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REVIEW

Role and activity of jasmonates in plants under in vitro conditions

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Abstract

Jasmonates (JAs), such as jasmonic acid and its methyl ester, are lipid-derived compounds with signal functions in plant growth and development, as well as in responses to stress. JAs are widely distributed in plants as natural plant growth regulators. JAs do not work independently but work as a part of a complex signaling network with other phytohormones. They are deployed to induce response during wounding and are often used for elicitation and stimulation of secondary metabolites production in different in vitro culture systems. Application of JAs seems to be promising during different steps of the micropropagation system for different species. JAs stimulate proliferation rate of shoots, roots, callus and induce microtubers and bulblets formation. However, negative effects of JAs on the condition of plant tissues are also reported, e.g. leaf senescence, reduced growth and inhibited somatic embryogenesis. This review summarizes the current knowledge of the application and properties of jasmonates under in vitro conditions in terms of cell division, explant growth, proliferation ability, storage organ formation and stress response.

Key message

The review summarized in detail the results achieved for plants cultivated in vitro in the presence of jasmonates and their possible mechanisms of action.

Keywords Cell proliferation · Micropropagation · Somatic embryogenesis · Storage organ formation · Abiotic stress

Introduction

Jasmonates (JAs) are widely distributed in plant tissues with high activity and growth rate, such as the stem tips, root tips, young leaves, flowers and unripe fruits. Endogenous JAs levels increase in response to the external stimuli, including mechanical damage, pathogen attack and osmotic stress (Sembdner and Parthier 1993; Creelman and Mullet 1995).

Jasmonic acid (JA) and its methyl ester (methyl jasmonates, MeJA) are linolenic acid (LA)-derived cyclopentanone-based compounds that belong to oxylipins (Creelman and Mullet 1995). It is believed that JA and MeJA represent a separate group of plant growth regulators with hormone-like properties (Sembdner et al. 1990). The initiation of JAs biosynthesis begins with the release of α-linolenic acid (Fig. 1) from chloroplast membranes, which undergoes multistage reactions catalyzed by enzymes present in plastids, peroxisomes and cytoplasm (Ghasemi Pirbalouti et al. 2014; Sharma and Laxmi 2016) and is regulated by light conditions (Zhai et al. 2007). Among exogenous JAs it was showed that more effective is MeJA due to its easier cell membrane crossing ability in comparison to JA and quick demethylation to free JA (Fattorini et al. 2018).

Bioactive form of JAs synthesized by JAR1 (Jasmonyl-L-amino acid synthetase; Fig. 1) is (7*S*,3*R*)-JA-Ile perceived by the COI1 receptor (the F-box protein CORONATINE INSENSITIVE 1) (Staswick and Tiryaki 2004; Fonseca et al. 2009; Wasternack and Hause 2013; Ueda et al. 2020). However, biochemical analysis indicated that *OsJAR1* encodes an enzyme conjugating JA not only to isoleucine (Ile) but also to tryptophane (Trp), leucine (Leu), methionine (Met), phenylalanine (Phe) and valine (Val) (Staswick 2009). JA-Ile binds to the Skp1-Cullin-F-box $(SCF)^{COI1}$E3 ubiquitin ligase complex which further recruits JAZ (JASMONATE

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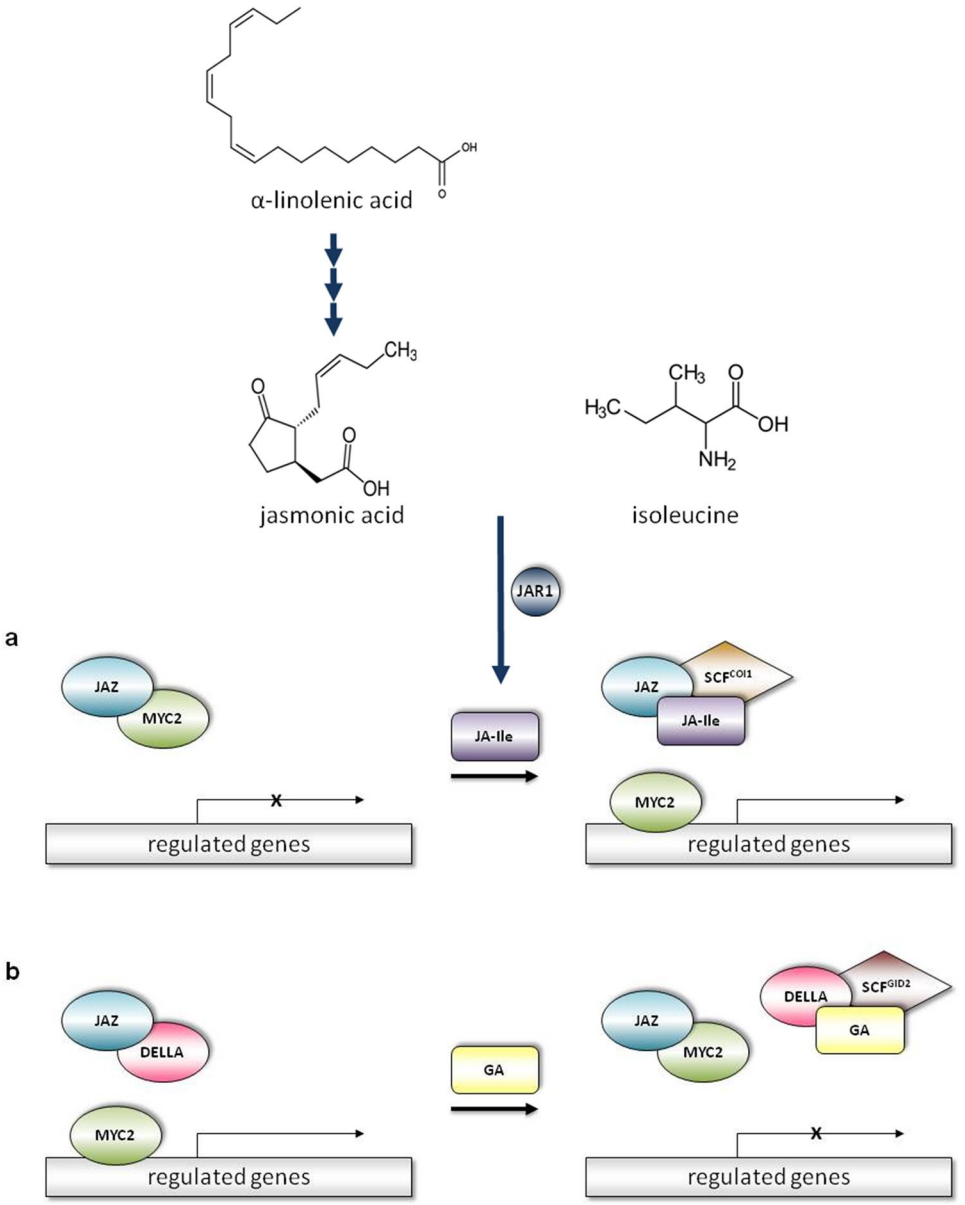

