ORIGINAL ARTICLE

Effect of jasmonic acid on cold-storage of *Taraxacum pieninicum* encapsulated shoot tips

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Abstract

Jasmonic acid is involved in plants response to various abiotic and biotic stresses. The aim of this study was to examine physiological response of *Taraxacum pieninicum* to JA-treatments during shoots micropropagation and during cold storage at 4 °C under reduced light or in the darkness. Obtained results indicated that JA during preculture reduced significantly growth of shoots without impact on proliferation rate. During cold storage JA (24–72 μM) limited effect of cold stress what was manifested by reduced accumulation of proline and TBARS. Growth inhibition of the stored tissue was more effective when JA was inside synthetic seeds structure than after preculture on medium supplemented with JA. Shoot proliferation and rooting were effective during regrowth after cold storage combined with JA exposure. Only elongation of roots was inhibited after storage in this conditions. However, length of roots did not affect acclimatization of plantlets to ex vitro conditions.

Keywords Jasmonic acid · Proline · Shoot proliferation · Slow-growth storage · *Taraxacum pieninicum* · TBARS

Abbreviations

BA	Benzylaminopurine
JA	Jasmonic acid
MDA	Malondialdehyde
MeJA	Methyl jasmonate
NAA	Naphthalene acetic acid
TBARS	Thiobarbituric acid reactive substances

Introduction

Cold during storage has a significant impact on a tissue condition. Abiotic stress causes significant reactive oxygen species accumulation, which cause oxidative damage and might result in cell death (You and Chan 2015). Low temperature affects all aspects of cellular function in plants (Yadav 2010; Theocharis et al. 2012). The major adverse effect of cold

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stress relates to the structure and integrity of the plasma membrane. Lipids containing polyunsaturated fatty acids are well-known targets to the free radicals attacks. Lipid peroxidation leads to the production of many primary products (mainly lipid hydroperoxides LOOH), which in further decomposition can form several low-molecular-weight products called thiobarbituric acid reactive substances (TBARS). The most common considered TBARS is malondialdehyde (MDA) which is a mutagen and is widely used as a biomarker for lipid peroxidation of omega-3 and omega-6 fatty acids (Ayala et al. 2014).

Plants possess cellular mechanisms that limit oxidative damages and increase cold tolerance. The most common strategy is based on accumulation of compatible osmolytes and osmoprotective compounds such as proline (Kishor et al. 2005). Proline has a diverse roles in plants e.g., is involved in stabilizing sub-cellular structures (membranes and proteins) and scavenging free radicals (Hayat et al. 2012). Thus, proline accumulation can effectively overcome lipid peroxidation.

Taraxacum pieninicum belongs to the *Asteraceae* family and is listed as critically endangered species. In view of its natural occurrence (Pieniny Mts., Poland), this species exhibits a potentially good resistance to cold in a field conditions. Conservation of *Taraxacum* species is very limited because seeds dramatically lose their vitality after 2 years, thus in vitro culture including storage in a slow growth

conditions seems to be the most appropriate method of protecting this genus. Synthetic seed technology is useful for plant species which are not able to produce seeds and plants that produce seeds with poor viability (Rihan et al. 2017). Synthetic seeds (synseeds) are defined as artificially encapsulated explants such as shoot tips or nods which possess the ability to convert into a whole plant after storage (Ara et al. 1999). Many gel agents such as agar, carrageenan, guar gum and sodium pectrate were used for encapsulation, although sodium alginate was discovered to be the most suitable and practicable for synseeds production. There are potential advantages of synthetic seed technology such as ease of production and transport. In addition, the use of this technique economizes upon time, space and medium requested by traditional tissue culture (Rihan et al. 2017). In our previous paper, we described efficient storage of *T. pieninicum* shoot tips and synthetic seeds in in vitro culture (Kamińska et al. 2016, 2018) and the protective effect of alginate coat during cold-storage has been documented. However, shoots overgrown the synseeds structure during storage, what limits the possible time of its storage and protective properties of the alginate coat.

During recent years numerous studies indicated that jasmonic acid (JA) is involved in biotic and abiotic stress response (Koo 2017), developmental processes of plant such as lateral root formation and positioning (Raya-González et al. 2012) but also in age-related leaf senescence (Morquecho-Contreras et al. 2010; Schommer et al. 2008). The aim of our study was to (1) investigate physiological response of *T. pieninicum* to jasmonic acid during shoot proliferation in the optimal growth conditions and during cold storage at 4 °C under reduced light or in the darkness. and (2) to assess whether jasmonic acid treatment enhance cold tolerance during slow-growth culture.

Materials and methods

Plant material and culture conditions

Seeds of *T. pieninicum* were obtained from the collection of the Polish Academy of Sciences Botanical Garden—Center for Biological Diversity Conservation in Powsin. Initial explants (shoot tips) were isolated from clusters obtained according to Trejgell et al. (2013) and subcultured every 4 weeks on basal MS medium supplemented with 3% sucrose and 1.1 µM BA and 0.14 µM NAA. Prior to the addition of 0.8% agar (w/v), the pH of the medium was adjusted to 5.8 before autoclaving. Cultures before storage were kept in continuous white fluorescent light (80 µmol m^{-2} s^{-1}) at 26 ± 1 °C (optimal growth conditions described by Trejgell et al. 2013).

