probability values of p ≤ 0.05, ≤ 0.01 and ≤ 0.001, respectively

During the initial test, the germination rate ranged from 92-95%. After 12 months of storage, it dropped to 81-90%, with the largest decrease occurring in the 'Jovana' genotype, which saw a 12% decline. Following exposure to accelerated ageing, the initial germination rate ranged from 89-95%, and after storage, it decreased to 76-89%, with the most significant loss observed in the 'Anna' genotype. In both cases, the percentage of atypical seedlings increased the most after storage in the Jovana genotype.

Even though examined genotypes had high germination percentages before storage, the difference in their longevity during storage was considerable in both cases of natural and artificial ageing. After 12 months of storage and natural ageing, all genotypes of oilseed rape—aside from 'Zorica'—showed a significant decline in germination (Table 2). In this genotype, there were no significant changes in the germination percentage and atypical seedlings. An increase in the number of non-germinated seeds was observed in the 'Zlatna', while in the other genotypes, natural ageing primarily affected the essential structures of the seeds and thus the increasing formation of deformed seedlings. Additionally, natural ageing had an impact on the decline of seedling growth parameters (shoot length, shoot fresh weight, root fresh weight), while there were no consistent changes in seedling root length.

Table 2. Germination and early growth parameters of oilseed rape genotypes after storage during natural aging

Genotypes/ Traits	Germination (%)	Atypical seedlings (%)	Non-germinated seeds (%)	Shoot length (mm)	Root length (mm)	Shoot fresh weight (g)	Root fresh weight (g)
Jovana start	93.00^{ab} ±1.53	3.75^{c} ±0.33	3.25^{ab} ±1.86	40.33^{a} ±2.31	56.67^{b} ±1.92	0.276^{ab} ±0.01	0.049^{abc}±0.01
Zorica start	$92,00^{ab}$ ±0.58	7.25^{bc} ±0.33	0.75^{bc} ±0.33	36.50^{a} ±1.04	56.33^{b} ±2.40	0.298^{a} ±0.01	0.046^{abc}±0.00
Zlatna start	95.50^{a} ±1.20	4.25^{c} ±0.88	0.25^{c} ±0.33	40.17^{a} ±2.46	70.17^{a} ±2.20	0.292^{a} ±0.02	0.062^{a} ±0.00
Anna start	92.00^{ab} ±0.58	7.00^{bc} ±0.58	1.00^{bc} ±0.58	38.33^{a} ±2.31	69.33^{a} ±2.03	0.267^{ab} ±0.01	0.045^{bc} ±0.00
Jovana after storage	81.25^{d} ±1.20	17.50^{a} ±1.53	1.25^{bc} ±0.33	24.33^{b} ±0.60	63.83^{ab} ±2.74	0.180^{c} ±0.00	0.035^{c} ±0.00
Zorica after storage	90.00^{bc} ±1.70	7.75^{bc} ±1.67	2.25^{abc} ±0.81	28.17^{b} ±0.88	66.50^{a} ±2.84	0.237^{b} ±0.01	0.040^{bc} ±0.01
Zlatna after storage	86.00^{cd}±1.00	9.00^{b} ±1.00	5.00^{a} ±1.00	30.17^{b} ±1.33	68.67^{a} ±3.41	0.258^{ab} ±0.01	0.054^{ab} ±0.00
Anna after storage	83.00^{d} ±3.00	14.75^{a} ±2.84	2.25^{abc} ±0.33	30.33^{b} ±3.17	62.00^{ab} ±3.17	0.259^{ab} ±0.02	0.042^{bc} ±0.01

Data are means of three replicates ± SE; the differences were statistically significant determined by Duncan's Multiple Range Test ($P < 0.05$). The same letters indicate no significant differences between means.

Observing the germination averaged after 12 months and accelerated ageing, the same trend was noticed with 'Zlatna', while 'Jovana' and 'Anna' had the greatest reduction (Table 3). Accelerated ageing treatment also initiated an increase in the number of atypical seedlings, while the percentage of non-germinated seeds was not changed. While root length and shoot fresh weight fluctuated, shoot length and fresh weight decreased.

