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The effect of exogenous methyl jasmonate on the fatty acid composition of germinating triticale kernels (x *Triticosecale* Wittmack, cv. Ugo)

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ABSTRACT

The influence of exogenous methyl jasmonate (MeJA) on the fatty acid composition of germinating kernels of triticale (x *Triticosecale* Wittmack, cv. Ugo) was analyzed in this study. The effect of different concentrations of MeJA (0, 1, 20, 100 and 1000 μM) on the viability and vigor of kernels and the fatty acid composition of seedlings after 24–96 h of kernel germination was evaluated. At high concentrations, MeJA inhibited the germination of triticale kernels with emergence of poorly developed seedlings of low number of roots. The content of saturated fatty acids decreased significantly after the first two days of germination under exposure to MeJA. Methyl jasmonate treatment increased the content of polyunsaturated fatty acids after the first two days of germination. The nutritional value of triticale kernels creates prospects for food production and human consumption. Methyl jasmonate can be used to increase the content of health-promoting components, such as polyunsaturated fatty acids, during germination of triticale kernels.

1. Introduction

The structure and biosynthetic pathway of jasmonates, mainly jasmonic acid (JA) and methyl jasmonate (MeJA), are like those of prostaglandins in animals [1,2]. Jasmonates provoke a wide range of plant responses, including morphological, developmental, and anatomical responses (such as seed germination, root and shoot growth, tuber formation, abscission of leaves, aging and embryogenesis), cellular and ultra-structural responses (such as cell division, disintegration of microtubules) and biochemical responses (such as Rubisco synthesis, photosynthesis, respiration, chlorophyll degradation and synthesis of phytoalexins and alkaloids [3].

According to Fonseca et al. [4] jasmonates regulate development and adaptation processes in plants by controlling their responses to biotic and abiotic stimuli, probably via their role in the biosynthesis of secondary metabolites, including flavonoids and anthocyanin [5,6]. Both abiotic stress such as mechanical damage and biotic stress such as infestation by insects and fungi provoke the release of linolenic acid from membrane lipids [7], which in turn can be converted to JA via the octadecanoid pathway. Elevated concentrations of JA in a cell promote the expression of genes that participate in defense processes. In terms of the induced effects, in particular stress responses in plants, jasmonates

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are similar to abscisic acid [8]. The JA-dependent wound signaling pathway is responsible for activating systemic responses, while the JA-independent wound signaling pathway is activated near the wound side and plays a role in repairing damaged tissues and defending against pathogens [9]. In wounded plant tissues, JA and MeJA are the major signaling compounds which induce the expression of genes encoding proteinase inhibitors, proteins that protect plants against insects [10]. Methyl jasmonate increases transcription levels of genes encoding defensins (PDE 1.2) and thionins (THI 2.1), proteins with antibacterial properties. Besides their role in protection of plants against insect invasion, jasmonates also influence herbivore feeding and behavior [11]. Moreover, MeJA influences the chemical composition of edible plant parts and plays a role in the treatment of serious plant diseases [12–14]. It has also been reported that jasmonates minimize the qualitative and quantitative losses in fruits and vegetables during long-distance transport of the produce [15].

In the context of our research, it is worth noting that currently a lot of attention is paid to the impact of jasmonates on human health and its uses in different aspects of life. It has been reported that, in humans, MeJA can inhibit the development of cancer [2,7,16–18] and this effect was manifested as inhibition of the growth of lymphoblastic leukemia cells, cervical cancer, breast cancer, prostate adenoma, and other neoplastic cells. Interestingly, in some cases the methyl ester (MeJA) was found to be more effective than jasmonic acid itself [19–22]. By virtue of its distinct aroma, MeJA has been implemented in many fragrance products [23]. Moreover, in recent years, the use of exogenous chemical inducers as pre- and post-harvest technologies to extend the shelf life of plant foods and improve their health-promoting properties has received increasing attention. Many inducers are described in the literature; among them, MeJA is the most commonly used [24,25].

Endogenous MeJA acts as a trigger molecule for the accumulation of secondary metabolites, particularly the phenolic substances including flavonols and anthocyanins, in edible plants [6,26,27]. Despite the growing awareness about the role of fatty acids, particularly the polyunsaturated fatty acids (PUFAs), in human health and disease resistance, the influence of MeJA on the fatty acid profile of plants has been occasionally studied. Many studies have positively linked PUFAs to reduced cardiovascular morbidity and mortality, enhanced infant development, cancer prevention, optimal brain and vision function and protection from arthritis, hypertension, diabetes mellitus, and neurological/neuropsychiatric disorders [28]. As a rule, vegetable oils are rich sources of PUFAs [28]. Some authors have reported significant changes in FA composition of plants after MeJA treatment [29–31].

Triticale grain is used in the production of feed for almost all types of livestock. The health benefits of triticale grain in human nutrition are well documented [32–34]. In recent decades, triticale has become a commercial crop grown worldwide under a wide range of environmental conditions. Triticale grain is rich in bioactive components that play an important role in human nutrition, including dietary fiber, phenolic acids, phytoestrogens, phytosterols, vitamins, tocopherols, tocotrienols, carotenoids, and diverse minerals [35–37]. The nutritional value of triticale creates prospects for food production and human consumption also due to the content of health-promoting components, such as polyunsaturated fatty acids. Moreover, triticale is a cereal crop of great sensitivity to aphid invasion and fungal infection, which justifies manipulation of exogenous jasmonates to confer resistance to the crop against biotic stress. Recently, we investigated the effect of exogenous MeJA on FA composition of the grains of winter triticale [38]. Nevertheless, the response of triticale seedlings during germination to exogenous MeJA has not been elucidated.

The aim of this study is to evaluate the influence of MeJA on germination parameters and the time-course changes in fatty acid composition of germinating triticale (x *Triticosecale* Wittmack, cv. Ugo) kernels.