Jasmonic acid treatment

Two different JA-treatments were examined: (1) 4-weeks preculture in the optimal growth condition on MS medium supplemented with 3% sucrose, 0.8% agar and 1.1 µM BA and 0.14 µM NAA and JA (further indication in the paper—preculture) or (2) jasmonic acid was mixed with the sodium alginate solution (inside) so that it was presented in the synseeds structure during storage. In each treatment four concentrations (24 µM, 48 µM, 72 µM, 96 µM) of JA were tested. After preculture proliferation rate (number of shoots per explant) was additionally evaluated.

Synthetic seeds production

For encapsulation shoot tips of *T. pieninicum* were obtained from 4-week in vitro culture with or without JA. Isolated shoot tips were suspended in 3% Na-alginate prepared in liquid MS medium. The shoot tips covered with alginate were dropped individually into 100 mM CaCl$_2$·2H$_2$O and kept for 25 min for polymerization. Thereafter, beads were retrieved from the calcium chloride solution using sterile sieve and washed with sterile distilled water.

Cold storage conditions

The synthetic seeds were transferred into Magenta® box containing 50 ml MS medium supplemented with 3% sucrose, 0.8% agar, without plant growth regulators (except JA in inside treatment) and stored under reduced continuous white fluorescent light (40 µmol m^{-2} s^{-1}) or in the darkness at 4 ± 1 °C for 3, 6 and 9 months. Synthetic seeds non-treated with JA were used as control.

Post-storage regrowth

After storage the alginate coat was removed and shoot tips from converted plants were transferred on fresh MS medium with full-strength nutrients supplemented with 3% sucrose, 1.11 µM BA, 0.14 µM NAA and 0.8% agar in the optimal growth conditions and subcultured twice. The proliferation rate was evaluated after each 4-week subculture.

For acclimatization the obtained shoots were rooted on MS medium without plant hormones. Ability of shoots to form roots was investigated on the base of roots number per shoot and root length. Formed roots were gently washed with sterile water to remove residual MS medium. Plantlets were then transplanted to plastic pots containing autoclaved mixture of vermiculite and sand (1:1 v/v), covered with a transparent boxes to maintain humidity (60–70%) and kept in a growth chamber at 23 ± 1 °C with white fluorescent

illumination (80 μmol m^{-2} s^{-1}). Plants were subsequently transferred to the pots containing sterile soil and then were transferred to the field conditions. Each step of the acclimatization was carried out after 4 weeks.

Biochemical analyses

Free proline determination was evaluated directly after cold-storage and after 1st subculture in the optimal conditions as described by Bates et al. (1973). Each sample contained about 50 mg tissue. Membrane lipid peroxidation was measured by the amount of TBARS. TBARS concentration was estimated directly after cold-treatment, following the protocol described by Song et al. (2011).

Data collection and statistical analysis

Proliferation rate after preculture with JA was evaluated for 8 explants. Stored microshoots were evaluated at 3 month intervals. In each variant of storage 16 encapsulated shoot tips were used. Proliferation rate in 1st subculture was obtained for shoots that survived the cold treatment for 3, 6 and 9 months. Proliferation rate in 2nd subculture and rooting rate were evaluated for 8 explants. Three replicates were performed for each analysis. Data were expressed as mean ± standard error (SE). Normality of variances was verified using the Shapiro–Wilk test. To examine significant differences among the treatments Kruskal–Wallis test at $p \leq 0.05$ was then performed, because of a non-normal data distribution and unequal sample sizes in post-regrowth part. Biochemical analyses were carried out in three replicates of the independent plants tissues and statistically significant differences were assess using Tukey's multiple range test at $p < 0.05$.

Results

Preculture with JA in optimal conditions

Before cold storage explants in the first JA-treatment were propagated for 4 weeks on MS medium supplemented with BA, NAA and JA. Obtained results indicated that shoots cultured on medium with JA added in the lowest concentration (24 μM) had the highest proliferation rate (26.7 ± 2.5 axillary shoots per explant) but the difference to the control plants (18.9 ± 2.2) was not statistically significant (Fig. 1a, b). The lowest proliferation rate (11.5 ± 1.2) was noted for the medium supplemented with the highest used concentration of JA (96 μM) and the difference in comparison to other concentration was significant. Increasing JA concentration led to limiting growth of the shoots. In addition, shoots on medium with JA in the highest used concentration were fragile with easily falling
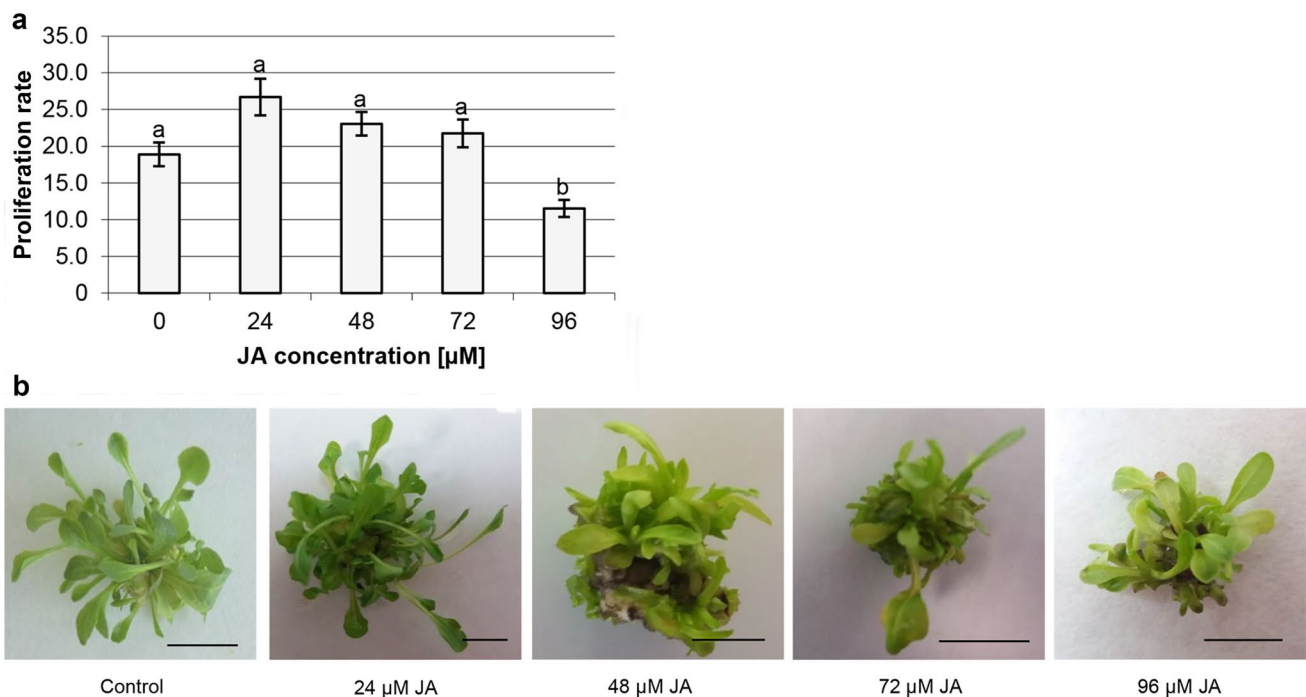