Fig. 1 Schematic representation of JA biosynthesis, conversion to the biologically active JA-Ile by JAR1 and interactions between JA and GA signaling pathways. In the absence of JA (**a**) repressors JAZ bind and inhibit the MYC family of transcription factors. JA-Ile binds to the SCF^{COI1} ubiquitin ligase complex and promotes degradation of JAZs, thus releasing MYC2 to trigger expression of JA-responsive genes. GA pathway is mediated through DELLA proteins. Without GA (**b**) DELLAs compete with MYC2 for binding to JAZs enabling expression of MYC2-regulated genes. In the presence of GA repressors DELLA are degraded through SCF^{GID2} complex, releasing JAZ to bind MYC2

ZIM-DOMAIN) transcriptional repressors for degradation through 26S proteasome, allowing the expression of JA-responsive genes (Zhai et al. 2017; Hyde et al. 2018; Fig. 1). JAZ repressors bind and inhibit the MYC family of transcription factors which ultimately leads to the growth promotion of leaves. However, JAZ-MYC interaction also takes part in plant growth inhibition during defense responses (Major et al. 2017; Guo et al. 2018). JA-Trp acts as an endogenous auxin inhibitor in *A. thaliana* and exogenously caused agravitropic root growth (Staswick 2009). The biological functions of other JA-amino acid conjugates are still unclear, although different COI1 homologs with variable preference perceive those bioactive molecules (Xiao et al. 2014; Yan et al. 2016).

The presence of JAs is associated with different changes in plant development and structure. Many studies have shown that JA and MeJA are involved in leaf senescence by stimulation of chlorophyll degradation. JA exposure causes damage to chloroplasts, decreases photosynthetic activity as a result of stimulation of RuBisCO degradation, stimulates destruction of cell membrane structure in the lipid peroxidation process and increases expression of senescence associated genes. The application of MeJA in turn, leads to an increase in the rate of cellular respiration, proteolytic and peroxidase activity in the leaves (Parthier 1990; Creelman and Mullet 1997; Liu et al. 2016). However, JAs are also involved in the defense responses to herbivore attack, promotion of shoot growth, storage organ formation: bulblets

and tubers, flowering processes, fruit and inflorescence number (Rohwer and Erwin 2008; Hummel et al. 2009).

Many studies on JAs effect were carried out on field or pot-grown plants, while its potential in in vitro culture need to be fully understood. The aim of this review is to summarize studies investigating the role of jasmonates in micropropagation, explants growth, storage organ formation and somatic embryogenesis in plants under in vitro conditions. This review might provide a starting point for further research using jasmonates.

Use of JAs during plant micropropagation

Basal culture medium provides all nutrients, energy and water necessary for plantlets, organs, tissues or cells growth. Regulation of developmental processes in plant tissue culture generally requires the addition of plant growth regulators (PGRs). Successful micropropagation strictly depends on a selection of appropriate PGRs and their concentration. The most commonly used PGRs are auxins and cytokinins which regulate growth and organize development of a plant tissue. In general, auxin mediates cell division and cytokinin mediates cell differentiation (Moubayidin et al. 2009). However, cultured plant tissues are also influenced by gibberellins (GAs), brassinosteroids (BRs), ethylene (ET), abscisic acid (ABA), salicylic acid (SA), jasmonates (JAs) and interactions among them (Gaspar et al. 1996; Phillips and Garda 2019). Exogenous application of JAs can affect a great variety of morphological and physiological responses in plants. Jasmonates, like all growth regulators, do not work independently but they are involved in a complex signaling network of interactions among multiple plant hormone signaling pathways (Yang et al. 2019). Different effects of exogenously applied PGRs, including JAs, may arise from modification of synthesis, catabolism, activation, sequestration, transport, or sensitivity to endogenous phytohormones of the same or other type (Gaspar et al. 1996).

A large number of studies conducted in different in vitro conditions have shown that exogenous JAs inhibit plant growth by suppression of the cell proliferation and expansion (Patil et al. 2014). However, high level of endogenous JAs was observed especially in young organs with high rate of cell division, therefore growth-promoting activity of JAs cannot be excluded and it was proposed that JAs-mediated physiological response might be a consequence of changes in endogenous cytokinins level which affects and regulates cell cycle (Avalbaev et al. 2016). Cell cycle is also under the gibberellins signaling control (Achard et al. 2009). Analysis of *Nicotiana attenuata* plants treated with exogenous JA and GA showed that JAs might indirectly repress shoot growth by antagonizing the GA pathway through specific DELLA-JAZ interactions and down regulation of photosynthesis (Machado et al. 2017). The GA signal is perceived by GID1 (GA-insensitive dwarf1). The GID1-GA complex stimulates plant growth and development by down-regulating DELLA repressors. In the absence of GA DELLAs compete with MYC2 for binding to JAZs, thereby releasing MYC2 to activate expression of MYC2-regulated genes. In the presence of GA DELLAs are degraded through $SCF^{GID2}E3$ complex leading to inhibitory JAZ-MYC2 interactions (Fig. 1; De Bruyne et al. 2014).

Cell cycle and cell proliferation

One of the first characterized physiological ex vivo effect of JAs was growth inhibition of the potted *Vicia faba* pericarp as a result of a cell cycle disturbance (Dathe et al. 1981). On this basis, a number of studies focused on the inhibitory effect of JAs on plant growth have been developed also under in vitro conditions. Ueda and Kato (1982) reported that JA and MeJA were powerful inhibitors of kinetin- and N-phenyl-N′-(2-chloro-4-pyridyl)urea-induced callus growth of *Glycine max.* Plant growth and development are related to cell expansion and cell differentiation, but also are strictly linked with cell division (Perrot-Rechenmann 2010). Świątek et al. (2002) compared the effect of JA with ABA on the cell cycle using *Nicotiana tabacum* BY-2 cell line. Their results showed that these phytohormones disturbed cell cycle progression by preventing DNA replication. Exogenous application of both compounds before the G1/S transition caused retention of cells in the G1 phase of the cell cycle. ABA application at a later stages did not affect further progression of the cell cycle, whereas JA effectively prevented cells from entering mitosis (cells arrested in G2 phase; Fig. 2). Those observations showed that the growth inhibition in response to JA might not resulted from a cell expansion in the elongation zone, but from a disruption of meristem activity (Świątek et al. 2002). Continued research confirmed that JA application led to tobacco BY-2 cell arrest in both G1 and G2 phases (Świątek et al. 2004). Analysis of a gene expression of Arabidopsis genome showed that also MeJA inhibited the activation of the M phase genes thus cells were arrested in the G2 phase of the cell cycle (Pauwels et al. 2008; Fig. 2). However, JAs treatment leads to reprogramming cells through the activity of specific transcription factors and proteins activity. It was indicated that MeJA primarily activates expression of the genes involved in jasmonate synthesis, thus cell cycle genes expression is suppressed in the later stages (Gumerova et al. 2015; Pauwels et al. 2008).

In asynchronously dividing *Taxus cuspidata* cultures addition of MeJA resulted in turn in four effects on the cell cycle: transient increase in G2 phase cells, transient decrease in S phase cells, and at later stages post-elicitation, increase in G0/G1 phase cells and decrease in G2 and S phase cells.