2. Materials and methods

2.1. Materials and methyl jasmonate treatment

The kernels of triticale (x *Triticosecale* Wittmack, cv. Ugo) used in the present work were harvested from the parent plants at the fully ripe stage, sun dried and stored in linen bags at 16–18 °C and average humidity of 60–65%.

Triticale kernels were incubated, for 96 h at 20 °C in the dark, on germination paper (Anchor Paper Company, St. Paul, USA) moistened with aqueous solutions of MeJA (Sigma Aldrich, cat. no. 392707) at concentrations of 0, 1, 20, 100 and 1000 μM. The experimental MeJA concentrations were based on preliminary experiments and on relevant studies for other plant species [30,31,38]. Each concentration was replicated four times and each replicate was a petri dish containing 100 kernels.

2.2. Evaluation of kernels germination and seedlings vigor

The germination capacity and germination rate of triticale kernels were calculated according to the International Seed Testing Association [39]. Germination was monitored by daily counting of the number of germinants, and germination capacity was expressed as the percentage of kernels which produced seedlings with the length of 1 cm after 8 days of incubation. Seedling vigor was assayed at the 72 h of germination period by measuring the fresh and dry weights of seedlings, length of epicotyl, length of the radicle, and the number of adventitious fibrous roots.

2.3. Total lipid extraction and fatty acid analysis

All chemicals and solvents used in the analysis were of analytical or HPLC grade (Supelco Bellefonte, Pennsylvania, USA; Larodan Fine Chemicals, Malmö, Sweden). Total lipids were extracted from seedlings by the modified method proposed by Folch et al. [40] using the chloroform: methanol extraction mixture (2:1 v/v). In brief, the samples were crushed in a porcelain mortar in an ice bath by combining 50 mg of the fresh material with 1 mL mixture of chloroform/methanol (2:1, v/v) with the addition of 0.005% butylated hydroxytoluene. After 15 min, 15 mL of chloroform was gradually added to the extraction mixture and the homogenate was passed through filter paper. The debris was rinsed several times with the extraction mixture, and the filtrate was combined with one-third the filtrate volume of 0.1 M aqueous KCl, stirred and allowed to stand at 2 °C for 12 h. The upper two of the three layers formed were discarded. The lower layer was passed through a filter paper, which was then rinsed three times with chloroform. The filtrate was evaporated in a rotary vacuum evaporator at 40 °C. The obtained lipids were re-dissolved in 1 mL chloroform, and the lipid solution was evaporated in a nitrogen atmosphere and stored in tight glass containers.

The water- and solvent-free lipids isolated from seedlings were converted to fatty acid methyl esters (FAMEs) in accordance with the European Standards (ISO12966–2:2017) [41]. In brief, fatty acids were converted to FAMEs by using 15% boron trifluoride solution (BF_3) in methanol as a catalyst. The FAMEs were separated by high-resolution gas chromatography (HR-GC) using Hewlett Packard 5890 Series II GC system equipped with a split/splitless injector and a flame-ionization detector (FID) on the Rtx 2330 chromatography column (105 m × 0.25 mm) (Restek, Bellefonte, Pennsylvania, USA). Helium was used as a carrier at a flow rate of 0.65 mL/min. Separation temperature was gradually increased from 180 °C (for 20 min) to 210 °C in the column, in stepwise increment of 1.5 °C/min, and maintained for 80 min at 250 °C both in the detector and the injector. A qualitative and quantitative analysis of chromatograms was carried out by comparing FAME retention times in the samples with the retention times of FAME standards (Supelco 37 Component FAME Mix, Supelco Bellefonte, Pennsylvania, USA; Larodan Fine Chemicals, Malmö, Sweden). Fatty acid percentages

were normalized with the use of internal standards and adjustment coefficients (to convert the percentage of peak area to the percentage of component weight) according to ISO12966–2:2017 [41]. Each sample was analyzed in four replicates.

2.4. Statistical analysis

The experiment was factorial with two factors and four replications in a completely randomized design. Each replicate was a petri dish containing 100 kernels. The main factors were 1) germination period with five levels: 0, 24, 48, 72 and 96 h and 2) MeJA concentration with five levels: 0, 1, 20, 100 and 1000 μM. The results were processed statistically by analysis of variance ANOVA using the STATISTICA software (v. 13.1, TIBCO Software Inc.). The significance of differences between mean values was estimated by Tukey's test ($p \leq 0.05$).

3. Results

3.1. Germination

The germination rate and germination capacity of triticale kernels incubated in aqueous solutions of MeJA were decreased compared to the control (Fig. 1 A, B). There was a threshold value of MeJA beyond which germination and seedling growth significantly decreased. This threshold was relatively broad (100 μM) for seedling dry weight (Fig. 2 B), moderate (20 μM) for germination rate, germination capacity, and number of embryonic roots (Fig. 1 A, B; Fig. 3 C) and narrow (1 μM) for seedling fresh weight, epicotyl length and the embryonic root length (Figs. 2 A; 3 A, B).

A significant decrease in germination rate was observed under exposure to highest concentration of MeJA i.e., 1000 μM, and germination capacity under 100 and 1000 μM (Fig. 1 A, B). Three-day-old seedlings exposed to the above concentrations of MeJA were characterized by the lowest fresh and dry matter content (Fig. 2 A, B). At high concentrations, MeJA significantly inhibited the elongation of epicotyls and radicle and reduced the number of adventitious fibrous roots (Fig. 3A-C).

The analysis of variance showed that the MeJA concentration had highly significant ($p < 0.01$) effect on the measures of germination and embryo growth of the germinating triticale kernels (Table 1).