Fig. 1 The effect of JA on shoot proliferation of *Taraxacum pieninicum* in the optimal growth conditions: proliferation rate (**a**) and phenotype of shoots clusters (**b**) on MS medium supplemented with 1.11 μM BA and 0.14 μM NAA and different concentration of JA after 4 weeks of the culture. Bar = 1 cm. Means with different letters are significantly different followed by Kruskal–Wallis test at $p \leq 0.05$

leaves. Furthermore, on the medium containing JA alone multiplication was not observed (data not shown).

Regrowth of stored plants under optimal conditions

Synthetic seeds in both JA-treatments showed reduced growth in comparison to the control plants during cold-storage. JA decreased leaf blade size in plants stored under light conditions (Fig. 2a). In turn, in the darkness exposure to JA in both treatments resulted in inhibition of leaf elongation but blade size slightly increased (Fig. 2b).

During regrowth, comparing to the control plants JA did not affect significantly shoots ability to proliferate in the 1st subculture in most treatments after 9 months of storage (Fig. 3a). Only for the explants with JA 24 μM inside synseed structure stored in darkness statistically significantly higher proliferation rate (20.9 ± 1.4 shoots per explant) was noted than for the control plants (15.1 ± 1.8 shoots per explant). Comparing treatments, it was noted that 24 μM and 96 μM JA inside synseed structure resulted in a significantly lower ability of shoots to proliferate after storage under light conditions than preculture with the same JA concentrations. Statistically significant differences between light conditions were observed for the control, for preculture with 24 μM JA and for the highest JA concentration in both treatments, regardless of the storage duration (Fig. 3a, Supplement 1).

In the 2nd subculture plants from inside JA-treatment and plants precultured with 24 μM JA showed reduced ability to proliferate (Fig. 3b). The inhibitory effect of JA was not recorded for shorter storage period (3 and 6 months) and even stimulation of the shoot proliferation was observed in the plants precultured with 24 μM JA (Supplement 2). Negative effect caused by light persisted also in the 2nd subculture.

JA in both treatments did not affect significantly rooting ability of shoots and number of roots per shoots after post-storage regrowth on MS medium without plant regulators, regardless of the storage time (Fig. 4a, b, Supplement 3, 4). However, after 9 months of storage inhibition of root elongation was observed for all JA treatments, except of 24 μM JA inside synseeds in both light conditions (Fig. 4c). After 3 months of storage, there was no inhibition of root growth (Supplement 5a), while after 6 months shorter roots were reported in the plants from JA-preculture treatment and in the variant with the highest used concentration of JA inside synseeds (Supplement 5b).

Obtained plantlets regardless of the JA-treatment, light conditions and duration of storage were successfully acclimatized and did not show any phenotypic changes to non-stored microcuttings (Fig. 5).

Biochemical analyses

In the optimal growth conditions, before cold-treatment, proline was accumulated on low level (1.3 ± 0.1 mg/g fresh weight) in *T. pieninicum* shoots (Fig. 6). JA-preculture did not affect proline accumulation, except for the highest JA concentration. Shoots precultured on MS medium supplemented with 96 μM JA contained 2.2 ± 0.1 mg proline/g FW. Cold storage generally stimulated biosynthesis of proline in all used variants (Fig. 7a). JA-preculture reduced accumulation of proline in shoots stored under light conditions, although significant difference to the control plants was reported only after preculture on medium MS with 24 μM JA. While the highest used concentration (96 μM) did not affect proline content in shoots in comparison to the control plants in both light conditions. Slightly more proline was accumulated during storage under light conditions in each treatment. However, statistically significant difference between light conditions was observed for the control and for the plants precultured with 96 μM. Similar data were recorded after 3 and 6 months storage (Supplement 6).

After 1st passage in the optimal growth conditions amount of accumulated proline decreased markedly. The highest proline level was noted in the shoots of plants stored under light conditions after preculture on 96 μM JA (Fig. 7b). Similar results were noted for material stored for 3 and 6 months (Supplement 7).

