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ORIGINAL PAPER

The effect of methyl jasmonate on accumulation of 2-phenylethylamine and putrescine in seedlings of common buckwheat (*Fagopyrum esculentum*)

Marcin Horbowicz · Ryszard Kosson · Wiesław Wiczkowski · Danuta Koczkodaj · Joanna Mitrus

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Abstract The effects of exogenously applied methyl jasmonate on content of biogenic amines: putrescine, spermidine, tyramine, cadaverine and 2-phenylethylamine in seedlings of common buckwheat (*Fagopyrum esculentum* Moench) were investigated. The studies have shown that methyl jasmonate stimulates the conversion of L-phenylalanine into 2-phenylethylamine and increases the endogenous levels of putrescine in hypocotyls and cotyledons of buckwheat seedlings. Simultaneous feeding the seedlings with L-phenylalanine and methyl jasmonate has indicated that conversion of L-phenylalanine into 2-phenylethylamine can be one of possible reasons, caused by the methyl jasmonate suppression of anthocyanins synthesis in hypocotyls. To our knowledge, the stimulation of conversion of L-phenylalanine into 2-phenylethylamine by methyl jasmonate, as found in the present study, is described for the first time in higher plants.

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M. Horbowicz (✉) · D. Koczkodaj · J. Mitrus
Department of Plant Physiology and Genetics,
Institute of Biology, University of Podlasie,
Prusa 12, 08-110 Siedlce, Poland
e-mail: mhorbowicz@ap.siedlce.pl

R. Kosson
Research Institute of Vegetable Crops,
Konstytucji 3 Maja 1/3, 96-100 Skierniewice, Poland

W. Wiczkowski
Institute of Animal Reproduction and Food Research,
Polish Academy of Sciences, Tuwima 10,
10-747 Olsztyn, Poland

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Abbreviations

JAs	Jasmonates
MJ	Methyl jasmonate
PAs	Polyamines
PEA	2-phenylethylamine
Phe	L-phenylalanine

Introduction

Biogenic amines are implicated in plant growth and developmental processes and in response to abiotic and biotic stress (Tabor and Tabor 1984; Bais and Ravishankar 2002; Walters 2003; Alcázar et al. 2006). These processes include stimulation of cell division, response to environmental stresses and regulation of embryogenesis, senescence, floral development and fruit ripening (Kakkar and Sawhney 2002; Kusano et al. 2008). Polyamines (PAs) belong to major biogenic amines in plants. PAs are synthesized by the decarboxylation of either arginine or ornithine, catalyzed by arginine decarboxylase or ornithine decarboxylase, respectively (Bagni and Tassoni 2001; Walters 2003). Aliphatic polyamines are involved in the delay of plant senescence, but the mechanism of this action is not fully known (Kaur-Sawhney et al. 1982). Although it is clear that PAs are essential for normal growth and have important physiological roles, the precise role(s) of polyamine metabolism in these processes remains not fully defined (Kakkar and Sawhney 2002).

Aromatic monoamines occurring in plants are the products of enzymatic decarboxylation of L-phenylalanine (Phe), L-tyrosine, and L-histidine to phenylethylamine (PEA), tyramine and histamine, respectively (Smith 1977; Tieman et al. 2006). PEA occurrence has been shown in marine algae (Percot et al. 2009), and some terrestrial plants (Shabana et al. 2006). The role of PEA in plants remains unclear. In common buckwheat PEA can be transformed into 2-phenylacetaldehyde which belongs to the compounds with the highest contribution to aroma of the plant (Janeš et al. 2009).

Jasmonic acid and its conjugates, such as methyl jasmonate (MJ)—collectively referred to as jasmonates (JAs), are specific for, but ubiquitous in the plant kingdom. JAs are signalling molecules implicated in the regulation of various biological processes, like ageing, and play an essential role in plant defense by regulating genes involved in cell growth and biotic and abiotic stress responses (Kazan and Manners 2008). Responses that depend on JAs signalling include not only defense against biotic stress, but also responses to UV radiation, ozone, and other abiotic stresses and senescing process (Ueda and Kato 1980; Wasternack 2007; Balbi and Devoto 2008).