3.2. Fatty acid composition

With the use of the HR-GC we confirmed the presence of 16 FAs in germinating triticale kernels. The composition of saturated (SFAs), monounsaturated (MUFAs) and polyunsaturated fatty acids (PUFAs), expressed as % w/w of total FAs, isolated from triticale kernels germinated at different concentrations of MeJA for different times at 20 °C, was presented in Tables 1–3.

The analysis of variance showed that the effect of the main factors (germination time and MeJA concentration) and their interaction on fatty acid composition of the germinating triticale kernels was statistically significant (Table 1). Only in case of pentadecanoic acid (C 15:0) the time of germination had no effect on the amount of this acid; however, significant differences were noted when comparing percentage of this acid between kernels germinating in different MeJA concentrations (Table 1).

The most common FAs in non-treated triticale kernels at the early stage of germination were the SFAs (72.0%), followed by PUFAs (18.9%) and MUFAs (9.1%) (Tables 2–4). At the end of the germination period (96 h), the pattern of FA dominance in the germinating kernels was shifted to PUFAs (48.6%), followed by SFAs (40.4%) and MUFAs (11%) (Tables 2–4). The most dominant FAs in non-treated germinating kernels were palmitic acid (C 16:0), octadecenoic/oleic acid (C 18:1 9c) and linoleic acid (C 18:2 *n-6*).

The saturated fatty acids isolated from the kernels of triticale in significant quantities (above 3% of the total fatty acid pool), except palmitic acid, were behenic acid (C 22:0), stearic (C 18:0), and margaric acid (C 17:0). Kernels exposed to various concentrations of MeJA were characterized by different proportions of the SFAs. After the first day of germination (24 h), a significant decrease was noted in the total percentage of SFAs in experimental kernels (Table 2). An analysis of the SFAs composition after 48 h of germination revealed similar trends which, however, were less regularly expressed in comparison with 24 h seedlings (Table 2). The results noted in samples exposed to the highest concentration (1000 μM) of MeJA differed considerably from the remaining samples exposed to MeJA.

Except at 72 h of germination, increasing concentration of MeJA from 0 to 1000 μM led to progressive reductions in myristic acid (C 14:0) concentration in triticale seedlings of 0.72%, 0.38% and 0.32% below the control, at 24, 48 and 96 h of germination, respectively. Only at 72 h, a 0.73% progressive increase was found across the whole range of MeJA concentrations (Table 2). For palmitic acid (C 16:0), increasing MeJA concentration from 0 to 1 μM led to 31.06%, 23.47%, 33.86% and 14.21% reductions at 24, 48, 72 and 96 h, respectively, which were followed by either 15.56%, 5.31% and 41.71% increases at 24, 48 and 72, respectively or a plateau at 96 h, with further decrease up to 18.62% in concentration up to 1000 μM (Table 1). For stearic acid (C 18:0), increasing MeJA concentration from 0 to 20 μM led to significant reductions at 24, 48, and 72 h of this compound, which were followed by an increase in concentration up to 1000 μM (Table 1). Only for 96 h the stearic acid amount was characterized by a decrease together with MeJA increasing concentration (Table 2).

In total six monounsaturated fatty acids (MUFAs) were identified in

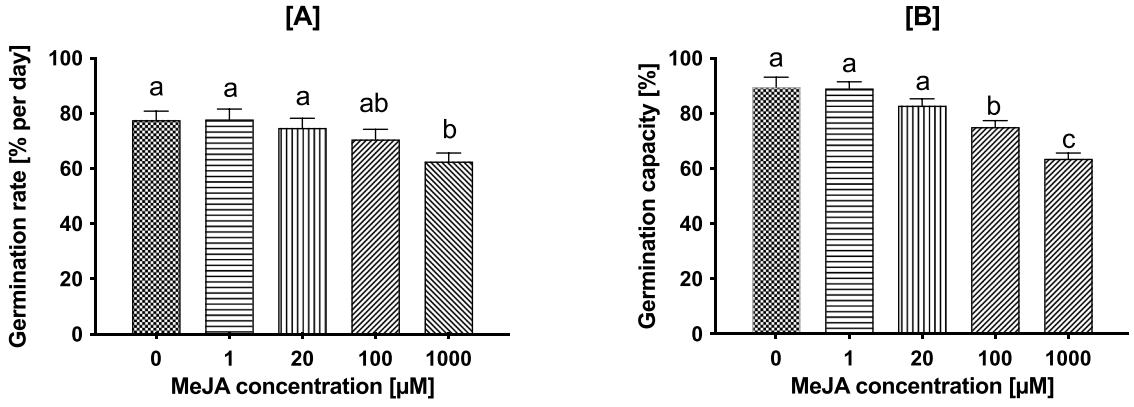

Fig. 1. Effect of MeJA on A) germination rate and B) germination capacity of triticale kernels. Each column represents the mean of four replicates ± SE. Means with common letters are non-significantly different at $p < 0.05$.

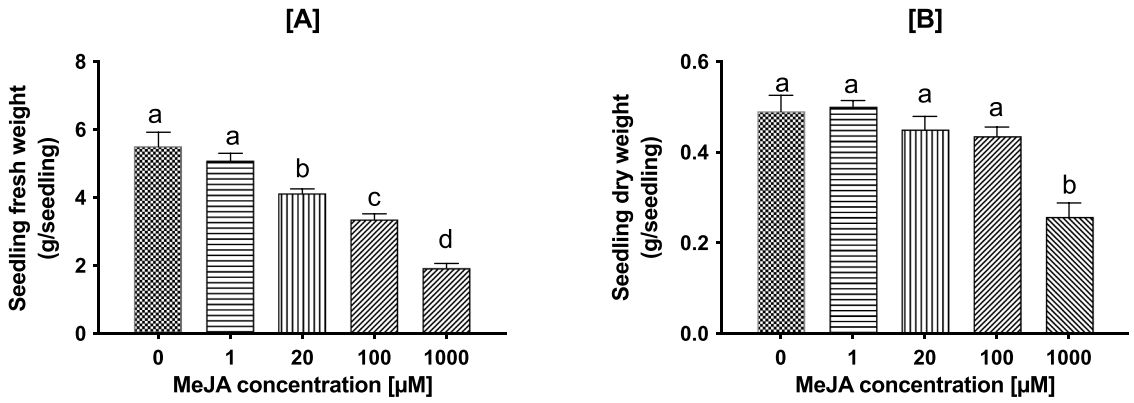

Fig. 2. Effect of MeJA on A) fresh weight and B) dry weight of triticale kernels after 3 days of germination. Each column represents the mean of four replicates ± SE. Means with common letters are non-significantly different at $p < 0.05$.