Prolonged storage time enhanced production of TBARS in the control plants under light conditions (Fig. 8). In the plants precultured on medium supplemented with JA it was reported that the highest used concentration increased TBARS content under light conditions, regardless of the storage duration (Supplement 8). In inside JA-treatment, the TBARS content decreased with increasing concentration of JA under light conditions. Furthermore, it was reported that JA decreased TBARS content in comparison to the control after storage in the dark lasting more than 3 months, regardless of the treatment and JA concentration.

Discussion

JA-like compounds occur widely in the plants, with highest activities in growing tissue such as stem apex, young leaves, immature fruits, and root tips (Sembdner and Parthier 1993).

Many studies showed that the effect of JA on growth and proliferation of plants in in vitro culture strictly depends of its concentration in the medium. In nanomolar range JA increased the explant size and the number of leaves in nodal explants of cabbage (Toro et al. 2003). JA added in concentrations from 0.01 to 1 μM increased the number and length of nodes of grapevine and potato, but the opposite effect was observed above this range (Ravnikar et al. 1990).
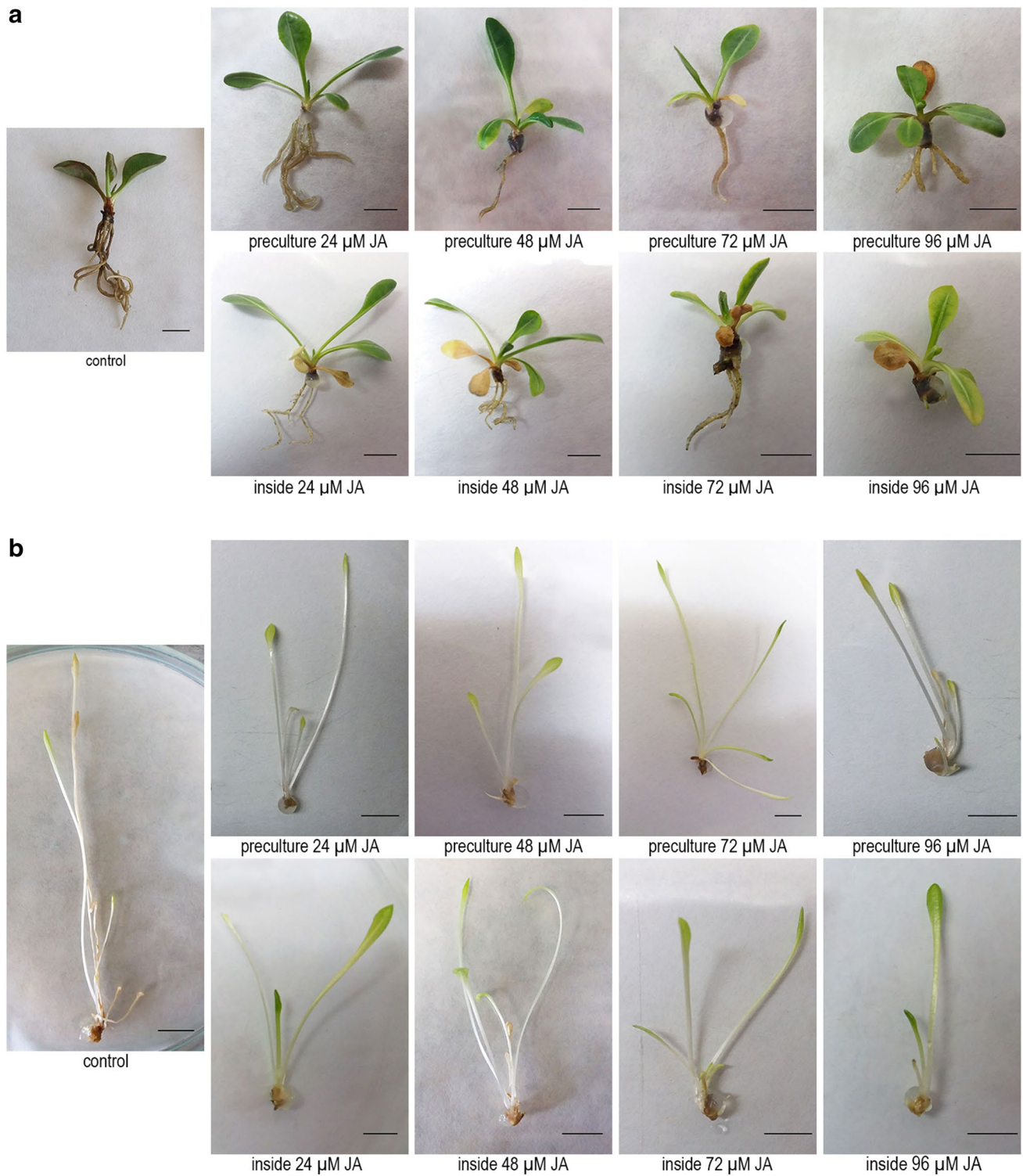
Fig. 2 Shoots converted from synthetic seeds during 9 months storage at 4 °C under light conditions (**a**) and in the darkness (**b**) after different treatment with JA. Bar = 1 cm