Table 3. Germination and early growth parameters of oilseed rape genotypes after storage and accelerated aging

Traits	Germination (%)	Atypical seedlings (%)	Non-germinated seeds (%)	Shoot length (mm)	Root length (mm)	Shoot fresh weight (g)	Root fresh weight (g)
Jovana start	87.25^{ab} ±0.88	4.25^{c} ±0.67	8.50^{a} ± 1.20	25.39^{bc} ±2.57	43.17^{c} ±3.21	0.190^{c} ± 0.02	0.042^{ab} ± 0.00
Zorica start	89.25^{ab} ±2.33	7.75^{bc} ±1.45	3.00^{b} ±1.15	30.66^{ab} ±2.20	55.17^{b} ±3.00	0.253^{ab} ± 0.02	0.048^{a} ± 0.01
Zlatna start	92.00^{ab} ±0.58	4.75^{c} ±0.33	3.25^{b} ±0.88	30.50^{ab} ±2.84	61.67^{ab} ±1.92	0.254^{ab} ± 0.01	0.051^{a} ± 0.01
Anna start	95.25^{a} ±0.67	3.75^{c} ±1.20	1.00^{b} ±0.58	35.33^{a} ±1.48	62.17^{ab} ±1.48	0.284^{a} ± 0.01	0.049^{a} ±0.00
Jovana after storage	76.00^{d} ±5.51	15.75^{a} ± 3.92	8.25^{a} ± 2.40	23.00^{c} ±0.72	68.21^{a} ±3.84	0.211^{b} ± 0.00	0.031^{b} ±0.00
Zorica after storage	89.00^{ab} ±2.28	9.00^{abc} ± 2.60	2.00^{b} ± 1.15	28.17^{bc} ±1.74	55.00^{b} ±2.47	0.257^{ab} ± 0.01	0.043^{ab} ±0.00
Zlatna after storage	85.75^{b} ±1.45	9.00^{abc} ± 2.08	5.25^{ab} ± 1.33	29.16^{bc} ±1.17	61.15^{ab} ±1.59	0.251^{ab} ± 0.02	0.039^{ab} ±0.00
Anna after storage	78.25^{c} ±1.85	13.75^{ab} ± 3.38	8.00^{a} ± 1.53	25.17^{bc} ±1.20	67.33^{a} ±1.48	0.237^{ab} ±0.01	0.047^{a} ±0.00

Data are means of three replicates ± SE; the differences were statistically significant determined by Duncan's Multiple Range Test ($P < 0.05$). The same letters indicate no significant differences between means.

Fatty acid content during natural and accelerate ageing oilseed rape seed

Oleic acid had the highest concentration of the fatty acids that were measured initially (54.3% to 60.3%), followed by linoleic acid (18.8% to 22.5%), linolenic acid (11.4% to 13.6%), palmitic acid (3.4-3.8), stearic acid (1.7% to 2.1%), echinosenic acid (1.0% to 3.3%), arachidonic acid (0.4%) and behenic acid (0.2% to 0.3%). Significant genotypic variation was detected for all fatty acids content without and with accelerated ageing treatment except for arachidonic and behenic acid amounts during natural ageing and behenic and stearic acid amounts after accelerated ageing. Similar regularity was found for a storage duration factor (Table 4). The absence of interaction between genotype and storage duration suggests that all genotypes exhibited similar behaviour in both the initial test and after 12 months of storage, following both natural ageing and accelerated ageing treatments.

