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Authors' contributions

The research idea was developed by JK and MH. Fatty acid analyses were performed by JK. Peroxidation was measured by MS. Plant experiments were conducted by DK and JM. The manuscript was written by MH and MS.

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Competing interests

No competing interests have been declared.

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ORIGINAL RESEARCH PAPER

Methyl jasmonate vapors affect the composition and peroxidation of major fatty acids in common buckwheat seedlings

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Abstract

The effect of methyl jasmonate (MJ) vapors on the composition and peroxidation of major fatty acids in the organs of common buckwheat seedlings was investigated. The composition of fatty acids in the hypocotyl and cotyledons of seedlings changed significantly under exposure to MJ vapors in closed jars. Four-day exposure to MJ led to a significant reduction in the concentrations of stearic, linoleic, and linolenic acids in the hypocotyl, whereas oleic acid levels increased approximately 3.5-fold. A decrease in stearic acid levels and an increase in the content of linolenic acid were noted in cotyledons, whereas oleic acid levels decreased in roots. Seven-day exposure to MJ vapor caused a further reduction in stearic acid content and an increase in oleic acid and linoleic acid levels in the hypocotyl. At the same time, the linoleic acid content of roots and linolenic acid levels in cotyledons were doubled, but a 5-fold reduction in linolenic acid concentrations was observed in roots. Methyl jasmonate intensified fatty acid peroxidation in cotyledons after 4 and 7 days and in roots after 4 days of exposure. Peroxidation was inhibited in the hypocotyl and roots after 7 days. The noted changes in the composition and peroxidation of fatty acids are probably indicative of senescence in buckwheat seedlings under the influence of MJ. Senescence seems to proceed faster in cotyledons than in other organs of buckwheat seedlings.

Keywords

methyl jasmonate; common buckwheat; seedling; fatty acid; peroxidation

Introduction

Methyl jasmonate (MJ) is a naturally occurring phytohormone involved in the signal transduction pathway and plant responses to environmental stressors [1]. Its influence on the production of phenolic metabolites has been widely studied [2]. The impact of MJ on the levels and composition of fatty acids in plant tissues is less known and ambiguous. Exogenous MJ clearly increased the content of free and bound oleic and linoleic acids in tulip stems, but it did not affect the levels of palmitic, stearic, and linolenic acids [3]. In tomato fruit, MJ significantly increased the content of linolenic acid and induced a less pronounced decrease in the concentrations of linoleic acid [4]. At the same time, MJ did not influence or provoked minor changes in the content of free and bound fatty acids in the petioles and blades of *Kalanchoe blossfeldiana* [5]. However, MJ decreased the content of free linolenic acid in intact tulip leaves [6].

Cell membrane lipids are the major target of environmental stressors [7]. In photosynthetic tissues, MJ can lead to disorganization of thylakoid membranes of chloroplasts [8]. Exogenous MJ inhibits growth and stimulates senescence processes in plants [9–11]. Senescence compromises the integrity of cellular membranes [12,13].

During senescence, membrane lipids undergo hydrolysis, and most of the released fatty acids are metabolized to acetyl-CoA [14]. Senescence is also accompanied by peroxidation of unsaturated fatty acids, which increases malondialdehyde (MDA) levels as the key indicator of the extent of lipid oxidation. However, MJ can also lower lipoxygenase activity and delay maturation of stored fruit [15]. The ratio of unsaturated to saturated fatty acids in MJ-treated fruit was also significantly higher than in control. The thiobarbituric acid (TBA) assay is most commonly used for measuring MDA and lipid peroxidation, although other substances may also react with TBA and thus contribute to the overestimation of peroxidation results [16–19].

The objective of this study was to evaluate the effect of MJ on the fatty acid profile and the rate of lipid peroxidation in the hypocotyl, cotyledons and roots of common buckwheat seedlings.