Furthermore, in lower concentration in the case of potato stem node culture stimulatory effect on the shoot length was observed. Addition of JA at higher concentration than 10 µM resulted in stunted plantlets without impact on the number of nodes (Ravnikar et al. 1992). Treatment with JA in concentration also up to 10 µM led to formation of plantlets
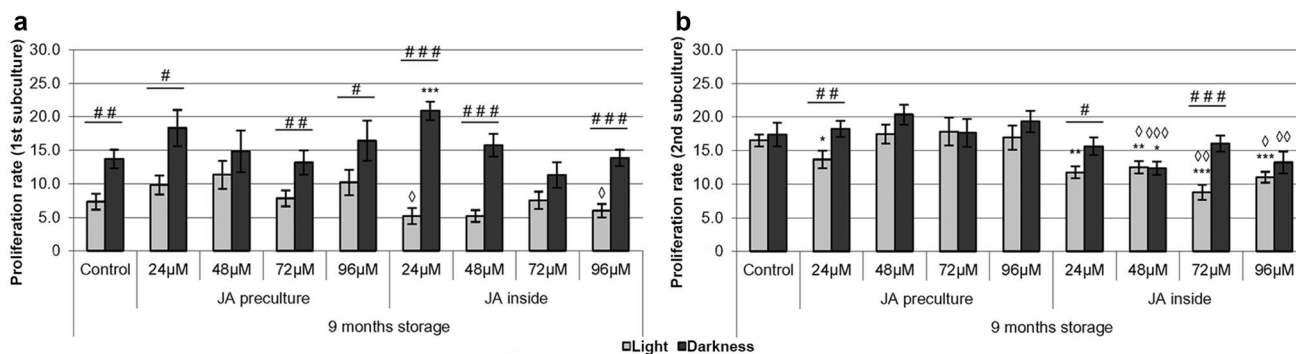
Fig. 3 The effect of light conditions and JA-treatment on *Taraxacum pieninicum* proliferation rate of shoots during regrowth on MS medium with 1.11 µM BA and 0.14 µM NAA in the 1st (**a**) and 2nd (**b**) subculture after 9 months storage at 4 °C. Statistically significant differences assessed using Kruskal–Wallis test at $p \leq 0.05$: to the control plants in the same light conditions are denoted *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$; between light conditions are denoted #$p < 0.05$, ##$p < 0.01$, ###$p < 0.001$; between JA treatment in the same light conditions are denoted ◊$p < 0.05$, ◊◊$p < 0.01$, ◊◊◊$p < 0.001$

with larger leaf surface and thicker stems in potato (Martín-Closas et al. 2000), pear and cherry cultures (Ružić et al. 2013) and to enhancement of the garlic shoots and bulbs development (Ravnikar et al. 1993). In *Pistacia vera* optimal concentration of MeJA for shoot multiplication was 1 µM. Higher concentration (10 µM) led to the leaf senescence and decrease in shoots ability to proliferate (Dolcet-Sanjuan and Claveria 1995). Our results indicated that increasing concentration of JA in the proliferation medium significantly limited the size of the plants what is highly desirable during long storage of a plant material in slow growth conditions. It was also noted that ability of the explants to proliferate decreased in the highest used concentration (96 µM). Similar results were obtained for JA-treated rice seedlings which growth was inhibited with increasing concentration up to 50 µM of JA in the MS medium (Cho et al. 2007). The effect of JA in represing shoot and root growth may be related to both cell division and elongation program, which may result from inhibition of the synthesis of the cell wall polysaccharides and reduction in mitotic activity in the meristem (Miyamoto et al. 1997; Raya-González et al. 2012).

On the basis of many observations, it was concluded that JA and its derivatives (MeJA and dihydro-MeJA) stimulate the induced systemic resistance (ISR), which improve production of stress and disease tolerance (Ghasemi Pirbalouti et al. 2014). Jasmonates are key signaling compounds in plant responses to biotic and abiotic stresses as well as in development. JA is involved in response to desiccation, ozone, UV, osmotic, cold and light stresses (Wasternack 2014). Under cold stress amount of endogenous JA increase in different plant species including rice (Du et al. 2013), wheat (Kosová et al. 2012) and *Arabidopsis thaliana* (Hu et al. 2013). Application of MeJA improves cold storage of subtropical fruits, e.g. mango (González-Aguilar et al. 2000) and lemon (Siboza et al. 2014) by reducing chilling injury.

Our study shown that JA application before cold-storage (preculture) or inside synthetic seeds reduce significantly growth of plantlets during storage. In addition, we reported stimulatory effect of JA-treatments (both type) on proliferation rate during regrowth, which indicated better condition of the stored material comparing to the control plants. Similar as in previously studies (Kamińska et al. 2016, 2018) higher proliferation rate of shoots was observed after storage in the darkness than under light conditions.

Effect of JA and its derivatives on rooting of plant is better documented. The ability to form roots is controlled by multiple endogenous and environmental factors, among which auxins plays the most important role (Gutierrez et al. 2012). It is well documented that auxin biosynthesis can be induced by jasmonate and vice versa. Furthermore, jasmonates increase local auxin accumulation in the basal meristem, essential for lateral root formation (Sun et al. 2009). Low concentration of JA and MeJA inhibited primary root growth and promoted lateral root formation in *Arabidopsis* (Wang et al. 2002; Woodward and Bartel 2005; Sun et al. 2009; Raya-González et al. 2012) and decreased adventitious rooting in *Arabidopsis* hypocotyls (Gutierrez et al. 2012). Our results indicated that JA exposure during cold-storage did not affect shoots ability to form roots and number of roots per shoot during regrowth. However, JA indirectly decreased adventitious root length after 9 months storage regardless of the JA-treatment (preculture or inside synseeds). Similar but directly effect was observed in *Pistacia vera* rooted on medium supplemented with MeJA (Dolcet-Sanjuan and Claveria 1995).