Table 4. Two-way ANOVA for the contents of fatty acids

Factor	Traits							
	Oleic acid	Linoeic acid	Linolenic acid	Palmitic acid	Stearic acid	Arachidonic acid	Eicosenoic acid	Behenic acid
	Control							
Storage duration (S)	***	***	NS	***	***	NS	***	***
Genotype (G)	***	***	***	***	*	NS	***	NS
S × G	NS	NS	NS	NS	NS	NS	*	NS
	Accelerate Ageing							
Storage duration (S)	***	***	*	***	***	NS	***	***
Genotype (G)	***	***	***	***	NS	*	***	NS
S × G	NS	NS	NS	NS	**	NS	NS	NS

Values with asterisk *, **, ***, are statistically different at probability values of p ≤ 0.05, ≤ 0.01 and ≤ 0.001, respectively.

The change in the content of fatty acids in seeds after 12 months of storage varied differently for certain fatty acids. Thus, the content of oleic and eicosenoic acid increased, the content of linoleic, stearic and behenic acid decreased, and the content of linolenic and arachidonic acid did not change natural ageing in storage. Similarly, accelerated ageing conditions after storage increased the content of oleic and eicosenoic acids, decreased the content of linoleic, palmitic and stearic acids, decreased the content of linolenic except for Anna, and did not affect the amount of arachidonic acid. Changes in the content of certain fatty acids in some genotypes were not statistically significant (Tables 5, 6).

Table 5. The fatty acid content of oilseed rape genotypes after storage during natural aging (%)

Traits	Oleic acid	Linoleic acid	Linolenic acid	Palmitic acid	Stearic acid	Arachidonic acid	Eicosenoic acid	Behenic acid
Jovana start	60.63^{b} ± 0.47	19.51^{e} ±0.14	12.23^{b} ±0.19	3.38^{e} ±0.03	2.11^{a} ±0.12	0.40^{ab} ± 0.02	1.02^{e} ±0.01	0.23^{ab} ± 0,02
Zorica start	54.93^{f} ±0.47	22.48^{a} ±0.24	13.57^{a} ±0.21	4.82^{a} ±0.09	1.67^{bc} ±0.08	0.39^{ab} ±0.03	1.43^{c} ±0.05	0.29^{a} ±0,05
Zlatna start	57.40^{de} ±0.43	18.80^{f} ± 0.14	11.42^{c} ± 0.20	4,53^{b} ± 0.09	1.82^{b} ±0.10	0.43^{a} ±0.02	3.33^{b} ±0.04	0.29^{a} ±0.04
Anna start	59.44^{c} ± 0.55	20.84^{c} ±0.30	11.47^{c} ±0.13	4.73^{a} ±0.06	1.81^{b} ±0.11	0.37^{b} ±0,.02	1.05^{e} ±0.02	0.29^{a} ±0.02
Jovana after storage	61.76^{a} ±0.00	19.04^{f} ±0.04	12.44^{b} ±0.01	3.85^{d} ±0.02	1.50^{cd} ±0.07	0.39^{ab} ±0.01	1.20^{d} ±0.02	0.17^{b} ±0.01
Zorica after storage	56.75^{de} ± 0.12	21.80^{b} ±0.02	13.44^{a} ±0.10	4.18^{c} ±0.07	1.28^{de} ±0.07	0.37^{b} ±0.00	1.49^{c} ±0.01	0.20^{b} ±0.04
Zlatna after storage	58.19^{d} ± 0.05	18.33^{g} ±0.03	11.36^{c} ±0.02	3.93^{d} ±0.01	1.55^{bcd} ± 0.04	0.40^{ab} ±0.00	3.61^{a} ±0.01	0.19^{b} ±0.00
Anna after storage	61.22^{ab} ± 0.05	20.10^{d} ±0.03	11.54^{c} ±0.03	4.11^{c} ±0.02	1.18^{e} ± 0,11	0.40^{ab} ±0.00	1.19^{d} ±0.01	0.21^{b} ±0.01

Data are means of three replicates ± SE; the differences were statistically significant determined by Duncan's Multiple Range Test ($P < 0.05$). The same letters indicate no significant differences between means.