Material and methods

Etiolated seedlings of common buckwheat (*Fagopyrum esculentum* Moench 'Hruszowska') were germinated for 4 days in darkness. The seedlings were transferred to a growth room with a 16-h photoperiod, 65 ±5% relative humidity and a temperature of 22 ±2°C / 18 ±2°C (day/night). High-pressure 400-W sodium lamps were the source of light (100 ±10 μmol m⁻² s⁻¹). During de-etiolation in the above conditions, the seedlings were exposed to MJ vapors for 4 or 7 days. A 50-μL drop of MJ was placed on a strip of filter paper which was suspended in a glass jar tightly capped with silicon foam, as described earlier [20]. Ambient MJ concentrations in closed jars were determined at 100 μmol on the assumption that the applied amounts were evaporated. After exposure, the seedlings were divided into roots, cotyledons and hypocotyls, and the organs were freeze dried separately. The samples were subjected to chemical analyses.

Lipids were extracted in a mixture of chloroform : methanol : 0.15 mol acetic acid (10:20:7.5, v/v/v) by the modified method of Bligh and Dyer [21]. The chloroform phase was evaporated to dryness under N₂, and the residue was dissolved in a small volume of chloroform. Fatty acids were methylated in a mixture of methanol, toluene, and sulfuric acid (80:20:2, v/v/v) [22]. Quantification of fatty acid methyl esters was carried out by gas chromatography on a 2.5 m × 3 mm ID column packed with 3% SP2300 on Supelcoport 100/120 mesh (Sigma-Aldrich, St. Louis, USA) with methyl heptadecanoic acid (C17:0) as an internal standard. The degree of lipid peroxidation was established by measuring the content of malondialdehyde (MDA) by the TBARS method [23]. All measurements were performed in three replicates, with the exception of MDA which was analyzed in five replicates. Differences between control and MJ-treated plants were determined by Student's *t*-test.

Results

The content of the following major fatty acids was analyzed in the organs of buckwheat seedlings: palmitic acid, stearic acid, oleic acid, linoleic acid, and linolenic acid. The remaining fatty acids occurred in very small amounts that are below the limit of detection. Stearic acid was the predominant saturated fatty acid in the tissues of buckwheat seedlings (Fig. 1). Linoleic acid was the major unsaturated fatty acid in the hypocotyl and cotyledons of control seedlings (Fig. 2). The content of linoleic and linolenic acids in roots was approximately equal.

In general, the influence of MJ on the fatty acid content of buckwheat seedlings was highly dependent on the type of evaluated tissue and length of exposure to MJ. Four-day exposure to MJ vapors decreased stearic acid levels and increased the content of linolenic acid in cotyledons (Fig. 1 and Fig. 2). The four-day exposure had a relatively minor effect on the composition of other fatty acids in buckwheat cotyledons, but it provoked significant changes in the fatty acid profile of the hypocotyl. In the organ, MJ induced a significant decrease in the content of stearic, linoleic and linolenic acids,