Enhanced accumulation of proline in plants tissue under different abiotic stress, including cold, is well documented. Proline increased in *Triticum aestivum* after 1 week of cold acclimation (3 °C) (Kamata and Uemura 2004) and in *Cucurbita pepo* after 2 weeks at 4 °C in (Carvajal et al.

Fig. 4 The effect of light conditions and JA-treatment on *Taraxacum pieninicum* rooting ability of shoots on MS medium after 9 months storage at 4 °C assessed by % of rooted shoots (**a**), number of roots per rooted shoots (**b**) and length of roots (**c**). Statistically significant differences assessed using Kruskal–Wallis test at p ≤ 0.05: to the control plants in the same light conditions are denoted *p < 0.05, **p < 0.01, ***p < 0.001; between light conditions are denoted #p < 0.05, ##p < 0.01, ###p < 0.001; between JA treatment in the same light conditions are denoted ◊p < 0.05, ◊◊p < 0.01, ◊◊◊p < 0.001
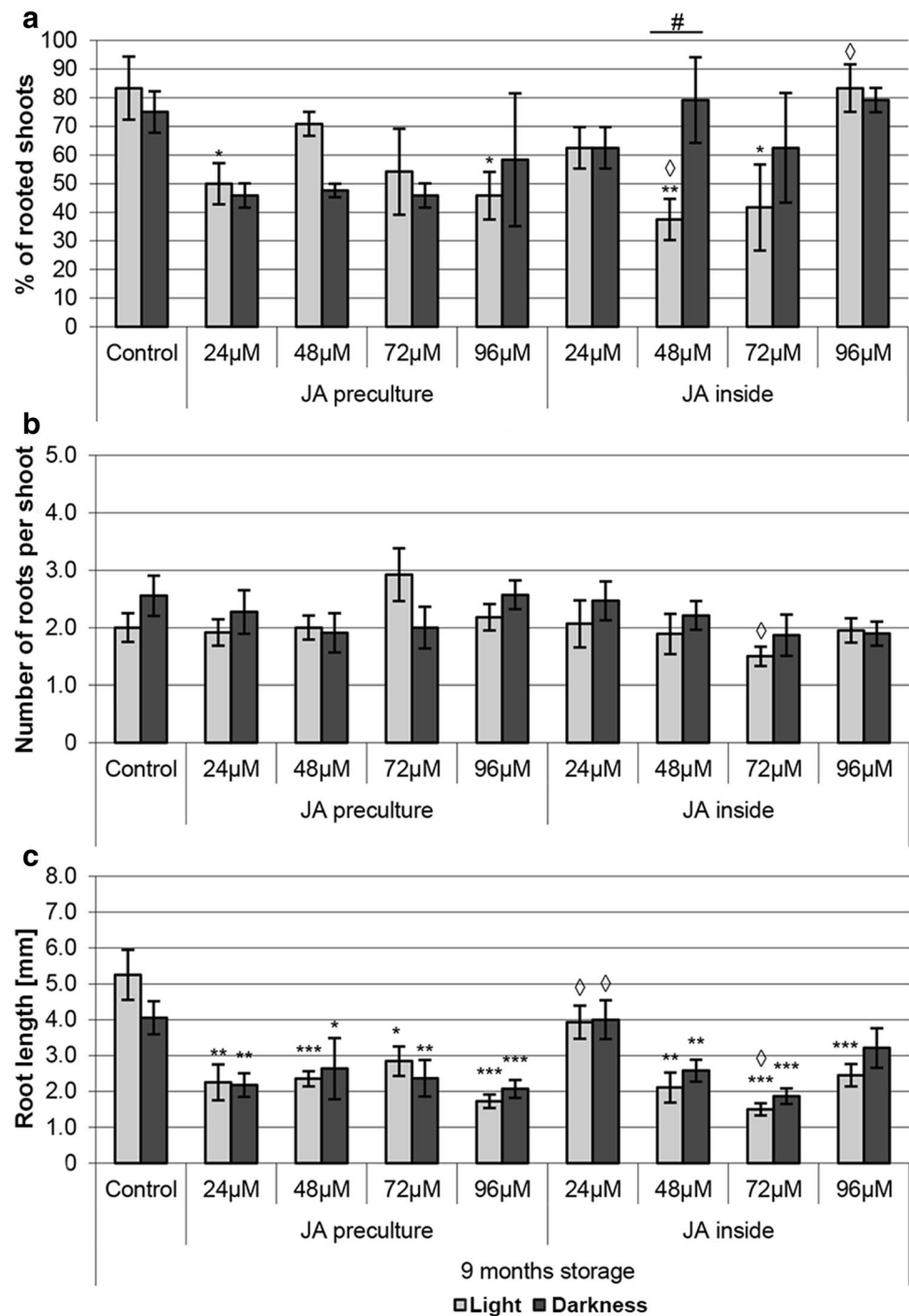
2015). Although in *A. thaliana* and *Vitis vinifera* proline level increased after only 4 h at 4 °C (Kaplan et al. 2007; Rooy et al. 2017). During first few weeks of storage of *Prunus persica* mesocarp at 0 °C and *Mangifera indica* at 10 °C proline content increased and decreased slightly afterwards (Shan et al. 2016; Li et al. 2014). In this study cold stress increased amount of proline almost 20-folds after 3 months and did not significantly change after longer storage. Furthermore, higher proline content was

reported in the plants stored under light conditions than in the darkness.