Table 6. The fatty acid content of oilseed rape genotypes after storage and accelerated aging (%)

Traits	Oleic acid	Linoleic acid	Linolenic acid	Palmitic acid	Stearic acid	Arachidonic acid	Eicosenoic acid	Behenic acid
Jovana start	60.47^{b} ±0,47	19.70^{d} ±0.14	12.01^{c} ±0.19	3.89^{c} ±0.03	2.10^{a} ±0.12	0.41^{ab} ±0.02	1.04^{e} ±0.01	0.28^{ab} ±0.02
Zorica start	55.47^{e} ±0.47	22.42^{a} ±0.24	13.15^{ab} ±0.21	4.84^{a} ±0.09	1.75^{a} ±0.08	0.39^{b} ±0.03	1.32^{cd} ±0.05	0.30^{a} ±0.05
Zlatna start	57.40^{d} ±0.43	18.32^{e} ±0.14	11.27^{d} ±0.20	4.30^{b} ±0.09	1.93^{a} ±0.10	0.42^{ab} ±0.02	3.72^{b} ±0.04	0.31^{d} ±0.04
Anna start	59.84^{b} ±0.55	20.55^{b} ±0.30	11.39^{d} ±0.13	4.73^{a} ±0.16	1.82^{a} ±0.11	0.39^{b} ±0.02	1.04^{e} ±0.02	0.25^{bc} ±0.02
Jovana after storage	62.13^{a} ±0.01	19.21^{c} ±0.04	12.69^{b} ±0.02	3.28^{d} ±0.02	0.68^{c} ±0.07	0.45^{a} ±0.01	1.28^{cd} ±0.02	0.22^{cd} ±0.01
Zorica after storage	56.65^{d} ±0.12	22.07^{a} ±0.02	13.53^{a} ±0.10	4.28^{b} ±0.02	1.10^{b} ±0.06	0.38^{b} ±0.00	1.37^{c} ±0.01	0.21^{cd} ±0.00
Zlatna after storage	58.53^{c} ±0.05	18.05^{e} ±0.03	11.21^{d} ±0.02	3.88^{c} ±0.01	1.33^{b} ±0.04	0.41^{ab} ±0.00	3.86^{a} ±0.01	0.19^{d} ±0.00
Anna after storage	60.12^{b} ±0.05	20.24^{b} ±0.03	11.59^{cd} ±0.10	4.21^{b} ±0.02	1.23^{b} ±0.11	0.38^{b} ±0.00	1.23^{d} ±0.01	0.20^{d} ±0.01

Data are means of three replicates ± SE; the differences were statistically significant determined by Duncan's Multiple Range Test ($P < 0.05$). The same letters indicate no significant differences between means

Tocopherol and glucosinolates composition during natural and accelerated ageing oilseed rape seed

The amount of total tocopherols in the tested genotypes ranged from 439.14 (Jovana) to 565.42 mg/kg (Anna). α-tocopherols content varied from 109.9 mg/kg to 196.19 mg/kg (Jovana and Anna, respectively), while γ-tocopherols represented 292.69-369.23 mg/kg (Zorica and Anna, respectively). The glucosinolate content in the examined genotypes varied between 20.07 mg/kg (Zorica) and 31.34 mg/kg (Anna) in dry matter (Table 8). Significant differences among genotypes were evident in the variability of tocopherol and glucosinolate contents, both with and without accelerated ageing treatment. A consistent pattern emerged with respect to the storage duration factor (Table 7). In the case of glucosinolates, no interaction was observed between genotype and storage duration, suggesting uniform behaviour among all genotypes during the initial test after natural ageing. However, an interaction between genotype and storage duration for tocopherol content was noted, indicating varied behaviour across genotypes during the initial test and after 12 months of storage, following both natural and accelerated ageing treatments. This interaction was also observed for glucosinolates after accelerated ageing treatments. (Table 7).

The alterations in total tocopherol and glucosinolate content in seeds exhibited diverse patterns after 12 months of storage. Across all tested genotypes, there was an increase in both total tocopherols and individual isomers (α- and γ-tocopherols), except for the 'Anna' genotype, where a decrease was noted. Conversely, accelerated ageing conditions post-storage had an inverse impact on glucosinolate content (both in dry and fresh material), resulting in a decrease for all tested genotypes, except for the Anna genotype (Tables 8 and 9).