MJ declined the level of free polyamines (putrescine, spermidine, spermine) in thin layers of *Nicotiana tabacum* and increased the content of hydroxycinnamic acid amides of the polyamine (Biondi et al. 2001). The treatment of barley (*Hordeum vulgare*) seedlings with MJ led to the increase of free polyamines and the hydroxycinnamic acid amides content (Walters et al. 2002). Cotyledons of sweet pepper treated with a solution of jasmonic acid exhibited inducible accumulation of caffeoylputrescine (Tebayashi et al. 2007).

Anthocyanin accumulation is stimulated by various environmental stresses, such as UV and blue light, high-intensity light, wounding, pathogen attack, drought, sugar and nutrient deficiency (Mancinelli 1984; Winkel-Shirley 2001). Anthocyanin accumulation is known to be regulated by light and plant hormones. Light acts both as an essential stimulus and as a factor that modulates the regulatory and structural genes of anthocyanin biosynthesis (Winkel-Shirley 2001). The major function of anthocyanins seems to be their photoprotective role (Steyn et al. 2002).

Anthocyanins play an important role in attracting insects or animals for pollination and seed dispersal. In addition, they play roles as anti-oxidants and in protecting DNA and the photosynthetic apparatus from high radiation fluxes (Gould 2004). Exogenously applied MJ enhanced the production of anthocyanins in tissues of many plants (Fang et al. 1999; Franceschi and Grimes 1991; Saniewski et al. 1998, 2003), but contrary to it declined their accumulation in hypocotyls of exposed to light seedlings of common buckwheat (Horbowicz et al. 2008). Looking for a possible reason of the last evidence we have shown that MJ had no influence on contents of apigenin, luteolin and quercetin glucosides in buckwheat tissues, but enhanced accumulation of condensed tannins in hypocotyls (Horbowicz et al. 2010). We suggested that MJ probably increases activity the leucocyanidin reductase or anthocyanidin reductase, possible enzymes in proanthocyanidins synthesis, or/and inhibits activity of anthocyanidin synthase, which transforms leucocyanidin into cyanidin.

This research has been undertaken to evaluate the effect of MJ on accumulation of 2-phenylethylamine and some polyamines and in seedlings of common buckwheat (*Fagopyrum esculentum* Moench). In order to explain the possible metabolic competition between anthocyanins and PEA forming, we also analysed the anthocyanin content in buckwheat seedlings simultaneously treated with Phe and MJ, as well as the influence of particular amines on the accumulation of anthocyanins. In the present paper, possible hypotheses were discussed, related to the reason of high accumulation of PEA in buckwheat tissues treated exogenously with MJ.

Materials and methods

Plant material

Seedlings of common buckwheat cv. Hruszowska were used in this study. Germination was carried out by placing buckwheat seeds between two layers of wet filter paper which were then rolled up and inserted in a 2-L beaker containing tap water at the bottom (Horbowicz et al. 2008). Germination was carried out in darkness at 24 ± 1°C during 4 days. After that, buckwheat seedlings were taken for experiments with MJ. In beakers with seedlings the water was replaced with water solutions of MJ at 10^{-8}, 10^{-6} or 10^{-4} M concentration. In the control sample the water was freshened. Because the MJ was added in a small volume (0.4 mL) of ethyl alcohol, the same amount of ethyl alcohol was added to the control sample. After 8-h pre-incubation in darkness the seedlings were grown for the next 4 days in growth chamber with a 16-h photoperiod and 65 ± 5% relative humidity. Chamber air temperature was maintained at 24 ± 2°C/16 ± 2°C (day/night). Light (100 μM m^{-2} s^{-1}) was provided by 400 W high-pressure sodium lamps.

In another experiment the etiolated buckwheat seedlings (after cutting off their roots) were placed in Hoagland nutrient solution containing various concentrations of PEA (10^{-5}, 10^{-4}, or 10^{-3} M), spermidine or putrescine. Another part of such seedlings was simultaneously treated with the solution of 5, 10, 15 or 25 mM of Phe and vapors of MJ (10^{-5} M). In these experiments the content of anthocyanins in the seedlings were measured, only.

HPLC determination of amines

Free amines were analysed according to the previously described, modified procedure by Flores and Galston (1982). Briefly, plant tissues were homogenized in 5% (*v*/*v*) perchloric acid in ice-cooled mortar. Homogenates were centrifuged, and amines in such obtained supernatant were derivatised with benzoyl chloride for 45 min at 35°C. Benzoyl derivatives of amines were extracted by shaking with ethyl acetate. The extraction was repeated twice, and pooled acetate layers were evaporated to dryness at 40°C in a stream of air. The residue was dissolved in a mobile phase used for HPLC analyses (acetonitrile–water, 45:55).