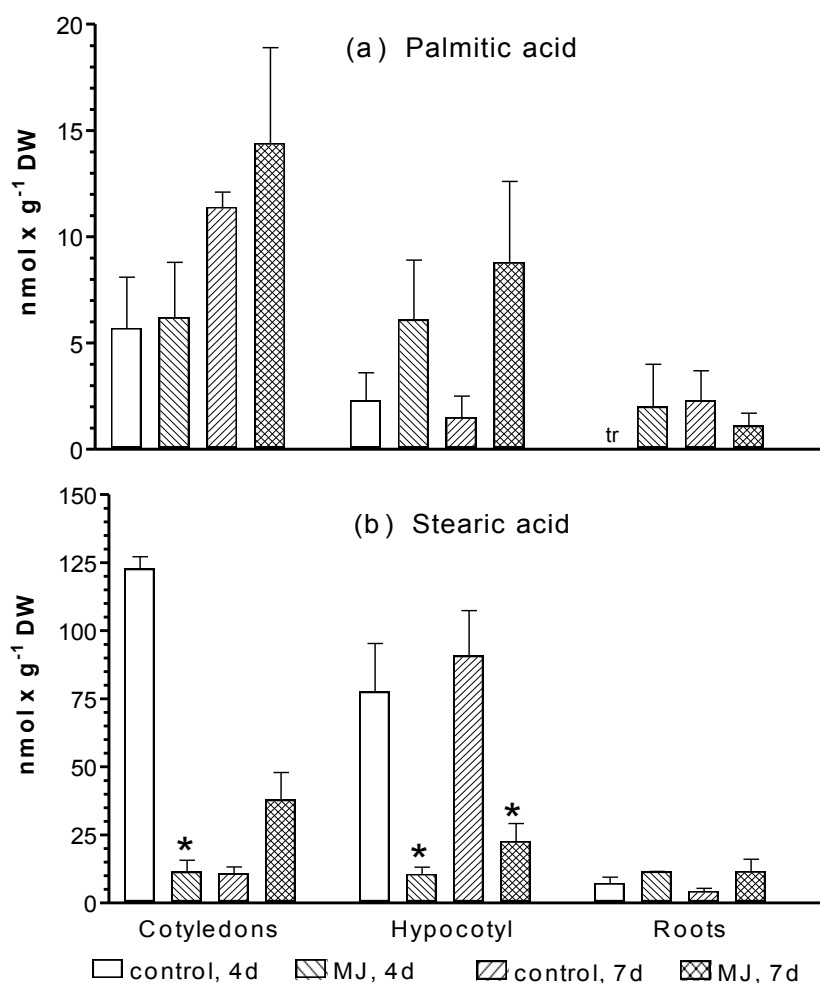


Fig. 1 The effect of 4-day (4 d) and 7-day (7 d) exposure to methyl jasmonate (MJ) vapors on the content ($\text{nmol g}^{-1} \text{DW}$) of major saturated fatty acids in the organs of common buckwheat seedlings (means $\pm \text{SD}$; tr – trace amount, below $1 \text{ nmol g}^{-1} \text{DW}$). Significant differences between control and MJ-treated plants are marked with asterisks * ($p < 0.05$).

and a marked increase in oleic acid levels. Oleic acid concentrations in roots decreased nearly 5-fold after 4 days of exposure to MJ vapors. A negligible decrease in linoleic acid levels and an increase in linolenic acid concentrations were also observed. The MJ-induced decrease in stearic acid levels and the accumulation of oleic acid were noted only in the hypocotyl.

Seven-day exposure to MJ led to a decrease in the content of stearic acid, an increase in the levels of oleic and linoleic acids, and a negligible decrease in linolenic acid concentrations in the hypocotyl (Fig. 1 and Fig. 2). Longer exposure to MJ provoked a 2-fold increase in the linolenic acid content of cotyledons, and a nearly 5-fold decrease in linolenic acid levels and an increase in linoleic acid concentrations in roots. After 7 days of exposure to MJ, roots exhibited severe symptoms of senescence, including brown discoloration and inhibition of growth.

The ratio of unsaturated to saturated fatty acids decreased in the cotyledons of buckwheat seedlings as a result of MJ exposure (Tab. 1). The above changes were particularly evident after 7 days of MJ treatment. Methyl jasmonate exerted an opposite effect in the hypocotyl and roots where an increase in the unsaturated/saturated fatty acid ratio was noted.

Malondialdehyde (MDA) concentrations were higher in cotyledons than in the hypocotyl and roots of buckwheat seedlings (Tab. 2). Methyl jasmonate vapors increased the MDA content of cotyledons after 4 and 7 days of exposure. Four-day exposure to MJ also increased MDA levels in roots. However, MJ inhibited the production of MDA in the hypocotyl, which was particularly evident after 7 days of treatment.