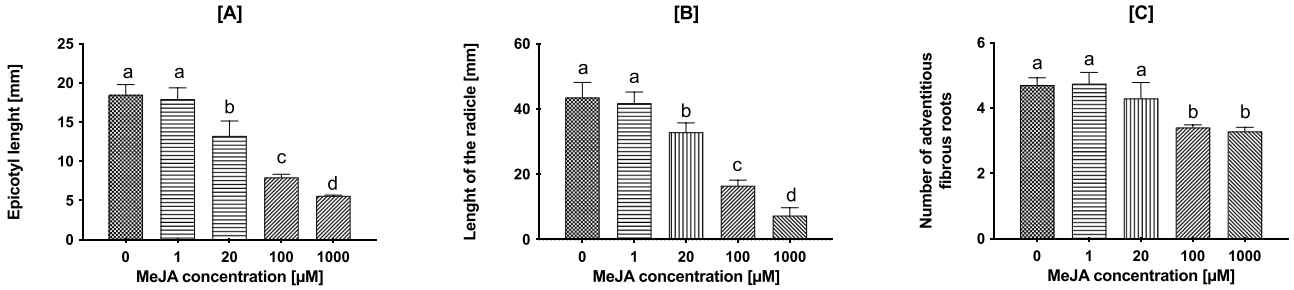

Fig. 3. Effect of MeJA on A) length of epicotyl, B) length of the radicle, and C) the number of adventitious fibrous roots in triticale kernels after 3 days of germination. Each column represents the mean of four replicates ± SE. Means with common letters are non-significantly different at $p < 0.05$.

Table 1
The two-way ANOVA to evaluate the effects of the main factors (germination time and methyl jasmonate concentration) and their interactions on triticale kernels germination, seedlings vigor, and lipid composition.

Parameter		Time of germination (Tg)	MeJA Concentration (MeJA_C)	Tg x MeJA_C
Triticale kernels germination	germination rate (4 days)	—	**	—
	germination capacity (8 days)	—	**	—
Seedlings vigor analysis (72 h)	seedling fresh weight (g/seedling)	—	**	—
	seedling dry weight (g/seedling)	—	**	—
	epicotyl length (mm);	—	**	—
	length of the radicle (mm)	—	**	—
	number of adventitious fibrous roots	—	**	—
SFAs	Myristic C 14:0	**	**	**
	Pentadecanic C 15:0	ns	***	**
	Palmitic C 16:0	***	***	***
	Margaric C 17:0	**	**	**
	Stearic C 18:0	**	**	**
	Arachic C 20:0	**	**	**
	Behenic C 22:0	**	**	**
	Together	**	**	**
MUFAs	Hexadecenoic C 16:1c	**	**	**
	Hexadecenoic/Palmitoleic C 16:1 9c	**	**	**
	Octadecenoic/Oleic C 18:1 9c	***	***	***
	Octadecenoic C 18:1 11c	**	**	**
	Eicosenoic C 20:1 *n-9*	**	**	**
	Erucic C 22:1	***	***	***
	Together	***	***	***
PUFAs	Linoleic C 18:2 *n-6*	***	***	***
	Linolenic C 18:3 *n-3*	***	***	***
	Eicosadienic C 20:2 *n-6*	ns	ns	ns
	Together	***	***	***

* Significant $p < 0.05$, ** highly significant $p < 0.01$, *** very highly significant $p < 0.001$, ns - not significant; — - no data

germinating kernels (Table 3). However, erucic acid (C 22:1) was detected only at 48 h (1 and 100 μM of MeJA) and 96 h (20 and 100 μM of MeJA) of germination (Table 3). The predominant MUFA was octadecenoic/ oleic acid (C 18:1 9c), and the percentage of the remaining five MUFAs did not exceed 3% in different samples (Table 3). The percentage of octadecenoic/ oleic acid (C 18:1 9c), in total MUFAs increased significantly in kernels after 24, 48, 72 and 96 h of germination, treated with 1 μM of MeJA, followed by progressive reduction only

Table 2
The saturated fatty acids composition (expressed as % of total fatty acids) isolated from triticale kernels germinated at different concentrations of MeJA for different times at 20 °C. Each value is the mean of four replicates ± SE. Means with common letters are non-significantly different at $p < 0.05$. tr. – trace.