Table 7. Analysis of variance for the contents of α-, γ-, total tocopherols, glucosinolates and oil content

Factor	Traits				
	α-Tocopherol	γ- Tocopherol	Total Tocopherols	Glucosinolates dry	Oil content
	Control				
Storage duration (S)	***	NS	***	*	***
Genotype (G)	***	***	***	***	***
S × G	***	***	***	NS	NS
	Accelerate Ageing				
Storage duration (S)	***	NS	***	***	NS
Genotype (G)	***	***	***	***	***
S × G	***	***	***	***	NS

Values with asterisk *, **, ***, are statistically different at probability values of p ≤ 0.05, ≤ 0.01 and ≤ 0.001, respectively.

Table 8. The tocopherols (mg/kg) and glucosinolates content (mmol/kg) of oilseed rape genotypes after storage during natural aging (mg/kg)

Traits	α-Tocopherol	γ-Tocopherol	Total tocopherols	Glucosinolates dry	Oil content
Jovana start	109.91^{e} ±0.40	329.23^{b} ±3.39	439.14^{e} ±2.95	23.00^{c} ±0.24	48.07^{a} ±0.07
Zorica start	156.10^{c} ±2.30	292.69^{d} ±3.00	448.79^{de} ±4.71	20.074^{de} ±0.13	44.87^{f} ±0.07
Zlatna start	146.97^{d} ±0.61	305.59^{c} ±4.22	452.56^{d} ±4.77	30.26^{a} ±0.34	45.81^{d} ±0.13
Anna start	196.19^{a} ±2.86	369.23^{a} ±3.70	565.42^{a} ±6.50	31.34^{a} ±0.36	46.24^{c} ±0.11
Jovana after storage	142.13^{d} ±3.33	370.13^{a} ± 3.24	512.26^{b} ±3.69	20.69^{cd} ±0.27	47.31^{b} ±0.13
Zorica after storage	186.43^{b} ±3.91	305.47^{c} ±4.23	491.90^{c} ±3.69	17.49^{e} ±0.24	44.31^{g} ±0.06
Zlatna after storage	180.98^{b} ±1.28	309.94^{c} ±4.91	490.92^{c} ±3.84	28.33^{b} ±0.36	45.37^{e} ±0.04
Anna after storage	186.24^{b} ±2.98	312.61^{c} ±1.59	498.89^{c} ±2.52	32.65^{a} ±2.35	45.64^{de} ±0.11

Data are means of three replicates ± SE; the differences were statistically significant determined by Duncan's Multiple Range Test ($P < 0.05$). The same letters indicate no significant differences between means

Linear regression indicated moderate associations between the content of certain compounds and seed viability after storage during natural ageing. The highest significant correlations were found between germination percentage and the contents of palmitic acid (r= 0.72), oleic acid (r=-0.47), linolenic (r=0.43), and arachidonic acid d (r=-0.75), while the correlation with ά-tocopherols, glucosinolate and oil content was not significant. Consequently, the same order was observed with the percentage of atypical seedlings. Non-germinated seeds were negatively correlated with palmitic acid.

In the case of accelerated ageing of seeds, the germination percentage was also significantly correlated with palmitic acid (r= 0.63), oleic acid (r= -0.48), arachidonic acid (r= -0.62), as well as with glucosinolate content (r= 0.44).