HPLC analysis was performed with liquid chromatograph (Agilent Technologies, model 1200 Series). The mobile phase was a mixture of acetonitrile–water (45:55, *v*/*v*) at flow rate of 1.0 mL min^{-1}. Benzoylated amines were eluted isocratically at the temperature of 30°C using a RP column Eclipse XDB—C_{18} analytical (4.6 × 150 mm, 5 µm particle size) and C_{18} guard column. The benzoyl derivatives were detected at 245 nm, diode array detector (DAD), and amine contents were calculated from standard curves of commercially available: putrescine, cadaverine, spermidine, tryptamine, spermine, histamine, tyramine, serotonine, 1,3 diamine propane, agmatine and PEA.

Identification of amines using LC/MS

Identification of plant amines was done by comparison of retention times of its benzoyl derivatives with commercially available standards (putrescine, spermidine, cadaverine, tyramine and PEA) as was described above, and their mass spectra by using a HPLC–DAD–MS system (Shimadzu, Kyoto, Japan). The mass spectrometer with electrospray ionization (ESI) was set at positive mode with the following parameters: CDL temperature 230°C, CDL voltage (−40 V), probe voltage (4.0 kV), nebulizer gas (N2) flow of 4.5 L min^{-1}, defragmentation voltage (45 V) and detector gain (1.8 kV). Aliquots (10 µL) of benzoylated amines from buckwheat tissue were injected into a liquid chromatograph equipped with a column 250 × 2.0 mm Luna C18, 5 µm (Phenomenex, USA). Identification analyses were performed at 45°C with the flow rate of 0.2 mL min^{-1}. Solvent for gradient elution was composed with water (A) and acetonitrile (B) as follows: 42–42–80–42–42% B at gradient time, t_G = 0–25–30–35–45 min.

Spectrophotometric determination of total anthocyanins

Total anthocyanin content was analysed by a method described by Mancinelli (1984) with some modifications (Horbowicz et al. 2008, 2009). The buckwheat tissue was extracted with 1% HCl–MeOH for 24 h at room temperature, in darkness with occasional shaking. The extracts were carefully decanted and their absorbance was measured at 530 and 657 nm. The formula $A_{530} - 0.25A_{657}$ was used to compensate for the absorption of chlorophyll degradation products (Mancinelli 1984). Anthocyanin content was expressed as µg of cyanidin 3-glucoside in 1 g of fresh matter, using 29,600 as molecular extinction coefficient.

Results

In tissues of buckwheat seedlings treated exogenously with MJ the presence of 2-phenylethylamine (PEA), the product of Phe decarboxylation was found. The identification of the PEA and all other amines was carried out by comparing retention times of plant origin compounds with commercially available standards, and confirmed by their mass-spectral data. Examples of such mass spectra obtained for benzoylated PEA were shown on Fig. 1a, b. Mass spectrum A contains fragmentation pattern of benzoylated compound isolated from buckwheat tissue, and B contains fragmentation of benzoylated PEA standard. The molecular ion for the compound was found at *m*/*z* 226 (M + H). This value corresponds to protonated $C_{15}H_{15}ON$ ($M = 225$), supporting the hypothesis that it is benzoylated 2-phenylethylamine. Both spectra contain the same signals: molecular ion, and *m*/*z* = 105—a benzoyl group (C_6H_5CO), major fragment of breakdown the PEA derivative. Moreover, the retention time of the substance found in buckwheat tissue was equal to benzoylated PEA standard. An example of HPLC chromatogram of benzoylated amines present in cotyledons of buckwheat seedlings treated with MJ is shown in Fig. 1c.

PEA contents increased dramatically in buckwheat hypocotyls and cotyledons as an effect of MJ treatment (Fig. 2). Only traces of PEA were found in the tissue of control hypocotyls, and around 30 nmol g^{-1} of fresh weight in cotyledons. The level of PEA in cotyledons of control seedlings was ca. fivefold lower than the level of putrescine or spermidine. Treatment with low concentration of MJ (10^{-8} M) caused enormous (ca. 20-fold in cotyledons) increase of the level of PEA (Fig. 2), which thus became major free amine in buckwheat tissues. Enhancing concentration of MJ to 10^{-4} M caused further increase of PEA level, which reached ca. 3,000 and 1,000 nmols g^{-1} of fresh weight in cotyledons and hypocotyls, respectively.