After 96 h of elicitation with MeJA, percentage of cells in the G2 and S phases decreased but in the G1/G0 phases increased, therefore it was suggested that cells treated with MeJA were not arrested in the G2/M transition but progression through the cell cycle was slowed down. A time lag between MeJA-mediated growth inhibition and cell death in asynchronously dividing *T. cuspidate* cell culture suggested that observed growth suppression in response to MeJA was not due to necrosis and/or rupturing of cell membranes, although the evidence indicated that JAs might affect cell walls (Capitani et al. 2005; Patil et al. 2014). Northern analysis and in situ hybridization using cDNA probes of the G1/S phase-specific genes confirmed enhanced proliferation growth of *N. tabacum* cells in response to relatively low concentrations of MeJA, whereas in highest concentration (10 µM) MeJA indicated transient effect and was more effective in enhancing defense-related processes such as cell wall thickening (Capitani et al. 2005). It was reported that MeJA elicitation increases content of cellular monolignols in *A. thaliana* (Pauwels et al. 2008) which polymerize into lignin according to the cell-wall class III peroxidases generating reactive oxygen species (ROS) from hydrogen peroxide. Peroxidase expression and activity is also stimulated by JA. These changes in response to JA are associated with a cessation of a growth and decreased cell expansion as a result of increased cross-linking of primary cell-wall components (Almagro et al. 2009; Napoleao et al. 2017; Hyde et al. 2018). An earlier report indicated that JAs delayed

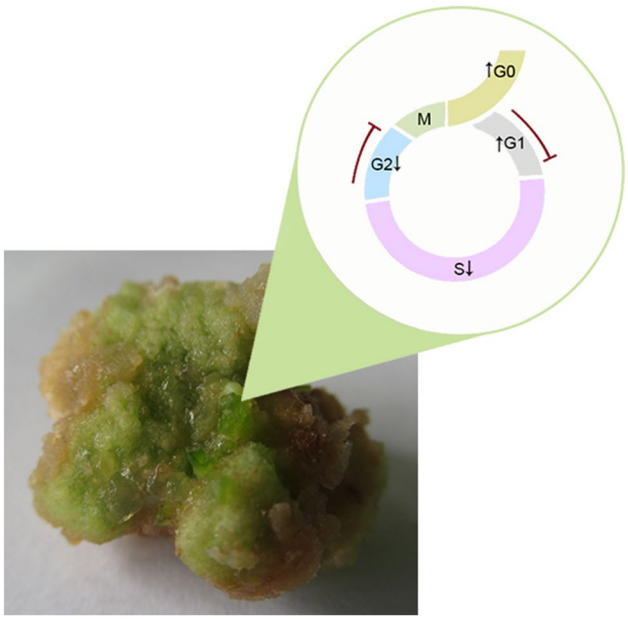

Fig. 2 Main effects of exogenous JAs on the cell cycle. JAs might cause retention of cells in the G1 and G2 phases, increase number of cells arrested in the G0 and G1 phases, and decrease number of cells entering the S and G2 phases

regeneration of the cell wall in protoplast of *Solanum tuberosum* (Ravnikar et al. 1992). In contrary to all these observations, it was reported that JA promotes division of mitotically less active cells in the root apical meristem named quiescent center (QC) in *A. thaliana.* Furthermore, JA pre-treatment increased number of new columella cell layer between QC and ablated cells, which suggest that JA stimulates stem cell replacement after ablation (Chen et al. 2011). JA-dependent regeneration network is highly important for plant response to parasitic infection (Zhou et al. 2019).

Effect of JAs on the cell division was also indirectly visualized during callus propagation under in vitro conditions. In higher concentration (5–50 µM) both JA and MeJA inhibited callus growth of *Medicago sativa* during differentiation stage (Ruduś et al. 2001; Table 1; Fig. 3). Elicitation with 10–100 µM MeJA significantly decreased cell viability of *T. cuspidata* and *Taxus baccata* suspension culture on $W_{B/A}$ medium supplemented with 6-benzylaminopurine (BA) and 1-naphthaleneacetic acid (NAA) (Bulgakov et al. 2011). Also 100 µM MeJA significantly decreased cell viability in protoplast culture of *A. thaliana* due to the rapid accumulation of H_2O_2 (Zhang and Xing 2008). Enhanced hydrogen peroxide and superoxide radical production was also detected in *Salvia miltiorrhiza* hairy roots (Liang et al. 2012) and *Panax ginseng* roots (Ali et al. 2006). In *Ricinus communis* gradual accumulation of H_2O_2 was indicated between 1 and 6 h after MeJA treatment of plants germinated under ex vivo conditions (Soares et al. 2010). High level of accumulated ROS leads to lipid peroxidation in cell membranes that might cause membrane damages, imbalance of cell homeostasis and further cell death (Pérez-Pérez et al. 2012). Correlation between oxidative stress and JAs is very complex. It was proposed that JA at a definite concentration can directly modify superoxide dismutase (SOD) structure that stimulates its activity (Maksymiec and Krupa 2006), thus JAs indicated both antioxidative and pro-oxidative activity (Ho et al. 2020). Exposure to JA and MeJA (50–200 µM) of *Mentha* × *piperita* cell suspension culture resulted in a less biomass accumulation than that of the control. Both elicitors suppressed growth of the cell suspension culture, although stronger inhibition was noted for MeJA application. Furthermore elicitation resulted in cultures color change from greenish to brown. Authors mentioned that this effect might be caused by increased accumulation of phenolic compounds and their oxidation what correlates with stimulatory effect of JAs on secondary metabolites accumulation (Krzyzanowska et al. 2011).

Earlier reports indicated that JAs not only have suppressing effect, but also have stimulating effect on cell division in various culture conditions or plant species, thus effect of JAs depends on its concentration, interaction with a specific PGRs and type of explant. In *S. tuberosum* JA (0.01–1.0 µM)

Table 1 Effect of jasmonates during plant micropropagation under in vitro conditions