Table 9. The tocopherols (mg/kg) and glucosinolates content (mmol/kg) of oilseed rape genotypes after storage and accelerated aging

Traits	α-Tocopherol	γ-Tocopherol	Total tocopherols	Glucosinolates dry	Oil content
Jovana start	105.86^{f} ±2.64	309.90^{d} ±3.79	415.76^{e} ±2.95	28.83^{c} ±0.49	47.64^{a} ±0.26
Zorica start	186.80^{b} ±1.30	357.11^{b} ±3.25	543.91^{ab} ±4.71	22.08^{e} ±0.45	44.09^{de} ±0.30
Zlatna start	122.92^{e} ±2.72	283.05^{e} ±3.48	405.97^{e} ±4.77	34.87^{a} ±0.05	44.76^{cd} ±0.45
Anna start	173.92^{c} ±6.61	381.39^{a} ±5.26	555.30^{a} ±6.50	32.39^{b} ± 0.68	45.82^{b} ±0.33
Jovana after storage	135.38^{d} ± 2.40	330.34^{c} ±5.09	465.72^{d} ±3.69	17.90^{f} ±0.15	47.52^{a} ±0.10
Zorica after storage	208.69^{a} ±5.16	305.62^{d} ±7.81	514.31^{c} ±3.69	16.32^{g} ±0.17	43.94^{e} ±0.03
Zlatna after storage	189.45^{b} ±2.40	349.93^{b} ±3.41	539.38^{b} ±3.84	25.19^{d} ±0.51	44.48^{de} ±0.06
Anna after storage	196.88^{b} ±4.01	395.00^{c} ±4.11	521.87^{c} ±2.52	25.53^{d} ±0.34	45.32^{b} ±0.02

Data are means of three replicates ± SE; the differences were statistically significant determined by Duncan's Multiple Range Test ($P < 0.05$). The same letters indicate no significant differences between means

Discussion

Seed ageing is a composite biological phenomenon that comprehends the coherence of molecular, biochemical, physiological, and metabolic processes (Fu *et al*., 2015). It comprises a progressive accumulation of damage to cellular and it is more pronounced when seeds are stored in unsuitable environments consequently causing impairment in seed viability and vigor (Wojtyla *et al*., 2016). This study focuses only on changes in the content of certain lipid compounds and their influence on germination performance during seed ageing. Intending to understand the mechanisms of oilseed rape seed ageing after short-term storage in terms of germination performance and changes in lipid composition and their connection, seeds of 4 oilseed rape genotypes were subjected to accelerated ageing. This treatment impaired germination and caused significant changes in seed lipid status.

The initial germination test is a fundamental and widely used method in the seed industry to quickly assess the quality of seeds. In combination with the assessment of other germination and early growth parameters, this test provides valuable information about the viability and potential performance of seeds. Our results demonstrated a high percentage of initial germination in all oilseed rape genotypes. Also, a reduction in germination percentage for all genotypes tested after one year of storage was observed, but this decline was more pronounced after exposure of seeds to double-stress conditions of high temperature and humidity. These conditions directly affect seed ageing leading to a rapid and sudden loss of seed vigour (Yin *et al*., 2015). Genotype 'Zorica' exhibited the highest level of tolerance among the tested genotypes, which indicates that it could perform better in the field, particularly when using aged seeds. At the same time, the most significant

decrease in germination occurred in 'Anna' genotype. These results may imply the existence of different mechanisms for preserving vitality under stressful conditions that contribute to seed deterioration.

According to research on oilseed rape seeds by Yin *et al*. (2015), germination decay may be brought on by the fact that the amount of ROS (Reactive Oxygen Species, the primary cause of stress in cells), decreased noticeably more slowly in artificially aged seeds than in non-aged seeds. Additionally, before the germination process began, the activities of some antioxidant enzymes (superoxide dismutase, catalase) were decreased in the accelerated-aged seeds. High temperature and relative humidity can oxidize the oil in the soybean seed, and transform it into free radicals, which initiate lipid peroxidation and reduce enzyme activity, directly affecting seed vitality (Bakhshandeh and Gholamhossieni, 2018). Furthermore, during seed ageing and in seedlings derived from aged seeds, DNA integrity was damaged (Mira *et al*., 2020) while impaired transcription results in incorrect enzyme synthesis crucial for seed germination (Kapoor *et al*., 2010).