The levels of all amines found in buckwheat seedlings (PEA, putrescine, spermidine and cadaverine) were much higher in cotyledons than in hypocotyls, with the exception of tryptamine (Fig. 2; Table 1). The treatment of seedlings with MJ clearly enhanced accumulation of putrescine in

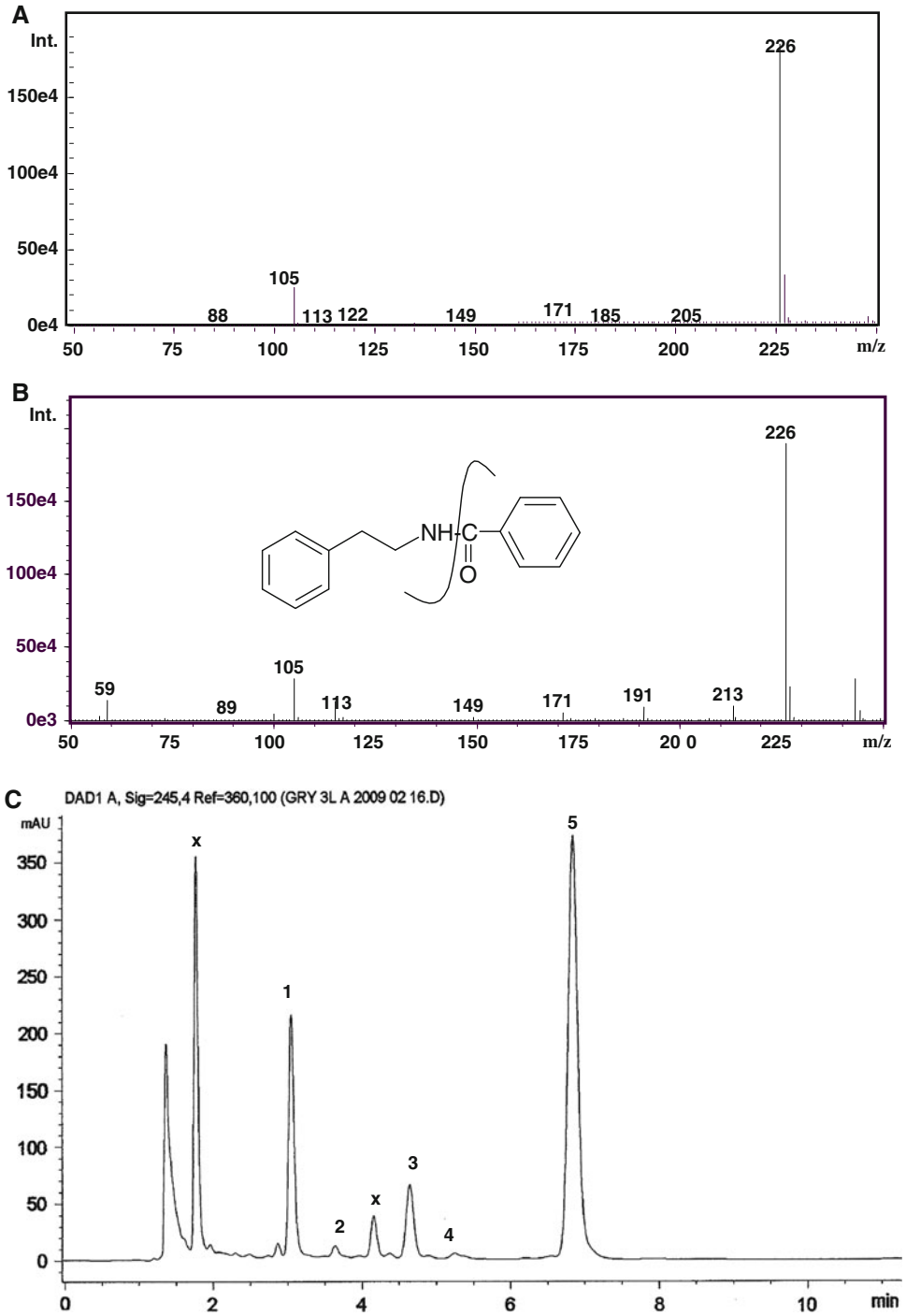

Fig. 1 **a** Positive-ion mass spectra of a benzoylated 2-phenylethylamine obtained from tissue of common buckwheat. **b** Positive-ion mass spectra of a benzoylated 2-phenylethylamine standard. Figure contains molecular structure of the analysed compound and major fragmentation pattern. **c** HPLC chromatogram of benzoylated derivatives of mono-, and polyamines isolated from seedlings of common buckwheat treated with methyl jasmonate (10^{-6} M): *1* putrescine, *2* cadaverine, *3* spermidine, *4* tryptamine, *5* 2-phenylethylamine, *x* unknown compounds

both analysed parts of buckwheat seedlings: hypocotyls and cotyledons (Table 1). Moreover, MJ stimulated the production of cadaverine in buckwheat cotyledons, but not in hypocotyls. In case of tryptamine there was noted decline its level in cotyledons only. However, the contents of both, tryptamine and cadaverine, were very low, and therefore any conclusions on base of such negligible amounts are uncertain (Table 1).