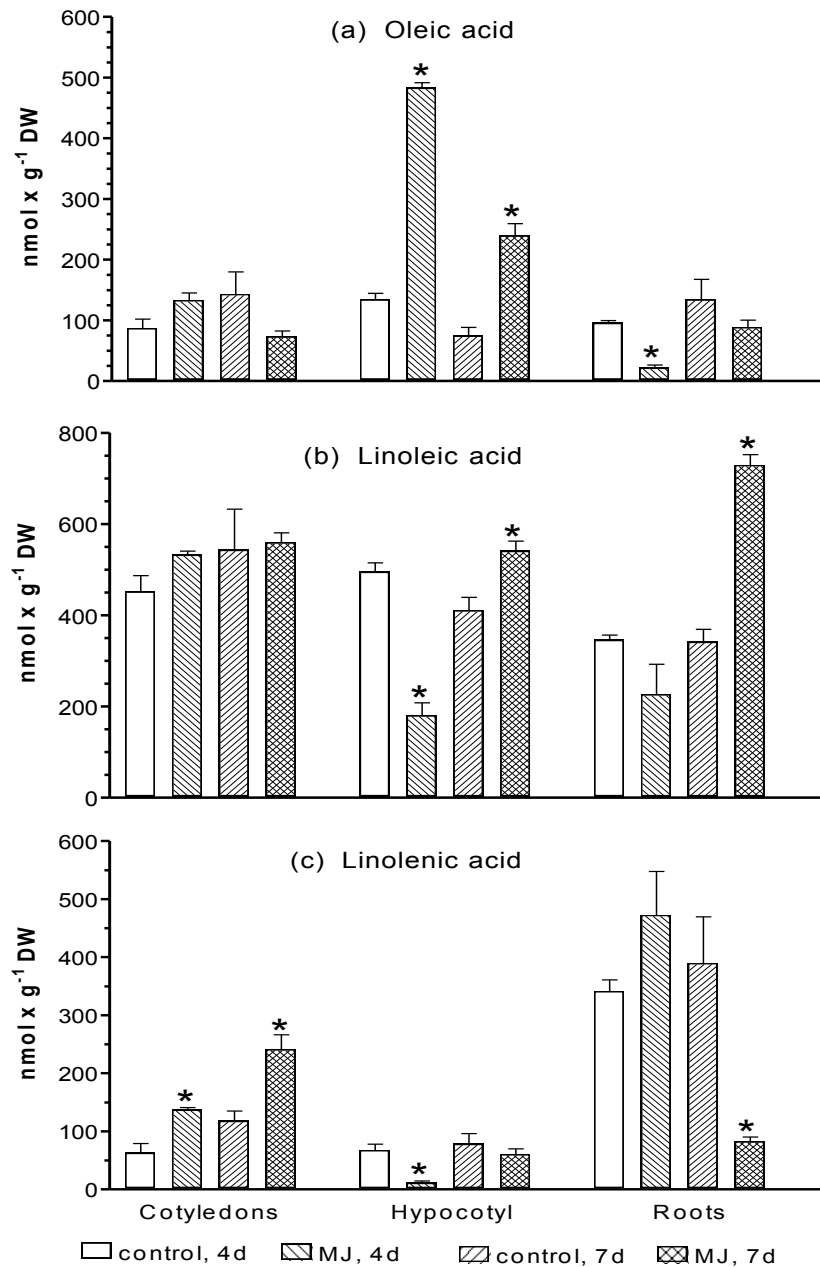


Fig. 2 The effect of 4-day (4 d) and 7-day (7 d) exposure to methyl jasmonate (MJ) vapors on the content ($\text{nmol} \text{g}^{-1} \text{DW}$) of major unsaturated fatty acids in the organs of common buckwheat seedlings (means \pm SD). Significant differences between control and MJ-treated plants are marked with asterisks * ($p < 0.05$).

Discussion

The results of this study indicate that linoleic acid was the major fatty acid in the organs of common buckwheat seedlings. Similar results were reported by Kim et al. [24] in the edible parts of etiolated buckwheat sprouts.

In our previous study, the addition of MJ to a growth medium inhibited the growth of roots in common buckwheat seedlings [20]. However, MJ had no effect on the growth of aerial parts. Methyl jasmonate had a varied effect on the fatty acids content of different seedling organs. According to our knowledge, the impact of MJ on the content and composition of fatty acids in buckwheat seedlings has not been investigated to date. A significant reduction in the concentrations of stearic, linoleic and linolenic acids was found in the hypocotyl exposed to MJ. Our results are only partially consistent with the previous observations made in tulip stems [3]. In these tissues, MJ clearly increased the content of oleic and linoleic acids, but it did not affect the levels

Tab. 1 The effect of 4-day and 7-day exposure to methyl jasmonate (MJ) vapors on the total content of saturated and unsaturated fatty acids (nmol g⁻¹ DW; means ±SD) in the organs of common buckwheat seedlings.