Saturated fatty acids (SFAs)								
Time period and MeJA concentration (μM)	Myristic C 14:0	Pentadecanoic C 15:0	Palmitic C 16:0	Margaric C 17:0	Stearic C 18:0	Arachidic C 20:0	Behenic C 22:0	Total
24 h								
0	0.72 ± 0.04^{ab}	tr.^{b}	50.06 ± 4.23^{b}	3.83 ± 0.22^{b}	9.63 ± 0.16^{a}	2.20 ± 0.17^{a}	5.60 ± 0.26^{a}	72.04 ± 4.32^{ab}
1	0.15 ± 0.02^{bcd}	0.06 ± 0.03^{ab}	19.00 ± 0.60 ^{g}	tr.^{e}	0.53 ± 0.03^{e}	tr.^{c}	1.03 ± 0.08^{de}	20.78 ± 1.01 ^{h}
20	0.17 ± 0.02^{bcd}	0.07 ± 0.02^{ab}	19.50 ± 0.57 ^{g}	tr.^{e}	0.58 ± 0.04^{e}	0.04 ± 0.06^{bc}	2.03 ± 0.09^{c}	22.39 ± 1.03^{gh}
100	0.07 ± 0.01 ^{cd}	tr.^{b}	28.36 ± 0.81^{efg}	1.15 ± 0.03^{de}	2.17 ± 0.09^{de}	tr.^{c}	1.08 ± 0.10^{d}	32.83 ± 1.50^{efgh}
1000	tr.^{d}	tr.^{b}	34.69 ± 0.59^{cdef}	2.75 ± 0.11^{bc}	4.86 ± 0.20^{bc}	tr.^{c}	tr.^{f}	42.30 ± 2.18^{de}
48 h								
0	0.38 ± 0.16^{abcd}	tr.^{b}	42.87 ± 3.59^{bc}	2.54 ± 0.95^{bc}	1.3 ± 0.21^{e}	tr.^{c}	2.06 ± 0.15^{c}	49.15 ± 3.76 ^{cd}
1	0.17 ± 0.11^{bcd}	0.08 ± 0.02^{ab}	19.40 ± 0.73 ^{g}	tr.^{e}	0.58 ± 0.20^{e}	tr.^{c}	0.87 ± 0.16^{de}	21.11 ± 2.43 ^{h}
20	0.17 ± 0.10^{bcd}	0.07 ± 0.02^{ab}	19.50 ± 3.11 ^{g}	tr.^{e}	0.58 ± 0.13^{e}	0.04 ± 0.05^{bc}	2.03 ± 0.23^{c}	22.39 ± 3.69^{gh}
100	0.10 ± 0.03^{bcd}	tr.^{b}	25.76 ± 3.43^{efg}	tr.^{e}	3.37 ± 0.22 ^{cd}	tr.^{c}	1.05 ± 0.08^{d}	30.35 ± 2.90^{efgh}
1000	tr.^{d}	tr.^{b}	24.71 ± 4.90^{efg}	2.75 ± 0.13^{bc}	4.76 ± 1.11^{bc}	tr.^{c}	tr.^{f}	32.22 ± 5.10^{efgh}
72 h								
0	tr.^{d}	tr.^{b}	54.73 ± 4.86^{ab}	tr.^{e}	4.18 ± 0.87^{bc}	tr.^{c}	tr.^{f}	58.91 ± 5.06^{bc}
1	0.22 ± 0.23^{bcd}	0.12 ± 0.10^{ab}	20.87 ± 3.03^{g}	tr.^{e}	0.58 ± 0.22^{e}	tr.^{c}	0.78 ± 0.27^{de}	22.57 ± 3.33^{gh}
20	0.26 ± 0.12^{bcd}	tr.^{b}	30.17 ± 4.11^{defg}	0.29 ± 0.20^{de}	0.78 ± 0.13^{e}	tr.^{c}	tr.^{f}	31.50 ± 4.18^{efgh}
100	0.43 ± 0.21^{abcd}	tr.^{b}	42.39 ± 5.38^{bcd}	13.12 ± 0.35^{a}	1.24 ± 0.24^{e}	tr.^{c}	tr.^{f}	57.18 ± 5.42^{c}
1000	0.73 ± 0.09^{a}	tr.^{b}	62.58 ± 5.22^{a}	13.93 ± 1.19^{a}	5.04 ± 1.26^{e}	tr$^{\cdot\ c}$	tr$^{\cdot\ f}$	82.28 ± 5.98^{a}
96 h								
0	0.51 ± 0.11^{abc}	tr.^{b}	37.41 ± 3.89^{cde}	0.79 ± 0.18^{de}	1.74 ± 0.19^{de}	tr.^{c}	tr.^{f}	40.45 ± 4.04^{def}
1	0.33 ± 0.22^{abcd}	0.13 ± 0.08^{a}	23.20 ± 2.76^{fg}	tr.^{e}	0.69 ± 0.16^{e}	tr.^{c}	0.69 ± 0.15^{de}	25.04 ± 2.97^{gh}
20	0.42 ± 0.10^{abcd}	tr.^{b}	29.90 ± 4.10^{efg}	1.48 ± 0.25 ^{cd}	0.87 ± 0.23^{e}	0.35 ± 0.16^{b}	2.61 ± 0.11^{b}	35.63 ± 4.11^{efg}
100	0.31 ± 0.10^{bcd}	tr.^{b}	25.16 ± 1.79^{efg}	1.02 ± 0.31^{de}	0.78 ± 0.21^{e}	0.22 ± 0.19^{bc}	1.13 ± 0.21^{d}	28.62 ± 1.84^{fgh}
1000	0.19 ± 0.16^{bcd}	0.10 ± 0.06^{ab}	18.62 ± 3.64 G	tr.^{e}	0.60 ± 0.37^{e}	0.24 ± 0.20^{bc}	0.55 ± 0.17^{e}	20.31 ± 4.03 ^{h}

Table 3
The monounsaturated fatty acids composition (expressed as % of total fatty acids) isolated from triticale kernels germinated at different concentrations of MeJA for different times at 20 °C. Each value is the mean of four replicates ± SE. Means with common letters are non-significantly different at $p < 0.05$. tr. – trace.".