The effect of JA on proline content depends on its concentration and plant species. In *Hordeum spontaneum* no significant differences were observed after exposure on 5 and 15 μM JA, but in *H. vulgare* application of 15 μM JA decreased proline content (Bandurska et al. 2003). However, Maslenkova et al. (1992) in studies on *H. vulgare* seedlings indicated increased proline content with

Fig. 5 Plantlets obtained after cold-storage acclimatized in mixture of vermiculite and sand after 9 months storage at 4 °C and regrowth in the optimal growth conditions. Control without cold-storage
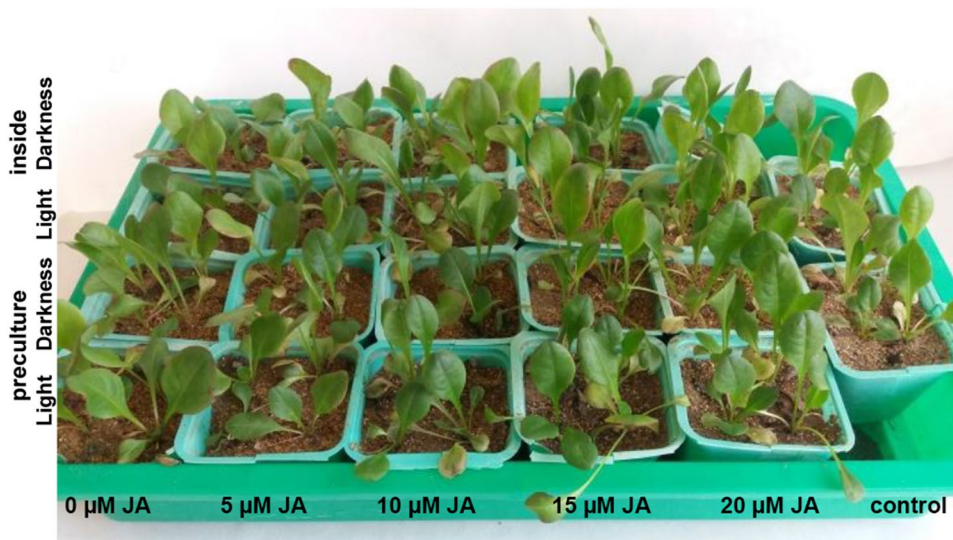

Fig. 6 Proline content in shoots after 4-week preculture on medium MS supplemented with 1.11 µM BA and 0.14 µM NAA and different concentration of JA. Means with different letters are significantly different followed by Tukey test at $p \leq 0.05$
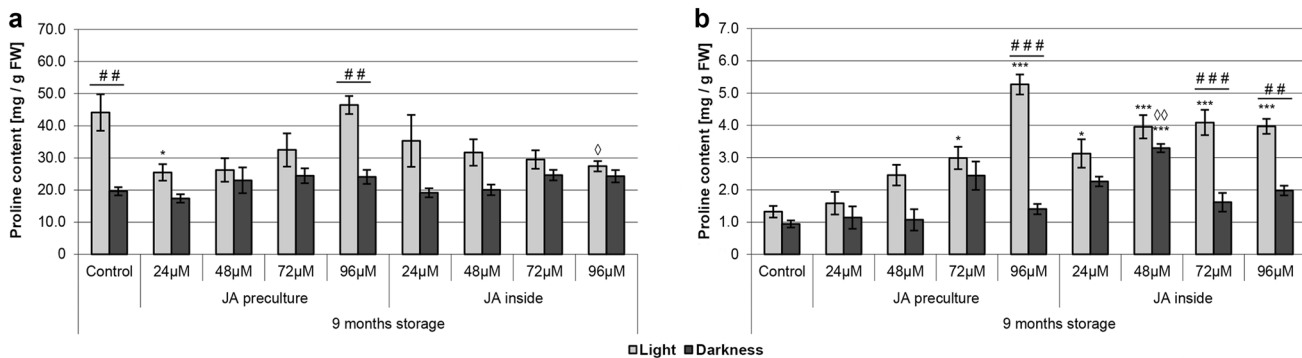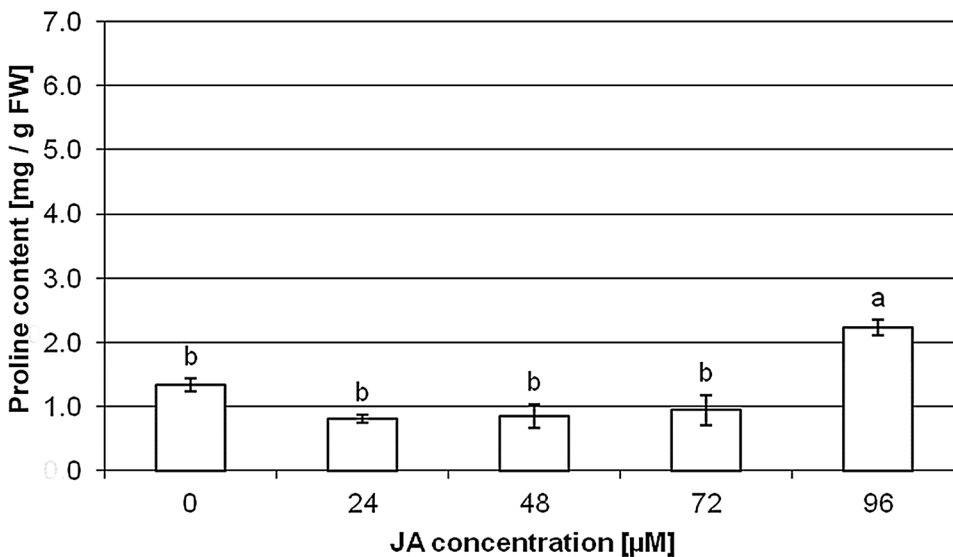