In hypocotyls treated simultaneously with MJ vapors and Phe solution enhanced production of anthocyanins was observed, in comparison with hypocotyls treated with MJ alone (Table 2). However, full reversion of MJ causing inhibition of anthocyanin accumulation was not found. Small concentration of Phe (5 and 10 mM, +MJ) caused even further decline of anthocyanins synthesis, than hypocotyls treated with MJ only. High concentration of

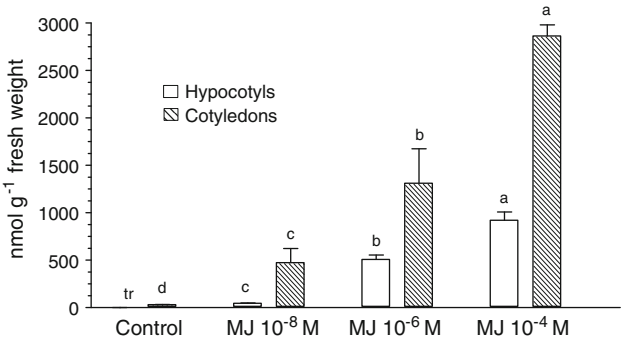

Fig. 2 Effect of methyl jasmonate (MJ) on 2-phenylethylamine level in cotyledons and hypocotyls of common buckwheat seedlings (means ± SD; *tr* traces). Mean results represent by *bars* marked by the various *letters* are significantly different at $\alpha = 0.05$ according to Newman–Keuls test

Table 1 Effect of methyl jasmonate (MJ) on content of polymines and tryptamine (nmols g^{-1} fresh weight; means ± SD) in hypocotyls and cotyledons of common buckwheat seedlings

	Putrescine		Spermidinie	
	Hypocotyls	Cotyledons	Hypocotyls	Cotyledons
Control	22.4 ± 2.8 b	160.1 ± 32.1 c	12.5 ± 0.7 a	146.4 ± 40.1
MJ 10^{-8} M	18.8 ± 0.5 b	322.4 ± 11.7 b	6.6 ± 1.2 b	176.1 ± 52.0
MJ 10^{-6} M	55.3 ± 3.8 a	432.8 ± 69.6 a	5.8 ± 0.5 b	164.6 ± 11.2
MJ 10^{-4} M	53.1 ± 7.5 a	452.7 ± 78.8 a	6.6 ± 2.8 b	136.2 ± 44.8
	Cadaverine		Tryptamine	
	Hypocotyls	Cotyledons	Hypocotyls	Cotyledons
Control	5.1 ± 1.4	14.2 ± 1.3 c	26.4 ± 2.7	18.6 ± 0.6 a
MJ 10^{-8} M	2.1 ± 0.7	15.6 ± 1.4 c	26.7 ± 1.2	10.5 ± 2.1 b
MJ 10^{-6} M	3.3 ± 0.5	30.9 ± 1.0 a	24.3 ± 1.3	6.9 ± 1.6 b
MJ 10^{-4} M	3.5 ± 0.7	22.1 ± 2.8 b	29.7 ± 3.0	8.6 ± 2.1 b

Means compared in columns followed by the various letters are significantly different at $\alpha = 0.05$ according to Newman–Keuls test