Monounsaturated fatty acids (MUFAs)							
Time period and MeJA concentration (μM)	Hexadecenoic C 16:1c	Hexadecenoic/ Palmitoleic C 16:1 9c	Octadecenoic/Oleic C 18:1 9c	Octadecenoic C 18:1 11c	Eicosenoic C 20:1 (*n*-9)	Erucic C 22:1	Total
24 h							
0	2.01 ± 0.22^{a}	0.72 ± 0.09^{c}	6.37 ± 0.81 ^{f}	0.00 ± 0.00 ^{h}	tr.^{g}	tr.^{d}	9.10 ± 0.42 ^{f}
1	0.20 ± 0.09^{hi}	0.19 ± 0.04^{gh}	14.01 ± 2.43^{a}	0.76 ± 0.20 ^{cd}	1.48 ± 0.09^{a}	tr.^{d}	16.65 ± 2.52^{ab}
20	0.26 ± 0.02 ^{h}	0.09 ± 0.01 ^{h}	13.93 ± 2.88^{a}	0.32 ± 0.11^{efgh}	1.49 ± 0.11^{a}	tr.^{d}	16.09 ± 1.38^{abc}
100	0.37 ± 0.09^{fgh}	tr.^{i}	12.50 ± 1.16^{abc}	tr.^{h}	tr.^{g}	tr.^{d}	12.88 ± 1.83^{bcde}
1000	tr.^{i}	tr.^{i}	10.23 ± 0.91^{bcde}	0.63 ± 0.22^{de}	tr.^{g}	tr.^{d}	10.86 ± 1.19^{ef}
48 h							
0	tr.^{i}	0.00 ± 0.00^{i}	7.07 ± 0.52^{ef}	0.64 ± 0.21^{de}	1.06 ± 0.13^{ef}	tr.^{d}	11.31 ± 2.06^{def}
1	0.41 ± 0.11^{efgh}	0.00 ± 0.00^{i}	14.02 ± 0.87^{a}	0.35 ± 0.09^{efg}	1.47 ± 0.12^{a}	2.54 ± 0.45^{a}	16.25 ± 1.27^{abc}
20	0.63 ± 0.10^{de}	0.26 ± 0.04^{fg}	6.45 ± 0.30 ^{f}	tr.^{h}	0.91 ± 0.06 ^{f}	tr.^{d}	10.20 ± 0.99^{ef}
100	0.41 ± 0.04^{efgh}	0.12 ± 0.02 ^{h}	9.89 ± 0.47^{bcde}	0.25 ± 0.11^{efg}	1.06 ± 0.07^{ef}	1.95 ± 0.34^{b}	17.37 ± 0.56^{a}
1000	0.20 ± 0.03^{hi}	0.18 ± 0.02^{gh}	10.23 ± 1.13^{bcde}	0.56 ± 0.20^{def}	1.43 ± 0.10^{ab}	tr.^{d}	12.60 ± 0.81^{bcde}
72 h							
0	0.92 ± 0.09^{c}	0.88 ± 0.10^{b}	8.08 ± 0.52^{ef}	2.37 ± 0.12^{a}	tr.^{g}	tr.^{d}	12.25 ± 0.86^{cdef}
1	0.42 ± 0.08^{efgh}	0.06 ± 0.01 ^{h}	12.24 ± 0.71^{abcd}	1.19 ± 0.08^{b}	1.35 ± 0.09^{abc}	tr.^{d}	15.26 ± 2.12^{abcd}
20	0.60 ± 0.05^{def}	0.61 ± 0.04^{c}	6.38 ± 0.55 ^{f}	0.26 ± 0.04^{fgh}	1.10 ± 0.08^{cdef}	tr.^{d}	8.95 ± 0.64 ^{f}
100	0.72 ± 0.06 ^{cd}	0.45 ± 0.03^{d}	7.26 ± 0.49^{ef}	0.16 ± 0.02^{gh}	1.11 ± 0.10^{cdef}	tr.^{d}	9.70 ± 0.88 ^{f}
1000	1.56 ± 0.10^{b}	1.27 ± 0.08^{a}	9.13 ± 0.31^{def}	1.07 ± 0.07^{bc}	tr.^{g}	tr.^{d}	13.03 ± 0.93^{bcde}
96 h							
0	0.73 ± 0.07 ^{cd}	0.66 ± 0.05^{c}	7.89 ± 0.53^{ef}	0.49 ± 0.05^{defg}	1.35 ± 0.11^{abc}	tr.^{d}	10.97 ± 0.98^{ef}
1	0.30 ± 0.01^{gh}	0.29 ± 0.01^{efg}	11.75 ± 0.90^{abcd}	0.34 ± 0.02^{efgh}	1.19 ± 0.08^{bcde}	tr.^{d}	14.02 ± 0.79^{bcde}
20	0.60 ± 0.04^{def}	0.40 ± 0.02^{de}	6.90 ± 0.47^{ef}	tr.^{h}	0.99 ± 0.08^{cf}	0.57 ± 0.22^{c}	9.46 ± 0.69^{f}
100	0.53 ± 0.06^{defg}	0.35 ± 0.03^{def}	9.23 ± 0.58^{cdef}	1.14 ± 0.08^{b}	1.09 ± 0.07^{def}	0.33 ± 0.11 ^{cd}	12.67 ± 1.04^{bcde}
1000	0.21 ± 0.02 ^{hi}	0.10 ± 0.02^{h}	13.07 ± 0.87^{ab}	0.76 ± 0.05 ^{cd}	1.32 ± 0.10^{abcd}	tr.^{d}	15.45 ± 2.17^{abcd}

at 24 h across the whole range of MeJA concentrations (Table 3). At the concentrations from 20 to 1000 μM of MeJA the increase was noted at all time periods from 48 to 96 h. The different concentration of MeJA caused significant changes in the percentage of MUFAs in experimental kernels. Differences were noted in the percentage of acids between the kernels germinating at different concentrations of MeJA at a certain time, as well as comparing the same concentration of MeJA and different times of the incubation i.e., 24 h, 48 h, 72 h, and 96 h (Table 3).