Plant species	JAs concentration	Explant	Medium (PGR)	Effect	References
Monocots					
Amaryllidaceae					
Allium sativum	0.01–10 µM JA	BP	B5	JA stimulated shoot development (EC = 10 µM)	Ravnikar et al. (1993)
Narcissus triandrus	4.76 µM JA	SH	MS (2-iP)	JA increased shoot multiplication	Santos and Salema (2000)
Asparagaceae					
Ruscus aculeatus	100 µM MeJA	SN	MS	Root growth completely blocked	Mangas et al. (2006)
Dioscoreaceae					
Dioscorea cayenensis–D. rotundata	10 µM JA	SN	MS (Kin)	Increased shoots number	Ovono et al. (2007)
Iridaceae					
Crocus sativus	1.43–4.76 µM JA	EC	MS (BA + NAA)	JA improved development of somatic embryos (EC = 2.38 µM) and plant regeneration via somatic embryogenesis	Blázquez et al. (2004)
Musaceae					
Musa acuminata	5–160 µM MeJA	ST	MS (BA)	MeJA increased proliferation rate of shoots up to 100 µM (EC = 40 µM); higher concentration indicated no significant effect	Mahmood et al. (2012)
Orchidaceae					
Cymbidium eburneum	0.01–10 µM MeJA	SH	MS	Stimulation of protocorm-like bodys (PLBs) formation (EC = 0.1 µM) but MeJA decreased shoot formation	Shimasaki et al. (2003)
Cymbidium kanran				Increased number of rhizome branches (EC = 1 µM)	
Poaceae					
Cymbopogon schoenanthus	0.095–213.06 µM MeJA	SE	MSB5 (NAA + BA)	10.65 µM MeJA increased number of regenerated roots Inhibitory effect on shoot production	Abdelsalam et al. (2018)
Oryza sativa	1–50 µM JA	SD	MS	Reduced growth of shoots and roots	Cho et al. (2007)
Zingiberaceae					
Curcuma longa	5–16 µM MeJA	PL	MS (BA)	MeJA decreased leaf, root and plant biomass	Cousins and Adelberg (2008)
Dicots					
Anacardiaceae					
Pistacia lentiscus	0.48–0.95 µM JA	ST	MS (BA)	JA reduced multiple shoot formation and elongation growth	Koç et al. (2014)
Pistacia vera	0.3–10 µM MeJA	SH	MSPV	0.3–3.2 µM MeJA improved shoot multiplication (EC = 1 µM) and favored leaf development; 10 µM MeJA led to leaf senescence	Dolcet-Sanjuan and Claveria (1995)

Table 1 (continued)

Plant species	JAs concentration	Explant	Medium (PGR)	Effect	References
Apiaceae					
Centella asiatica	100 µM MeJA	SN	MS	Over 50% reduced weight of aerial parts and more than 70% reduced roots growth	Mangas et al. (2006)
	50–100 µM MeJA	HR	MS	MeJA inhibited growth of the hairy roots (EC = 50 µM)	Nguyen et al. (2019a, b)
Apocynaceae					
Catharanthus roseus	118.89–475.58 µM MeJA	C	MS (BA + NAA)	MeJA increased fresh and dry weight of callus (EC = 356.68 µM)	Al-Zuhairi and Ghanm (2017)
Asteraceae					
Artemisia annua	2–5 µM MeJA	SD	MS	MeJA increased plant height and dry weight (EC = 5 µM)	Alam and Albalawi (2020)
Stevia rebaudiana	50–200 µM MeJA	SN	WPM	MeJA decreased shoot and root development and growth	Moharramnejad et al. (2019)
Taraxacum pieninicum	24–96 µM JA	ST	MS (BA + NAA)	JA increased proliferation rate of shoots (EC = 24 µM), but increasing JA concentration led to limiting growth of the shoots	Kamińska et al. (2018)
Brassicaceae					
Arabidopsis thaliana	100 µM MeJA	PP	W5	Significant decreased cell viability	Zhang and Xing (2008)
	50 µM MeJA	SD	1/2 MS	MeJA inhibited leaf growth (reduced cell number and size) and also inhibited root-cell proliferation and elongation	Noir et al. (2013)
Brassica napus	0.95–23.8 µM JA	MC	NLN-13	Incubation with 4.78 µM JA for 24 h was the best combination for microspore embryogenesis	Ahmadi et al. (2014)
Brassica oleracea	0.002–6 µM JA	SN	MS	0.002–0.05 µM JA increased explant size and number of leaves; 0.01 µM JA stimulated root growth; 1.25–6 µM JA inhibited explants growth	Toro et al. (2003)
Caryophyllaceae					
Dianthus caryophyllus	10–40 µM MeJA	LC	MS (2,4-D + Kin)	MeJA increased callus growth rate	Matter et al. (2017)
Fabaceae					
Medicago sativa	5–50 µM JA, MeJA	C	SH	JAs inhibited callus growth during differentiation stage and reduced somatic embryo production	Ruduś et al. (2001)
	0.5–500 µM MeJA	SC	B5 (2,4-D + NAA)	MeJA inhibited callus induction, callus growth, proliferation of embryogenic suspension as well as germination and conversion of somatic embryos	Ruduś et al. (2006)

Table 1 (continued)

Plant species	JAs concentration	Explant	Medium (PGR)	Effect	References
Medicago truncatula	0.1–10 µM JA	SD	BNM	JA reduced nodulation and elongation growth of the roots	Sun et al. (2006)
Vigna mungo	0.95–11.9 µM JA	H	MS	JA stimulated root primordial and subsequent root formation with lateral branches. JA increased organogenic callus production	Lingakumar et al. (2014)
Lamiaceae					
Lavandula angustifolia	0.48–4.78 µM JA	SH	MS	JA decreased shoots production, increased polyphenol and chlorophyll content	Miclea et al. (2020)
Mentha×piperita	50 – 200 µM JA, MeJA	SC	LS (2iP + 2,4-D)	JAs decreased biomass accumulation and caused culture browning, no effect on cell aggregation	Krzyzanowska et al. (2011)
Ziziphora persica	50–150 µM MeJA	SH	MS (NAA + BA)	MeJA decreased shoot proliferation rate but stimulated its elongation growth (EC = 50 µM); 100 µM MeJA decreased number of roots but 150 µM MeJA stimulated their elongation growth	Zare-Hassani et al. (2019)
Malpighiaceae					
Galphimia glauca	100 µM MeJA	SN	MS	Reduced plant growth, accelerated symptoms of senescence and necrosis mainly in roots	Mangas et al. (2006)
Polygonaceae					
Fagopyrum tataricum	0.01–10 µM MeJA	SC	B5 (2,4-D + IAA + NAA + Kin)	MeJA in low concentrations (0.01 and 0.1 µM) stimulated accumulation of biomass but inhibited somatic embryogenesis after the transfer onto PGRs-free medium	Gumerova et al. (2015)
Rheum rhabarbarum	4.76×10^{-5} to 4.76 µM JA	SH	MS	4.76×10^{-5} to 4.76×10^{-3} µM MeJA induced minirhizomes formation	Rayirath et al. (2011)
Rosaceae					
Malus pumila	0.45–4.5 µM JA	D	B5 (BA + NAA)	JA promoted callus formation only at 15 DAFB (days after blooming); at 25 and 35 DAFB JA inhibited callus induction	Kondo et al. (2001)
Prunus avium	0.45–4.5 µM JA	D	B5	JA increased the weight of the callus (up to 1 µM)	Kondo et al. (2002)

Table 1 (continued)