Table 2 Effect of methyl jasmonate (MJ) and L-phenylalanine (Phe) on content of anthocyanins (μg g^{-1} fresh weight; means ± SD)

Treatment	Hypocotyls	Cotyledons
Control	240.9 ± 15.6 a	366.6 ± 47.5 a
MJ 10^{-5} M	65.5 ± 4.9 d	276.9 ± 52.4 ab
MJ 10^{-5} M, 5 mM Phe	37.5 ± 1.1 e	200.2 ± 45.3 b
MJ 10^{-5} M, 10 mM Phe	49.4 ± 4.1 de	226.8 ± 45.5 b
MJ 10^{-5} M, 15 mM Phe	85.8 ± 4.2 c	280.8 ± 52.1ab
MJ 10^{-5} M, 25 mM Phe	113.4 ± 6.5 b	312.7 ± 47.8 ab

Means compared in columns followed by the various letters are significantly different at $\alpha = 0.05$ according to Newman–Keuls test

Table 3 Effect of 2-phenylethylamine (PEA) and polyamines on content of anthocyanins (μg g^{-1} fresh weight) in hypocotyls and cotyledons of common buckwheat seedlings (means ± SD)

Treatment	Hypocotyls	Cotyledons
2-Phenylethylamine treatment		
Control	240.9 ± 15.6 b	366.6 ± 47.5 c
PEA 10^{-5} M	306.7 ± 16.1 a	521.9 ± 49.5 ab
PEA 10^{-4} M	329.0 ± 12.7 a	600.3 ± 41.8 a
PEA 10^{-3} M	268.0 ± 33.5 ab	410.6 ± 32.2 bc
Polyamine treatment		
Control	255.3 ± 11.0 b	448.4 ± 58.3 a
Spermidine, 10^{-3} M	312.9 ± 15.2 a	355.7 ± 34.7 ab
Putrescine, 10^{-3} M	316.9 ± 12.9 a	327.7 ± 18.9 b

Means compared in columns followed by the various letters are significantly different at $\alpha = 0.05$ according to Newman–Keuls test

Phe (15 and 25 mM) partly reversed the phenomena of the MJ-caused decline of anthocyanins in hypocotyls.

The PEA in moderate concentration (10^{-4} M, 10^{-5} M) exhibited some stimulatory influence on anthocyanin accumulation in hypocotyls and cotyledons of buckwheat seedlings (Table 3), but the treatment with high concentration of PEA (10^{-3} M) did not affect the level of anthocyanins. Feeding experiments with putrescine and spermidine caused also slight stimulation of the synthesis of anthocyanins in hypocotyls, and its decrease in cotyledons of buckwheat seedlings (Table 3).

Discussion

Our earlier studies have shown that MJ inhibits synthesis and accumulation of anthocyanins in hypocotyls of etiolated seedlings of common buckwheat (*Fagopyrum esculentum* Moench) exposed to light, but had no effect on phenylalanine ammonia-lyase activity (Horbowicz et al. 2008). The results are contrary to many earlier published data (Fang et al. 1999; Franceschi and Grimes 1991; Saniewski et al. 1998, 2003). The phenomenon is difficult to explain. MJ inhibited accumulation of anthocyanins in buckwheat hypocotyls, but had no effect on phenylalanine and tyrosine ammonia-lyases activities, what suggests that it can act not in first, but in later steps of anthocyanin formation pathway (Horbowicz et al. 2008). Feeding buckwheat seedlings with intermediates of the pathway: *trans*-cinnamic acid, *p*-coumaric acid and naringenin, did not diminish the declining of anthocyanin level caused by MJ added simultaneously (Horbowicz et al. 2009). Moreover, according to our other studies MJ did not affect levels of quercetin, apigenin and luteolin glycosides in cotyledons and hypocotyls of buckwheat seedlings, but did affect the

stimulation of proanthocyanidins synthesis in hypocotyls (Horbowicz et al. 2010). The last fact can be a major reason of declining of anthocyanin accumulation in buckwheat hypocotyls treated with MJ.