Only three polyunsaturated fatty acids (PUFAs) were detected in triticale kernels unexposed and exposed to MeJA: linoleic (C 18:2 *n-6*), linolenic (C 18:3 *n-3*) and eicosadienoic (C 20:2 *n-6*) (Table 4). The presence of eicosadienoic acid was determined only in the control sample after 24 h of germination. After the first day of germination, MeJA increased the percentage of PUFAs relative to the control sample (Table 4). This trend was also maintained after 48 h, 72 h, and 96 h of seedlings germination. In successive days of germination, exposure to 1 μM of MeJA clearly increased the percentage of linoleic acid in germinating triticale kernels (Table 4). After 24, 48, and 72 h the

Table 4
The polyunsaturated fatty acids composition (expressed as % of total fatty acids) isolated from triticale kernels germinated at different concentrations of MeJA for different times at 20 °C. Each value is the mean of four replicates ± SE. Means with common letters are non-significantly different at $p < 0.05$. tr. – trace.".

Polyunsaturated fatty acids (PUFAs)				
Time period and MeJA concentration (μM)	Linoleic C 18:2 (*n*-6)	Linolenic C 18:3 (*n*-3)	Eicosadienoic C 20:2 (*n*-6)	Total
24 h				
0	16.55 ± 0.23 ^{g}	2.01 ± 0.21^{j}	0.30 ± 0.21^{a}	18.86 ± 0.23^{gh}
1	52.64 ± 4.98^{ab}	9.93 ± 0.93^{de}	tr.^{a}	62.57 ± 5.12^{ab}
20	51.61 ± 3.74^{ab}	9.91 ± 0.73^{de}	tr.^{a}	61.52 ± 5.83^{abc}
100	47.81 ± 2.91^{abc}	6.48 ± 1.30^{gh}	tr.^{a}	54.29 ± 4.43^{abc}
1000	42.14 ± 2.78^{bcd}	4.70 ± 0.22^{ij}	tr.^{a}	46.84 ± 3.86^{cde}
48 h				
0	30.49 ± 3.05^{ef}	9.05 ± 0.57^{fg}	tr.^{a}	39.54 ± 4.02^{def}
1	52.35 ± 4.08^{ab}	10.29 ± 0.78^{de}	tr.^{a}	62.64 ± 5.13^{ab}
20	51.10 ± 5.06^{ab}	16.31 ± 1.40^{a}	tr.^{a}	67.41 ± 6.37^{a}
100	47.28 ± 3.19^{abc}	10.64 ± 2.2 ^{cd}	tr.^{a}	57.92 ± 5.23^{abc}
1000	45.63 ± 3.27^{abc}	9.55 ± 3.00^{ef}	tr.^{a}	55.18 ± 6.02^{abc}
72 h				
0	23.00 ± 2.05^{fg}	5.84 ± 1.55^{hi}	tr.^{a}	28.84 ± 2.16^{fg}
1	50.49 ± 5.25^{ab}	11.68 ± 1.07^{bcd}	tr.^{a}	62.17 ± 5.38^{ab}
20	42.58 ± 4.75^{bcd}	16.97 ± 2.39^{a}	tr.^{a}	59.55 ± 5.91^{abc}
100	17.33 ± 0,92 ^{g}	15.79 ± 1.19^{ab}	tr.^{a}	33.12 ± 2.95^{efg}
1000	4.69 ± 1.19 ^{h}	13.27 ± 1.44^{abcd}	tr.^{a}	4.69 ± 1.19 ^{h}
96 h				
0	34.37 ± 2.67^{de}	14.21 ± 1.12^{abc}	tr.^{a}	48.58 ± 4.40^{bcd}
1	47.18 ± 3.81^{abc}	13.76 ± 2.03^{abcd}	tr.^{a}	60.94 ± 5.89^{abc}
20	39.37 ± 3.16^{cde}	15.54 ± 1.97^{ab}	tr.^{a}	54.91 ± 5.38^{abc}
100	54.66 ± 3.05^{a}	10.41 ± 1.00 ^{cd}	tr.^{a}	58.71 ± 6.11^{abc}
1000	50.54 ± 6.52^{ab}	13.70 ± 0.49^{abcd}	tr.^{a}	64.24 ± 5.27^{a}

decrease in kernels treated with 20 – 1000 μM of MeJA was observed. However, the analysis of linoleic acid percentage in germinating triticale kernels after 96 h showed decrease up to 39.37% under the influence of 20 μM of MeJA, followed by increase in concentration up to 1000 μM (Table 4). The increasing concentration of MeJA from 0 to 20 μM led to a progressive increase in linolenic acid (C 18:3 n-3) concentration in triticale seedlings, followed by a decrease of acid percentage in triticale seedlings germinating at all the remaining MeJA concentrations during the whole period of the experiment (24–96 h) (Table 4).

4. Discussion

Methyl jasmonate is a signal molecule that controls different developmental processes of the plant such as seed germination, root growth, flowering, fruit ripening, and senescence [42]. Methyl jasmonate, through controlling plant metabolism and chemical composition, plays an outstanding role in the defense mechanisms of the plant against several diseases [12–14]. Depending on the organ, species, and age of the plant, the content of jasmonate compounds varies greatly, ranging from 3 to 10 μg per g fresh weight [43]. Relatively high jasmonate levels are present in the generative parts of the plant, i.e., the pericarp, fruit, and seeds compared with the vegetative organs, i.e., the stems and leaves. Several biological and physicochemical factors as well as mechanical damage have a great influence on the plant content of jasmonate [44,45]. Generally, the content of jasmonates in the plant decreases with age [46].

There is a lot of information dealing with the role of jasmonates in lipid transformations during germination of oily seeds; but little information is available concerning seeds of low lipid content. Therefore, the present work was conducted to fill this gap and the aim of this study was to evaluate the effect of exogenous application of MeJA in an in vitro experiment on the content and composition of fatty acids in germinating kernels of winter triticale (x *Triticosecale* Wittmack, cv. Ugo).