The findings of our study reveal that both natural and artificial ageing of seeds not only declaim germination but also significantly lead to an increased occurrence of atypical seedlings. Atypical or abnormal seedlings are those that deviate from the typical development patterns expected during the germination process and early seedling growth. Specifically, among the various abnormalities observed, the deformation or absence of the radicle (the embryonic root) is particularly pronounced, suggesting that this vital structure is most susceptible to damage caused by the ageing process. The genotype 'Zorica' not only exhibited the highest preservation of germination throughout storage and accelerated ageing but also resisted the increase in the formation of abnormal seedlings, further demonstrating the high vigour of the seeds. The study of Veselova and Veselovsky (2003) highlights specific research finding regarding the effects of accelerated ageing treatment on pea seed germination and the formation of atypical seedlings. According to their research, these effects are attributed to changes in the permeability of cell membranes, particularly involving the opening and closing of aquaporin channels, rather than alterations in the properties of membrane lipids.

The examined oilseed rape genotypes showed various seedling performances both after natural and accelerated ageing treatments. All genotypes developed longer shoots and roots following initial testing under optimal and accelerated ageing conditions than the same treatment did after a year in storage. After 12 months of storage, root length slightly increased or did not change in both natural and accelerated ageing, but root weight was reduced, indicating unusual radicle formation. It can be assumed that the cells have elongated, but the development of the cellular compartments was not complete. The genotype 'Zlatna' was an exception, where both parameters declined or remained unchanged. Strong and vigorous seedlings with a long radicle can play a crucial role when adverse conditions occur in the field, e.g. if a drought strikes after germination, and water is available in the deeper layers of the soil (Čanak *et al*., 2020).

Although many studies show the relationship between lipids and the process of germination and initial seedling growth oilseed rape (Yin *et al*., 2015; Jovičić *et al*. 2017), *Arabidopsis* mutant lines (Oenel *et al*., 2017), safflower (Onder *et al*., 2020), oat (Xia *et al*., 2015), vetch (Jovičić *et al*., 2018), wheat (Wiebach *et al*., 2020), cabbage and lettuce seeds (Adetunji *et al*., 2020), the influence of changes in fatty acid composition on seed vigour is still quite unclear (Seyyedi *et al*., 2015). Considering that over 90% of the total fatty acids found in oilseed rape seeds are oleic, linoleic, and linolenic acids, these acids are deemed the most significant unsaturated fatty acids. Consequently, it is believed that these acids play a crucial role in preserving the seed vigor of this crop, implying that unsaturated fatty acids exert a more substantial impact on seed vigor than saturated fatty acids (Seyyedi *et al*., 2018). The authors suggest that unsaturated fatty acids are anticipated to undergo faster degradation compared to saturated fatty acids. This expectation arises from the observation that accelerated ageing seems to induce oil oxidation, compromising the structural integrity of unsaturated fatty acids. However, contrary to this expectation, our study reveals that the levels of several investigated unsaturated fatty acids decreased during both accelerated and natural ageing. Furthermore, given the observed increase in levels of oleic and eicosenoic acid in seeds exposed to both natural and accelerated ageing across all genotypes, it is reasonable to speculate that the combination of seed storage and elevated temperatures might enhance the

activities of certain enzymes involved in lipid production. The assertions provided by Seyyedi *et al*. (2015), and Seyyedi *et al*., 2018 suggest that oils with higher linoleic and linolenic acid content may undergo quicker oxidation. Additionally, it's noted that these fatty acid composition traits may result in declined oilseed rape seed germination. However, the specific instance of the 'Zorica' genotype seems to have shown a minimal decrease in germination percentage despite having the mentioned fatty acid composition. There are also speculations that the cause of the declined germination in naturally aged seeds is different from that in seeds that are artificially aged. Namely, the germination of tomatillo seeds decreased after accelerated ageing, but there was no discernible change in the amount of fatty acids present. However, in naturally aged seeds, the germination percentage also decreased along with a change in the amount of fatty acids (Pichardo-Gonzalez *et al*., 2010, 2014). Contradictory results among available research within the same plant species, as well as between different species, emphasise the complexity of the relationship between fatty acid composition and seed vigour and certainly imply additional research on this topic.