Fatty acids ratio	After 4 days		After 7 days	
	control	MJ treated	control	MJ treated
Cotyledons				
Saturated (S)	7.2 ±2.3	13.5 ±2.1	4.4 ±0.6	12.8 ±3.3
Unsaturated (U)	602.0 ±54.5	803.0 ±15.5*	804.3 ±36.1	874.0 ±43.4
Ratio U/S	89.9 ±30.2	60.5 ±9.5	184.9 ±25.5	69.0 ±15.0*
Hypocotyl				
Saturated (S)	117.7 ±27.4	19.1 ±2.2*	92.1 ±15.7	16.9 ±3.3*
Unsaturated (U)	697.3 ±30.0	675.0 ±17.1	564.0 ±23.6	841.0 ±5.3*
Ratio U/S	6.1 ±1.5	35.6 ±4.1*	6.2 ±1.1	51.1 ±10.2*
Roots				
Saturated (S)	128.4 ±6.3	10.3 ±1.4*	23.1 ±1.4	52.3 ±14.4
Unsaturated (U)	783.0 ±30.8	721.0 ±75.6	865.7 ±77.0	900.3 ±28.9
Ratio U/S	6.1 ±0.7	70.9 ±9.7*	37.6 ±5.7	18.2 ±5.1

* Significant differences between control and MJ-treated plants ($p < 0.05$).

Tab. 2 The effect of 4-day and 7-day exposure to methyl jasmonate (MJ) vapors on the concentrations of malondialdehyde (nmol g⁻¹ DW; means ±SD) in the organs of common buckwheat seedlings.

Analyzed organ	After 4 days		After 7 days	
	control	MJ treated	control	MJ treated
Cotyledons	400.3 ±16.2	566.7 ±43.3*	371.8 ±35.5	565.5 ±107.2*
Hypocotyl	260.8 ±34.4	246.4 ±14.4	232.5 ±20.6	107.8 ±19.3*
Roots	191.0 ±9.4	241.0 ±23.7*	65.0 ±6.5	38.1 ±17.0

* Significant differences between control and MJ-treated plants ($p < 0.05$).

of palmitic, stearic, and linolenic acids. Exposure to MJ decreased the concentrations of free linolenic acid in tulip leaves [6], and led to a marked increase in linolenic acid levels and a decrease in the linoleic acid content of green tomato fruit [4]. The results of our study differ from previous observations made in petioles and blades of *Kalanchoe blossfeldiana*, where exposure to MJ applied in lanolin paste led to only minor changes in the content of fatty acids [5]. These differences could be attributed to the various forms of MJ application in vapors and lanolin paste.

The noted changes in the ratio of saturated to unsaturated fatty acids may affect the regulation of cell growth and cell differentiation due to changes in cell membrane permeability [25]. The above probably impairs the transport of nutrients across membranes, and it inhibits seedling growth, which was demonstrated in our previous studies [20,26]. One of the first discovered biological activities of MJ was the promotion of senescence in oat (*Avena sativa*) leaves [9,10]. In the present study, clear symptoms of senescence were also noted in the roots of buckwheat seedlings. During leaf senescence in *Arabidopsis*, *Brachypodium distachyon*, and switchgrass (*Panicum virgatum*), a progressive decrease in the content of all fatty acids occurs [14]. The most pronounced changes were observed in linolenic acid levels. The unsaturated/saturated

fatty acid ratio is also lower in senescent leaves. In vegetative plant organs, most fatty acids occur as components of cytoplasmic membranes, and changes in their composition may affect membrane properties. The above could be one of the reasons for the decrease in the anthocyanin content of hypocotyl tissues exposed to MJ vapors [20]. Anthocyanins are transported across the tonoplast to vacuoles where they are stored as anthocyanic vacuolar inclusions [27,28].

In this study, the unsaturated/saturated fatty acid ratio decreased in cotyledons, and increased in the hypocotyl and roots of buckwheat seedlings exposed to MJ, which could imply that MJ induces other processes that provoke organ-dependent responses. Our findings could also be attributed to the fact that MJ affects many metabolic processes and therefore objective conclusions are difficult to formulate. One of such processes involves the accumulation of large amounts of 2-phenylethylamine [20,29]. According to Seltman et al. [30], natural senescence differs from stress-induced senescence. The authors suggest that exogenous application of biologically active compounds is not necessarily related to the effect and function of endogenous compounds.