Plant species	JAs concentration	Explant	Medium (PGR)	Effect	References
Pyrus communis *Pyrus cerasus* × *Pyrus canescens*	1–10 µM JA	SH	MS (BA + IBA/NAA)	JA increased leaves growth, fresh and dry weight of shoots	Ružić et al. (2013)
Solanaceae					
Lycopersicum esculentum	0.01–100 µM JA	R	MS	0.01–0.1 µM JA promoted frequency of lateral root initiation and elongation; > 0.1 µM JA inhibited root growth	Tung et al. (1996)
Nicotiana tabacum	0.1–10 µM MeJA	TCL	MS (IAA + BA)	0.1–1.0 µM MeJA increased explant fresh weight but ≥ 1.0 µM decreased number of developed shoot	Biondi et al. (2001)
Solanum tuberosum	0.01–100 µM JA	SN	MS	Increasing JA concentration decreased main roots length; > 10 µM JA inhibited roots formation; 0.1–1 µM JA increased shoot length; > 10 µM JA resulted in stunted plantlets	Ravnikar et al. (1992)
	0.01–1 µM JA	PP	ST (BA + 2,4-D)	0.01–0.1 µM JA delayed regeneration of cell walls; 0.01–0.1 µM JA stimulated cell division (number of microcalli)	
	0.95–238 µM JA	SN	MS	9.5 µM JA increased fresh weight of shoot and root, roots number and length; > 9.5 µM JA inhibited growth	Zhang et al. (2006)
	0.5–2 µM JA	SN	MS	JA shortened time for shoot initiation, increased shoot and root elongation, number of nodes, leaves and roots	Kumlay (2016)
Withania somnifera	50–250 µM MeJA	SH	MS (BA)	MeJA reduced biomass production of shoots	Sivanandhan et al. (2013)
Gymnosperm					
Pinaceae					
Pinus radiata	0.001–1000 µM JA	CT	SH (BA)	0.001–1 µM JA had no effect; 100 µM JA decreased number of shoots, nodules, maximum shoots length, fresh and dry weight; 1000 µM JA inhibited shoots and nodules formation	Tampe et al. (2001)
Polypodiaceae					
Platycerium bifurcatum	0.1–100 µM JA	L	MS	JA stimulated development of rhizoids and adventitious shoots (EC = 10 µM)	Camloh et al. (1999)
	0.01–100 µM JA	G	Knop	JA inhibited growth of gametophytes after 40 days of culture	Camloh et al. (2001)

Table 1 (continued)

Plant species	JAs concentration	Explant	Medium (PGR)	Effect	References
Taxaceae					
Taxus cuspidate; Taxus baccata	1–100 µM MeJA	SC	$W_{B/A}$ (BA + NAA)	≥ 10 µM MeJA inhibited growth of suspension cell culture	Bulgakov et al. (2011)
Fern					
Anemiaceae					
Anemia tomentosa	0.1–10 µM JA	G	1/2 MS	JA promoted sporophyte development from spore-derived gametophyte	Castilho et al. (2018)

Medium: *B5* Gamborg's B5 medium, *BNM* buffered nodulation medium, *Knop* Knop's medium, *LS* Linsmayer and Skoog medium, *MS* Murashige and Skoog medium, *MSB5* Murashige and Skoog medium including Gamborg B5 vitamins, *MSPV* modified Murashige and Skoog medium, *NLN-13* Nitsch and Nitsch medium with 13% sucrose modified by Lichter, *SH* Shenk and Hildebrandt medium, *ST* Shepard and Totten medium, *W5* W5 solution, *WPM* woody plant medium, $W_{B/A}$ W_0 Bulgakov's medium supplemented with BAP and NAA

Plant growth regulators: *2,4-D* 2,4-dichlorophenoxyacetic acid, *2-iP* 6-(γ,γ-dimethylallylamino)purine, *BA* 6-benzyloaminopurine, *IAA* indole-3-acetic acid, *IBA* indole-3-butyric acid, *Kin* kinetin, *NAA* 1-naphthaleneacetic acid

Explants: *BP* basal plates, *C* callus, *CT* cotyledons, *D* discs from pulp, *EC* embryogenic callus, *G* gametophytes, *H* hypocotyls, *HR* hairy roots, *L* leaves, *LC* leaf callus, *MC* microspore suspension, *PL* plantlets, *PP* protoplasts, *R* roots, *SC* suspension cell culture, *SD* seedlings, *SE* seeds, *SH* shoots, *SN* stem nodes, *ST* shoot tips, *TCL* thin cell layers

EC the most effective concentration

combined with BA and 2,4-dichlorophenoxyacetic acid (2,4-D) stimulated cell division manifested by increased number of microcalli (Ravnikar et al. 1992). Similar results were obtained for *Prunus avium* and *Vigna mungo* callus cultures propagated on B5 and MS medium, respectively, supplemented with JA in the comparable concentrations (Table 1), although without any other hormonal additives (Kondo et al. 2002; Lingakumar et al. 2014). Addition of the ester derivative of JA also affected callus growth. MeJA (10–40 µM) combined with 2,4-D and kinetin (Kin) increased callus growth rate from *Dianthus caryophyllus* leaf explants (Matter et al. 2017). Even ten times higher concentration (118.9–475.6 µM) of MeJA in MS medium with BA and NAA increased fresh and dry weight of *Catharanthus roseus* callus (Al-Zuhairi and Ghanm 2017). The JAs effect might also depend on the growth stage of the plants. In *Malus pumila* growing in an open field, the endogenous level of JA is high in the early stages of pulp development, thus effect of exogenous JA under in vitro conditions varied between samples from ex vivo plants collected in different days after blooming (DAFB). It was indicated that only at 15 DAFB, when the plant tissue was still in the cell division stage, JA promoted callus formation. At 25 and 35 DAFB, JA in turn inhibited callus formation probably because endogenous JA concentrations increase with time of fruit growth. These results indicated that only low endogenous JA level promotes callus formation, whereas increasing JA concentration inhibits this process (Kondo et al. 2001).

Organogenesis

Analyzing JAs addition during plant micropropagation, it was reported that these compounds perform varied effects, either promoting or inhibitory. For example, JA in concentrations of 0.5–2.0 µM shortened time for shoot initiation, increased shoot and root elongation, number of nodes, leaves and roots in stem nodes of *S. tuberosum* placed onto MS medium (Kumlay 2016; Table 1). In turn, growth of the *Oryza sativa* seedling was inhibited with increasing concentration of JA in MS medium, even in the presence of 1 µM JA root growth was reduced twofold over the control (Cho et al. 2007). As it was noticed role of JAs seems to be species- and context-dependent (Lakehal and Bellini 2018) and mentioned JA and GA growth-defense balance should be considered during analyzing the JAs effect on the propagation effectiveness. Generally it is presupposed that JA prioritizes defense, in turn GA—prioritizes growth. Inhibited plant growth as a results of JA treatment is probably related with suppression of GA-mediated pathway (Hou et al. 2013; Nguyen et al. 2019a). It was indicated that MeJA-mediated growth inhibition might results also from the perturbations in mitochondrial membrane integrity, decreases in the