The fatty acid composition of ripe triticale grains has been fully described [38] but not during kernel germination. Triticale kernels are relatively low in lipids, with a lipid content of 1.4–2.2% (w/w) [38], most of which occurs in the embryo [47]. Lipids of triticale kernels contain 20 fatty acids (FAs) with the highest proportion being of linoleic acid [38], followed by palmitic acid and oleic acid [47]. Methyl jasmonate applied twice (stages 54 and 73 on BBCH-scale used to identify the phenological development stages of plants) to winter triticale (*Triticosecale* Wittmack cv. Dinaro) did not exert a significant effect on the composition of FAs of the grains [38]. However, high concentrations (100 and 1000 μM) of exogenous MeJA during seed germination induced changes in the phospholipid profile and inhibited lipid biosynthesis in yellow lupine [48]. Moreover, MeJA increased the content of isoflavones in three-day old yellow lupine seedlings [49]. The present findings indicate that at the high concentrations relative to the other studies, MeJA accelerates the decomposition of saturated fatty acids during the first days of triticale kernel germination, in favor of unsaturated fatty acids, mostly PUFAs (Table 2 and Table 3). Enzymatic hydrolysis of storage food (starch, proteins, and lipids) is an essential process in germinating kernels. At the initial stages of germination, lipases in wheat and barley kernels hydrolyze triacylglycerols to free fatty acids which are further metabolized by other enzymes. For example, PUFAs are subjected to β-oxidation by lipoxygenases via the JA biosynthesis pathway, leading to the production of acetyl-CoA [47,50]. Under exposure to exogenous MeJA, the breakdown of SFAs may be accelerated by two independent processes: a) direct stimulation of lipase activity by MeJA which, similarly to gibberellins, enhances the activity of α-amylase, and b) inducing the expression of genes responsible for the biosynthesis of lipase protein. Both hypotheses require experimental validation. Lipases and other enzymes have been commercially isolated from animal sources; but recently they are also isolated from plants. Dietary supplementation with active lipases is particularly recommended for people suffering from gallbladder problems, celiac disease and Crohn's disease [51]. Further studies confirming participation of lipases in SFAs breakdown in germinating triticale kernels, as well as stimulation of lipase activity by MeJA is necessary.

Cereal seedlings are not widely consumed, but the consumption of sprouted grains is claimed to have a positive effect on human health, which has recently led to a growing positive perception of sprouted grains among consumers and brought new foods and beverages to the market [52]. In our study, we confirmed high percentage of PUFAs at the expense of SFAs in germinating triticale kernels (Tables 2, 3). Foods rich in PUFAs with minority of SFAs are highly recommended [53]. Studies have shown that consumption of saturated fat has a deleterious effect on serum lipids by increasing low-density lipoprotein (LDL) cholesterol

levels [54]. There is some evidence that short-chain fatty acids (less than 10 C) are less likely to affect serum cholesterol levels, while longer-chain fatty acids (12, 14, or 16 C) are more likely to increase LDL levels. An exception is stearic acid (18 C), which does not appear to increase serum LDL cholesterol levels [53,55]. Increased consumption of SFAs is also associated with an increased risk of coronary heart disease (CHD). Various studies and reports support the increased consumption of PUFAs for the prevention of CHD [56]. It has been shown that PUFAs also provide some benefit to patients with cystic fibrosis, and may have a protective effect against dementia [57,58]. Moreover, PUFAs can lower triglyceride and LDL in patients with diabetes [59] and contribute to the prevention of cancer and life-style diseases [53,60]. In line with the recommendations formulated by the Nutrition Committee of the American Heart Association [61] and by the European Union authorities [62], the food industry is encouraged to replace SFAs and trans-unsaturated fatty acids with PUFAs and MUFAs, which also affect a number of risk factors for CHD, including lowering total and LDL cholesterol levels, thus protecting against thrombogenesis, reducing LDL susceptibility to oxidation, and producing a more favorable glycemic profile [63].

Moreover, in human body, the PUFAs eicosapentaenoic acid and docosahexaenoic acid can be synthesized in low quantities from exogenous linoleic and linolenic acids [64,65]. Similarly, production of several PUFAs was enhanced in germinating triticale kernels after the treatment with MeJA (Table 3). This increased content of PUFAs, along with the decrease in SFAs and the possibly higher lipase activity in germinating triticale kernels after treatment with MeJA might justify recommending consumption of cereal seedlings as a food supplement. Nevertheless, despite the above benefits of MeJA application, Kubicka and Zadernowski [66] argued that jasmonate-treated foods can exert negative health effects. Therefore, further research is necessary to guarantee the safety and quality of jasmonate-treated foods.

5. Conclusions

Although application of MeJA to the germinating triticale kernels impeded kernel germination and embryo growth to different extents, yet it improved the nutritional quality of the emerging seedlings. The adverse effect of MeJA was stronger on embryo growth than on kernel germination. The beneficial effect of MeJA application to germinating triticale kernels was manifested as increased unsaturated fatty acids, mainly PUFAs, at the expense of SFAs. Methyl jasmonate could activate lipases, which play an essential role in the digestion, transport, and processing of dietary fats, but this issue requires further detailed research. Methyl jasmonate-treated triticale seedlings may have a greater health-promoting effect than wheat seedlings which are currently being marketed as a health-promoting product.

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CRediT authorship contribution statement

Kazimierz Zalewski: Conceptualization, Resources, Writing – original draft, Supervision. **Sylwester Czaplicki**: Methodology, Software, Formal analysis, Investigation. **Ryszard Rafałowski**: Methodology, Software, Formal analysis, Investigation. **Stryinski Robert Stryiński**: Software, Data curation, Writing – review & editing, Visualization. **Adam Okorski**: Software, Data curation, Visualization. **Bartosz Nitkiewicz**: Validation, Investigation, Resources. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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