Apart from shifts in fatty acid composition, there may also be changes in the levels of non-enzymatic antioxidants as seeds undergo ageing. The ageing process can subject seeds to oxidative stress triggered by various factors. This oxidative stress can lead to the production of free radicals, which can damage cellular components and affect seed viability. Antioxidants like tocopherols help neutralize these free radicals, preserving the integrity of essential biomolecules within the seed (Mesa and Munne-Bosch, 2023). Hence, α-tocopherol plays a vital role in maintaining the optimal redox state within chloroplasts, ensuring the integrity and functionality of thylakoid membranes during plant growth and in the face of stress-induced challenges (Munne-Bosch, 2005). α-tocopherol, collaborating with diverse antioxidants, plays a pivotal role in reducing ROS levels within photosynthetic membranes. Additionally, it inhibits lipid peroxidation by transforming lipid peroxyl radicals into corresponding hydroperoxides, thereby safeguarding membrane integrity (Giurizatto *et al*., 2012). Our investigations reveal an upward trend in tocopherol levels in seeds as they undergo both natural and artificial ageing. This phenomenon is indicative of the seed's inherent defence mechanism against oxidative damage. Increased levels of antioxidants, such as tocopherols, during natural and accelerated seed ageing contribute to the seed's ability to withstand oxidative stress and maintain its viability (Giurizatto *et al*., 2012). The enhanced presence of tocopherols in aged seeds indicates their role in mitigating oxidative stress and maintaining seed quality. Understanding the dynamics of antioxidants, including tocopherols, during seed ageing is essential for seed conservation and storage practices. By harnessing the protective properties of antioxidants, researchers and agriculturists can develop strategies to extend the shelf life of seeds and ensure the preservation of their genetic integrity for future planting.

The elevated glucosinolate content within the seeds of numerous Brassicaceae species serves a dual-purpose during germination, functioning both as an antioxidant and as a reservoir of nutrients (Artes-Hernandez *et al*., 2022). A decline in the dry glucosinolate content was noted in response to both natural and accelerated ageing across all cultivars, except for the Anna genotype during natural ageing conditions. Baenas *et al*. (2012) documented a decrease in glucosinolate levels during the germination of diverse varieties of Brassicaceae vegetable seeds. This decline is likely linked to the selective metabolism of glucosinolates and the concurrent dilution of glucosinolate concentrations due to tissue expansion. The decrease in glucosinolate levels during germination is a result of the plant's transition from a storage phase to an active growth phase, where energy and resources are reallocated to support seedling development rather than the production of defense compounds. Oilseed rape seeds containing a higher content of glucosinolates showed reduced production of normal seedlings negatively affecting the viability of seeds during long-term storage (Nagel *et al*., 2018). Our results showed a moderate relationship between the glucosinolate amount and germination percentage.

Conclusions

The findings in this study suggest that alterations in seed lipid composition may impact seed viability and seedling morphology, particularly under short-term storage and seed deterioration conditions. Further research on this topic would provide valuable insights into the effects of ageing on seedling development and offer a deeper understanding of how specific seed structures, such as the radicle, are affected. Overall, our study's observations shed light on the intricate relationship between seed ageing and seedling abnormalities, particularly focusing on the role of the radicle in this process and demonstrating the existence of differences between genotypes within the same plant species.

Authors' Contributions

DJ: Conceptualization; Investigation; Data curation; Formal analysis; Writing original draft; NG: Contributed to experiment design; Formal analyses; Validation; Writing- original draft; AMJ: Initiated and guided research; Supplied seed materials, Writing original draft; ZN: Literature review; Provided critical insights during the manuscript revision process; GT: Contributed to conducting analyses, Writing- review and editing; DP: Contributed to conducting analyses, Literature review; Writing- review and editing; MI: Contributed to conducting analyses; Literature review; Writing- review and editing.

All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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