Atmospheric MJ has been found to increase the activity of lipoxygenase (LOX), a key enzyme in jasmonate biosynthesis [31,32]. The activation of LOX induces lipid peroxidation, leads to the formation of reactive oxygen species, and an increase in malondialdehyde (MDA) concentrations [33], which was observed in the cotyledons of buckwheat seedlings exposed to MJ. Methyl jasmonate in the gaseous phase increased LOX activity in tobacco leaf tissues [31]. At the same time, MJ vapors decreased MDA levels in the hypocotyl, which was particularly evident after 7 days of exposure. The causes of the above have not been fully elucidated, but the results of previous studies indicate that under certain conditions lipid peroxidation leads to inhibition of MDA synthesis. Exogenous jasmonic acid (JA) enhanced salt stress tolerance and decreased MDA concentrations in wheat seedlings [34]. According to the cited authors, JA protects seedlings from stress damage by stimulating antioxidant enzymes and increasing antioxidant levels. The protective role of jasmonates against lipid peroxidation induced by abiotic stress was also reported in other studies [15,35,36].

The concentrations of MDA were significantly lower in the roots of control plants and in seedlings exposed to MJ for 7 days, which points to the inhibition of peroxidation processes. This is probably related to a lower metabolic rate, which could have been caused by accelerated senescence.

In conclusion, our data provide evidence that MJ directly or indirectly affects the profile and content of fatty acids in buckwheat seedlings. Methyl jasmonate exerted the most profound effect on the fatty acid composition of the hypocotyl where linoleic acid concentrations decreased significantly. In cotyledons, the observed changes in fatty acid content were less evident, but the accumulation of MDA is indicative of advanced senescence. The noted differences in the responses of various organs of buckwheat seedlings exposed to MJ confirm earlier reports that plant organs differ considerably in their sensitivity to MJ [31].

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Wpływ par jasmonianu metylu na skład i peroksydację głównych kwasów tłuszczowych w siewkach gryki zwyczajnej

Streszczenie

Badano wpływ par jasmonianu metylu (MJ) na skład głównych kwasów tłuszczowych i stopień ich peroksydacji w siewkach gryki zwyczajnej (*Fagopyrum esculentum* 'Hruszowska'). MJ powodował duże zmiany w składzie kwasów tłuszczowych w poszczególnych tkankach siewek. I tak, 4-dniowe traktowanie MJ doprowadziło do dużych spadków zawartości kwasów: stearynowego, linolowego i linolenowego w hipokotyli siewek gryki, zaś zawartość kwasu oleinowego wzrosła ok. 3.5-krotnie. W przypadku liścieni wykazano obniżenie zawartości kwasu stearynowego oraz podwyższenie poziomu kwasu linolenowego, natomiast w tkankach korzeni stwierdzono obniżenie zawartości kwasu oleinowego. Dłuższe, 7-dniowe traktowanie również prowadziło do obniżenia zawartości kwasu stearynowego i wzrostu poziomu kwasu oleinowego w hipokotyli, lecz wówczas zawartość kwasu linolowego wzrosła. W tym samym czasie zawartości kwasów linolowego w korzeniach oraz linolenowego w liścieniach uległy podwojeniu, ale wystąpiło 5-krotne obniżenie poziomu kwasu linolenowego w korzeniach. MJ powodował wzrost peroksydacji kwasów tłuszczowych w liścieniach po 4 i 7 dniach stosowania, zaś w przypadku korzeni jedynie po 4 dniach. W hipokotyli i korzeniach 7-dniowe stosowanie MJ powodowało zahamowanie procesu peroksydacji. Zmiany składu kwasów tłuszczowych oraz stopnia ich peroksydacji są zapewne objawem procesów starzenia siewek gryki pod wpływem MJ. Wydaje się, że proces starzenia zachodzi szybciej w liścieniach, niż w pozostałych organach siewek gryki.