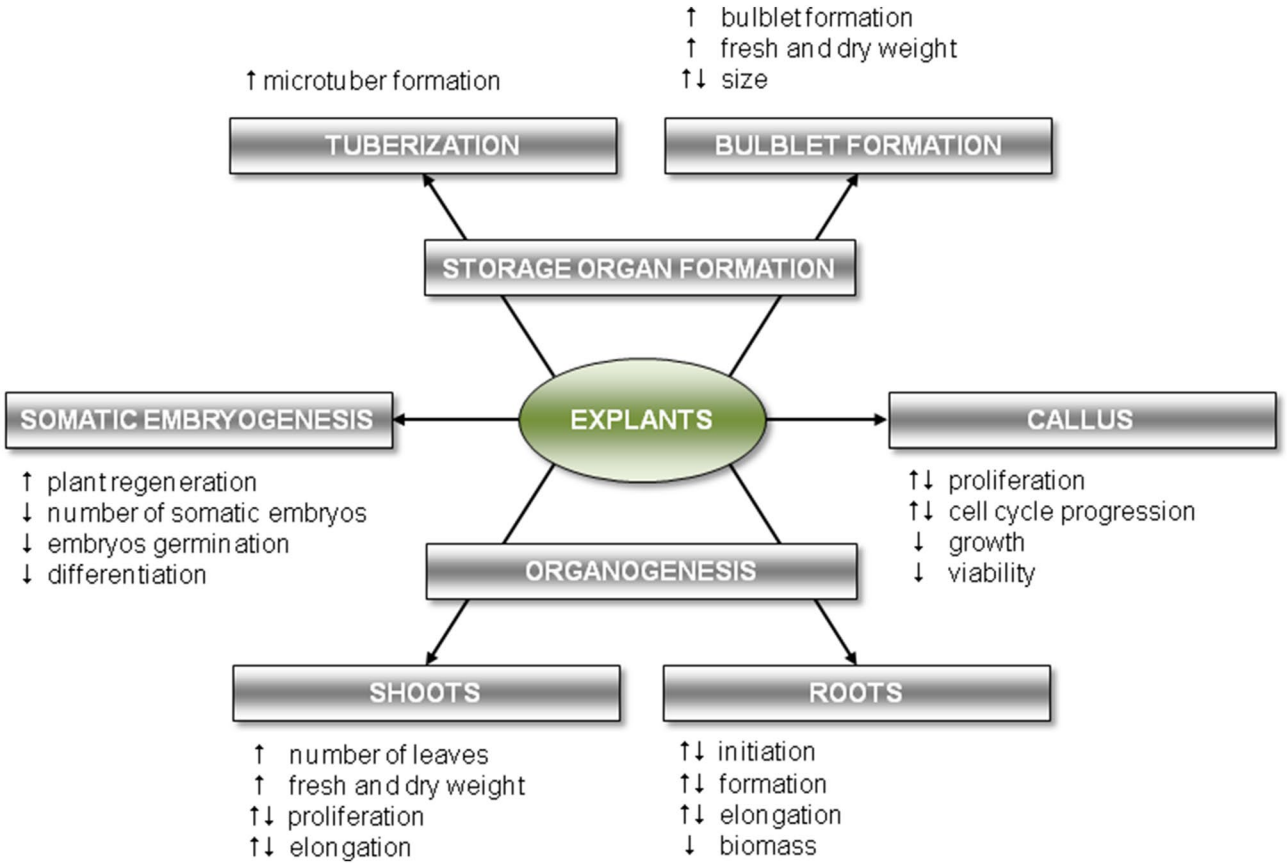

Fig. 3 Diagrammatic representation of the effects of exogenously applied JAs under in vitro conditions (promoting and inhibitory effects)

biosynthesis of ATP and proteins involved in energy metabolism (Ruiz-May et al. 2011; Cho et al. 2007).

Shoots proliferation and growth of the aerial parts

In the shoot induction, development and proliferation cytokinins play a vital role. In *S. tuberosum* stem node cultures it was indicated that exogenous JA increased the ratio between physiologically active and inactive cytokinins without changing its total content (Dermastia et al. 1994). In turn, *Triticum aestivum* seedlings treated with MeJA showed twofold increased accumulation of cytokinins without changes in ABA and auxins levels (Avalbaev et al. 2016). It was also reported that MeJA increased accumulation of cytokinins, despite the antagonistic interaction between JA and cytokinin noted in xylem development of *A. thaliana* (Jang et al. 2017). JAs were considered as inhibitors of cytokinin-induced plant growth manifested by reduced biomass in *A. thaliana* (Yan et al. 2007,2009; Zhang and Turner 2008; Noir et al. 2013; Attaran et al. 2014; Table 1; Fig. 3) and in *O. sativa* (Yang et al. 2012; Hibara et al. 2016). JA suppresses cell proliferation in wounded *A. thaliana* plants leading to a reduced leaf size with fewer and smaller epidermal cells giving a "bonsai effect" (Zhang and Turner 2008; Noir et al. 2013; Yang et al. 2019). JAs act as a growth inhibitors even in combination with exogenous BA. Repressed growth of the shoots was observed for *Pinus radiata* (Tampe et al. 2001), *Curcuma longa* (Cousins and Adelberg 2008) and *Withania somnifera* (Sivanandhan et al. 2013). No shoot production was observed for *Lavandula angustifolia* treated with 4.78 µM JA (Miclea et al. 2020). Addition of JA even in concentrations lower than 1 µM into MS medium with BA reduced multiple formation and elongation of *Pistacia lentiscus* shoots (Koç et al. 2014). JA in concentrations up to 0.05 µM increased dry weight of shoots, leaves and roots developed from single nodes explants and number of leaves of *Brassica oleracea* cultivated in MS medium. In higher concentrations (1.25–6. µM) JA inhibited explant growth (Toro et al. 2003). MeJA in concentrations 0.1–1.0 µM also increased explant fresh weight but in higher concentration decreased number of developed shoots in *N. tabacum* cultured on MS medium supplemented with BA and IAA. Histological analyzes indicated that loss of the thin layer tobacco explants ability to regenerate in response to MeJA treatment was due to a strong hypertrophy of the cells and

disappearance of meristemoids (Biondi et al. 2001) and reduced shoot primordial development (Capitani et al. 2005).

For various species JA stimulated shoot proliferation rate and growth when it was added into a medium in concentrations up to 10 µM (Table 1). JA supplementation of a medium containing N6-(2-Isopentenyl)adenine (2-iP) increased shoot multiplication and development in *Allium sativum* (0.1–10 µM JA) and *Narcissus triandrus* (4.8 µM JA) (Ravnikar et al. 1993; Santos and Salema 2000). Combined with Kin, 10 µM JA increased shoot number of *Dioscorea cayenensis—D. rotundata* (Ovono et al. 2007). In *Pyrus communis* and *P. cerasus* × *P. canescens* shoots addition of 1–10 µM JA into MS medium supplemented with BA and IBA or NAA increased leaf growth, fresh and dry weight of shoots (Ružić et al. 2013). MeJA (0.3–3.2 µM) also improved shoot multiplication and favored leaf development of *Pistacia vera* propagated onto MSPV medium containing BA and IBA, although 10 µM MeJA led to the leaf senescence and decreased shoot proliferation (Dolcet-Sanjuan and Claveria 1995). On the other hand in *Musa acuminata* increasing concentration of MeJA up to 100 µM also stimulated proliferation rate of shoots in presence of BA (Mahmood et al. 2012). Similarly proliferation rate of *Taraxacum pieninicum* shoots on MS medium supplemented with BA and NAA was stimulated by JA in higher concentrations (24–96 µM). However, it was reported that increasing concentration of JA limited the growth of the obtained shoots (Kamińska et al. 2018). The opposite effect was obtained for *Ziziphora persica* multiplied shoots on MS medium supplemented with the same PGRs, where MeJA decreased shoot proliferation rate but stimulated its elongation (Zare-Hassani et al. 2019). Increased height and dry weight of the seedlings probably by a rapid and significant increase of cytokinins level was observed also for *T. aestivum* and *Artemisia annua* treated with only MeJA in low concentrations (0.01–1 µM and 2–5 µM, respectively) (Avalbaev et al. 2016; Alam and Albalawi 2020), but high MeJA concentrations (10 and 100 µM) inhibited wheat seedlings growth (Avalbaev et al. 2016). Reduced growth of the shoots in response to JA or MeJA alone in MS medium was also reported in *S. tuberosum* (Ravnikar et al. 1992), *O. sativa* (Cho et al. 2007), *Centella asiatica* and *Galphimia glauca* (Mangas et al. 2006). In *A. thaliana* inhibited leaf growth as a result of treatment with 50 µM MeJA was manifested by both cell number and cell size reduction (Noir et al. 2013). Furthermore, it was indicated that exogenous MeJA suppresses hypocotyl elongation in a SCF ^{COI1}-dependent pathway in Arabidopsis under various light conditions, particularly effectively under red light (Chen et al. 2013). Signal cross-talk between JA and the red-light receptor phytochrome B (phyB) is thought to intermediate growth stimulation in neighboring plants competing for light. However, in further research it was shown that growth restriction at high level of endogenous JA was independent of phyB but involved dysregulation of Trp biosynthesis (Major et al. 2020).