Fig. 7 The effect of light conditions and JA-treatment on accumulation of proline in *Taraxacum pieninicum* shoots directly after 9 months storage at 4 °C (**a**) and after 1st subculture on MS medium with 1.11 µM BA and 0.14 µM NAA in the optimal growth conditions (**b**). Statistically significant differences assessed using Tukey test at $p \leq 0.05$: to the control plants in the same light conditions are denoted *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$; between light conditions are denoted #$p < 0.05$, ##$p < 0.01$, ###$p < 0.001$; between JA treatment in the same light conditions are denoted ◊$p < 0.05$, ◊◊$p < 0.01$, ◊◊◊$p < 0.001$

Fig. 8 The effect of light conditions and JA-treatment on accumulation of TBARS in *Taraxacum pieninicum* shoots after 9 months storage at 4 °C. Statistically significant differences assessed using Tukey test at $p \leq 0.05$: to the control plants in the same light conditions are denoted $*p < 0.05$, $**p < 0.01$, $***p < 0.001$; between light conditions are denoted $^\#p < 0.05$, $^{\#\#}p < 0.01$, $^{\#\#\#}p < 0.001$; between JA treatment in the same light conditions are denoted $^\Diamond p < 0.05$, $^{\Diamond\Diamond}p < 0.01$, $^{\Diamond\Diamond\Diamond}p < 0.001$
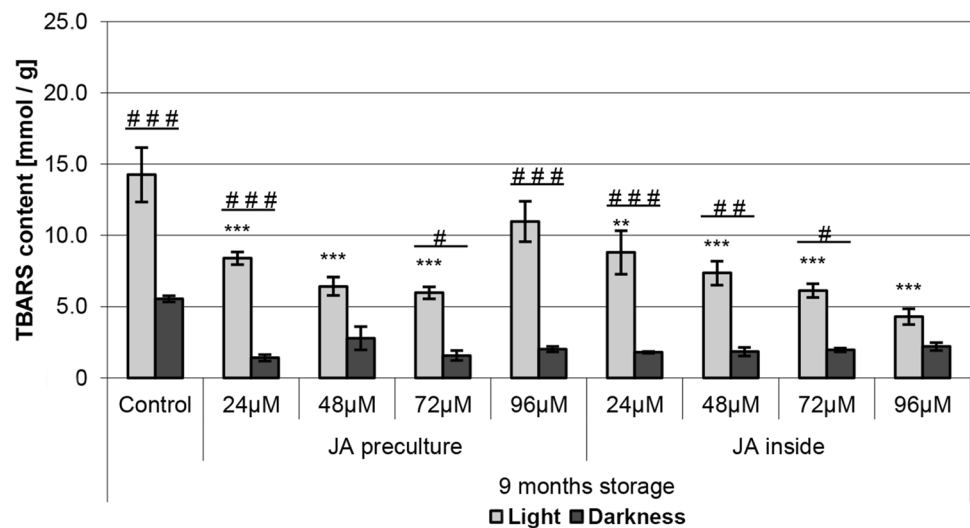
increasing JA concentration (2.5–250 μM). In our study JA did not affect significantly proline accumulation in the stored explants compared to non-treated plants, except for preculture on 96 μM JA. No increase of proline content was also observed in rice leaves exposed to MeJA in the darkness and in light conditions (Chen et al. 1994).

Some studies indicate that lipid peroxidation in cell membranes, expressed as MDA content, can be activated by the action of lipoxygenase, which is stimulated by jasmonates (Piotrowska et al. 2010). In the present study TBARS content in the plant tissue, as indices of damage, increased more noticeably during storage under light conditions than in the darkness. Furthermore, prolonging storage time resulted in increase of TBARS content under light conditions, but decreased in the darkness. Preculture before storage on medium supplemented with 24–72 μM JA decreased production of TBARS under light conditions. In higher concentration (96 μM) amelioration of a cold stress was not observed what correlates with results obtained during post-storage shoots proliferation and proline accumulation. These results are in agreement with Piotrowska et al. (2010), where JA in low concentration (0.01–0.1 μM) directly stimulated increase in fresh weight and decrease in TBARS production in aquatic plant *Wolffia arrhiza*, but above this concentration (10–100 μM) JA reduced plants growth and stimulated formation of lipid peroxides. In turn, JA in higher concentration effectively ameliorated drought stress in *Brassica* seedlings (2000 μM JA) and salt stress in wheat (500 μM JA) through a significant reduction in MDA content (Alam et al. 2014; Qiu et al. 2014). Furthermore, in our study, when JA was inside synseed structure, TBARS content decreased with increasing JA concentration under light conditions.

Conclusions

In conclusion, the results indicated that exogenous application of JA slightly induced cold tolerance by decrease in TBARS level, but did not induced proline accumulation during *T. pieninicum* storage in the slow-growth conditions. Moreover, JA inhibited overgrowing the synseeds structure during storage what may extend the protective effect of the alginate coat and thus extend time of synseeds storage. Inhibition of the tissue growth was more effective when JA was inside synthetic seeds structure than after preculture on medium supplemented with JA. Furthermore, limited growth during storage did not affect quality of the stored material in post-storage regrowth.

Compliance with ethical standards

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