Looking for another possible reason of anthocyanin decrease in hypocotyls of buckwheat seedlings treated with MJ, we decided to check if the hormone has an effect on products of aminoacids decarboxylation—amines. Amines extracted from the buckwheat tissues, after derivatization with benzoyl chloride, were analyzed using a previously described method (Flores and Galston 1982). As a result, putrescine, spermidine, cadaverine and tryptamine were found. Other amines, like spermine, serotonine, 1,3-diaminopropane, agmatine, histamine and tyramine were not present in detectable levels. However, the major amine which was accumulated in tissues of MJ-treated seedlings was identified as 2-phenylethylamine (PEA) (Fig. 1; Table 1).

High increase of PEA level, and use of large amounts of Phe as substrate, could have an impact on the synthesis of phenylpropanoids, including anthocyanins. Feeding the buckwheat seedlings with high concentration of L-phenylalanine (Phe) partly suppressed inhibitory effect of MJ on accumulation of anthocyanins in buckwheat hypocotyls (Table 2). However, low dose of Phe reduced the accumulation of the anthocyanins. It can be a result of synergistic with MJ enhancing of decarboxylation of Phe to PEA, but we have not studied the hypothesis. It seems like high concentration of Phe can be enough for production of both: PEA and *trans*-cinnamic acid, a basic substrate for synthesis of all flavonoids classes, including anthocyanins. It seems also that in buckwheat hypocotyls treated with MJ decarboxylation of Phe to PEA is predominant, in comparison with *trans*-cinnamic acid synthesis.

Although PEA is quite rare in plant kingdom, there are some reports on its presence in algae (Rolle et al. 1977; Percot et al. 2009) and plants (Smith 1977; Shabana et al. 2006). PEA has been mainly studied as a metabolite of neurotransmitters in animals and in the human brain (Blau 1978; Saavedra 1978). In plants PEA can be transformed into 2-phenylacetaldehyde, and further converted to 2-phenylethanol (Tieman et al. 2006). According to recently published data PEA can be substrate to synthesis of 2-phenylacetaldehyde—compound with the high contribution to the common buckwheat aroma (Janeš et al. 2009). It means that in buckwheat tissues there exists a metabolic route for conversion of Phe, not only into phenylpropanoids, but also into PEA and to further metabolites.

PAs frequently accumulate in plants in response to abiotic and biotic stresses (Walters 2003; Alcázar et al. 2006). Exogenously supplied PAs protected plants from abiotic stress, and transgenic plants with overexpressed PAs genes exhibited stress tolerance (Walters 2003). On the other hand, loss-of-function mutant of PAs biosynthetic genes resulted in the decrease of stress tolerance (Kusano et al. 2008). The results presented by us indicate that concentration of Phe in tissues of buckwheat cotyledons and hypocotyls can be also stress-induced process.

The level of PAs is high in young leaves and declines with age and can be an indicator of senescence (Kaur-Sawhney et al. 1982). As the MJ is a plant hormone active in the senescence processes, enhanced accumulation of putrescine and PEA can be a defense response against MJ and its stimulation of senescence and ageing processes. This hypothesis needs further studies if level of the PEA can be indicator of senescence and/or ageing processes in buckwheat tissue.

Moreover, we decided to check whether the PEA and/or major PAs are directly involved in the process of declining of anthocyanins and therefore we carried out experiments with feeding the buckwheat seedlings with PEA, putrescine and/or spermidine. Obtained results have shown that PEA had some stimulatory effect for accumulation of anthocyanins in buckwheat hypocotyls and cotyledons. Similar effect was obtained in hypocotyls when spermidine and putrescine were fed to buckwheat seedlings (Table 3).

In conclusion, our results indicate that exogenous MJ has a great stimulatory impact on the synthesis of PEA in buckwheat hypocotyls and cotyledons. MJ stimulated the putrescine production as well. Enormous production of PEA under influence of MJ was accompanied by a decline of anthocyanins in buckwheat hypocotyls (Horbowicz et al. 2008). The possible reason of decline in the anthocyanin accumulation is probably enhanced production of condensed tannins (proanthocyanidins) (Horbowicz et al. 2010). However, simultaneous treatment of buckwheat seedlings with Phe and MJ indicates that production of PEA can be another reason for the suppression of anthocyanin synthesis. Confirmation of the hypothesis requires further detailed, enzymatic and genetic studies.

High concentration of PEA in buckwheat tissues is probably the plant response to stimulating the senescing and ageing processes caused by exogenous MJ. To our knowledge the accumulation of 2-phenylethylamine effect by methyl jasmonate, as found in our studies, has been described for the first time.

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