Rooting of the plantlets

The most important PGRs during rooting process of in vitro derived shoots are auxins, especially indole-3-butyric acid (IBA) and indole-3-acetic acid (IAA) (Goel et al. 2018). Increased accumulation of endogenous JA might be stimulated during adventitious root (AR) formation by conversion of the IBA to IAA in NO-mediated upregulation of JA biosynthetic genes (Fattorini et al. 2017). It was suggested that MeJA acts during dedifferentiation phase by increasing sensitivity to auxin of the founder cells which divide and the descendent cells become increasingly determined to root formation under the auxin signal (De Klerk 2002). However, it was documented that JA and auxins antagonize root growth through interaction between JAZ protein and transcription factor MYC2 (Yang et al. 2019; Fig. 1). Furthermore, MeJA induced root growth inhibition through the reduction of Arabidopsis root cell length with involvement of *COI1* in this process (Adams and Turner 2010). These results suggest that JAs modulates root formation via whole JAs pathway COI1-JAZs-MYC2 (Chini et al. 2009), but it was also reported that JA inhibits auxin-induced lateral root (LR) formation independently of the COI1 receptor (Ishimaru et al. 2018). Inhibition of AR initiation induced by JAs involve cytokinin-dependent pathway in *A. thaliana* (Lakehal et al. 2020). In turn auxin increases JA conjugation efficiency lowering free JA level. This auxin-JA interaction supports the hypothesis that JA signaling pathway negatively regulates AR in *Arabidopsis* hypocotyls (Gutierrez et al. 2012). Other studies indicated that JAs inhibits primary root (PR) elongation but promotes LR formation (Lakehal and Bellini 2018) and it was reported that IAA biosynthesis is required for MeJA to promote LR formation (Sun et al. 2009; Cai et al. 2014). Furthermore, it was shown that JA affect PR and LR growth by an auxin-independent pathway. The inhibiting effect of JA on a root system was found to be caused by a reduced cortex cell length and the low rate of the root-meristem cell formation in *Helianthus annuus* seedlings (Monzón et al. 2012). It was also suggested that the effect of JAs on the root growth may result from the reorganization of the root meristem, decreased cell division, inhibited cell elongation and premature cell maturation (Xue and Zhang 2007; Tung et al. 1996).

As for all micropropagation steps concentration of PGR does matter, but for some species, e.g. *O. sativa*, JA regardless of its concentration reduced root growth (Cho et al. 2007). In *Medicago truncatula* in turn only 0.1–10 µM JA inhibited nodulation and suppressed roots elongation growth (Sun et al. 2006). Similarly MeJA (5–16 µM) decreased root biomass in *Curcuma longa* plantlets (Cousins and Adelberg

2008). However, suppressed rooting process was mainly associated with the high concentrations of JAs (Table 1). Addition of 100 µM MeJA into MS medium reduced roots growth of *C. asiatica*, *Ruscus aculeatus* and *G. glauca* (Mangas et al. 2006). Furthermore, MeJA (50–100 µM) inhibited hairy roots growth of *C. asiatica* (Nguyen et al. 2019b). Supplementation of WPM medium with MeJA in concentrations of 50–200 µM led to decreased roots and shoots development and growth on nodal explants of *Stevia rebaudiana* (Moharramnejad et al. 2019). In turn in *Z. persica* 100 µM MeJA decreased number of roots, although at higher concentration (150 µM) stimulated root elongation (Zare-Hassani et al. 2019). Stimulation of root formation by JAs was also noted for low concentrations (up to 1.0 µM) in *S. tuberosum, B. oleracea* and *Lycopersicum esculentum* (Ravnikar et al. 1992; Tung et al. 1996; Toro et al. 2003; Zhang et al. 2006; Table 1). In *Cymbidium kanran* 1 µM JA increased number of rhizome branches (Shimasaki et al. 2003). Even in lower concentrations (4.76×10^{-5} to 4.76×10^{-3} µM) JA induced minirhizomes formation in shoot clusters of *Rheum rhabarbarum* (Rayirath et al. 2011). JA also stimulated root primordium and subsequent root formation with lateral branches in *V. mungo* hypocotyls placed onto MS medium (Lingakumar et al. 2014). Addition of 10.65 µM MeJA into MS medium supplemented with Gamborg's B5 vitamins, BA and NAA increased number of regenerated roots in *Cymbopogon schoenanthus* seedlings but showed negative effect on a shoot production (Abdelsalam et al. 2018).

It was indicated that JA derived by the demethylation of MeJA, applied at 0.01 µM in combination with IBA and Kin enhanced AR in *N. tabacum* and *A. thaliana* seedlings and thin cell layers (TCLs) under dark conditions. The endogenous IAA levels increased in the TCLs at the time of the first AR-cell cluster formation under MeJA treatment. Furthermore, it was shown that also xylogenesis in *Arabidopsis* TCLs is under the JAs control. Role of JAs in these processes was related to crosstalk between JA- and ET-signalling (Fattorini et al. 2009, 2018). It was proposed that JA at high concentrations promote xylogenesis rather than AR formation, and mentioned cross-talk between JA and ET may decide which of these competing processes will occur (Druege et al. 2019). These results were confirmed by Betti et al. (2019) who showed that during AR formation in *Arabidopsis* stem explants cultured with IBA the antagonism between JA and ET is based on an involvement of the EIN2 (Ethylene Insensitive2) and COI1 cross-talk. It was also assumed that JAs cooperate with cytokinins to repress initiation of AR formation in *Arabidopsis* under constant red light conditions thus JAs effect on AR formation might also depend on light conditions during culture (Lakehal et al. 2020; Fig. 3).

Somatic embryogenesis

Somatic embryogenesis (SE) is the developmental process in which a competent cell or a cell group undergoes biochemical and molecular changes resulting in the formation of a somatic embryo (Yang and Zhang 2010). Somatic embryos are bipolar structures with an apical pole (the future shoot) and a basal pole (the future root), both with its own meristem (Horstman et al. 2017). This regeneration system is preferred over organogenesis due to a low frequency of chimeras, a high number of regenerants and a limited level of somatic variation (Gaj 2001; Carra et al. 2019). One of the determining factors during induction of SE is IAA metabolism in the cells. Acquisition the embryogenic potential by pro-embryogenic mass is dependent on auxin homeostasis at a specific level (Nic-Can and Loyola-Vargas 2016). In Arabidopsis SE is a two-step process. In the first step early cotyledonary zygotic embryos are placed on medium supplemented with auxins to stimulate formation of the embryogenic tissue. In the next step formation of the somatic embryos is stimulated by the removal of auxins from the medium. JA is a key component of embryogenesis regulation in the pathway including phytoglobin 2 (PGB2), NO and several JA-responsive intermediates (Bassuner et al. 2007; Mira et al. 2016). It was suggested that JAs inhibit embryo germination in angiosperm (Białecka and Kępczyński 2003), although high endogenous level of JA is essential for somatic embryo formation in *M. sativa*. A relatively high and stable JA content was reported in somatic embryos developed from globular through torpedo till early-cotyledonary stage (Ruduś et al. 2009). Exogenous MeJA not only inhibited callus growth of this species during differentiation stage, but also negatively affected the proliferation of embryogenic suspension and reduced somatic embryos production (Ruduś et al. 2001, 2006; Table 1; Fig. 3). Tokuji et al. (1995) showed that MeJA markedly delayed somatic embryo differentiation from cell clusters to torpedo stage and repressed their further regeneration in *Daucus carota*. Cells of *Fagopyrum tataricum* from suspension culture after MeJA treatment were almost completely unable to produce somatic embryos. Proposed explanation was based on possible suppression of the cell cycle genes expression and cells arrest of entry into mitosis. On the other hand it cannot be excluded that exogenous MeJA induced perturbations in the level of endogenous hormones which after cells transfer onto hormone-free medium prevent activation of the embryogenesis process (Gumerova et al. 2015). In contrast to these results, Reinbothe et al. (1994) indicated that MeJA induces embryogenesis-related proteins and mRNA in *Nicotiana plumbaginifolia.* Improved microspore embryogenesis was obtained for *Brassica napus* treated with 4.8 µM JA for 24 h. At higher level (9.5 and 23.8 µM) JA improved embryogenesis and callogenesis only after 6 h incubation.

Longer incubation decreased microspore embryogenesis and microspore-derived embryos germination (Ahmadi et al. 2014). Blázquez et al. (2004) indicated that JA also in low concentration (2.4 µM) significantly improved SE and plant regeneration in *Crocus sativus*. Equivalent to somatic embryos in orchids, protocorm-like bodies (PLBs) formation was improved as a result of a MeJA treatment, although PLBs formation decreased as MeJA level increased (Teixeira da Silva 2012). Similar results were obtained in shoots culture of *Cymbidium eburneum* where addition of MeJA into MS medium stimulated PLBs formation with simultaneous decreased shoot formation (Shimasaki et al. 2003).

Microtuber and bulblet formation

For some species culture through bulblets or microtubers has become a more effective method of propagation due to the genetic purity (Wang and Hu 1982; Sultana et al. 2010). Formation of this both storage organs under in vitro conditions might be affected by several factors such as sucrose levels, photoperiods and PGRs and is controlled by biochemical and genetic factors (Gheisari and Miri 2017; Islam et al. 2017).

Several phytohormones are associated with the processes associated with the tuberization. Especially significant role was assigned to GA_3 which regulates the change in cell growth orientation from longitudinal to radial swelling of the stolon tip what is characteristic step during tuber formation (Hannapel et al. 2017). JAs also induce changes of the cell division marked by cortical microtubules reorientation and radial expansion direction during initiation of storage organs formation (Shibaoka 1991; Matsuki et al. 1992; Podwyszyńska et al. 2015). JAs involvement in this process was repeatedly confirmed not only in tuber formation from stolon apex in plants from soil cultivation (Koda 1997; Cenzano et al. 2003) but also during further cell expansion of medullary tissue in *S. tuberosum* microtuber discs cultured in vitro (Takahashi et al. 1994; Table 2). Pruski et al. (2002) pointed out that JA induction of tuberization and microtuber bulking on *S. tuberosum* nodal cuttings was most pronounced under tuberization-inhibiting 16 h photoperiod. As can be seen different studies indicated that JA and its derivatives stimulated microtuber formation (Hamberg and Gardner 1992; Fig. 3) not only in potato, but also in *D. rotundata* (Jasik and Mantell 2000), *D. cayenensis* (Ovono et al. 2007) and *Pterostylis sanguinea* (Debeljak et al. 2002), although a number of studies indicated that JA was not directly involved in process of tuberization in *Solanum* spp. (Helder et al. 1993; Jackson and Willmitzer 1994; Jackson 1999). This process is also controlled by light, temperature and GA (Lin et al. 2013). It suggests that tuberization is indirectly controlled by JAs through crosstalk with GA signaling (Koda 1997; Wasternack and Hause 2013; Siddiqi and Husen 2019). However, increased accumulation of JA in pretuberous roots of *Manihot esculenta* planted in the field inhibited tuberous root formation. Those inconsistencies might be due to the differences between potato (i.e., stem tuber) and cassava (i.e., root tuber) and contrasting JAs impact on the cell processes in tissues that differ e.g. in sensitivity to this phytohormone and endogenous level of other PGRs (Utsumi et al. 2020), e.g. cytokinins which were reported to antagonize the JAs effect on *S. tuberosum* microtuber growth after induction. Furthermore JAs effect on microtuber formation is also maturity-specific. The late maturing cultivar may have lower response to JAs (Sarkar et al. 2006).

Commercially grown cultivars are also propagated by other vegetative tissue, such as bulbs. Conventionally bulbs are produced from scales since a long period of time. Micropropagation is similar to the scaling, although under in vitro conditions small scale-explants are used and excised scales from the new bulblets can be used as initial material thus propagation cycles can be performed few times per year (Askari et al. 2018). It was shown that increased JAs level occurs also in bulb forming plants suggesting that this phytohormone is involved in the formation of storage organs other than tubers. JAs plays role in the formation and enlargement of bulblets on *N. triandus* (Santos and Salema 2000), *A. sativum* (Bekheet 2006), *Allium victorialis* (Park et al. 2004) shoot explants placed on MS medium, and *A. sativum* basal plates transferred onto B5 medium (Ravnikar et al. 1993) (Table 2; Fig. 3). For *A. sativum* and *Narcissus papyraceus* it was also noted that JA and MeJA, respectively, stimulated bulblet formation and increased number and weight of bulblets in combination with NAA (Kim et al. 2003; Hosseini et al. 2013), although in *N. papyraceus* MeJA showed an inhibitory effect on a size of bulblets (Hosseini et al. 2013). Interestingly JA combined with cytokinin 2-iP stimulated bulblets production and its growth in *Hyacinthus orientalis* (Doğan et al. 2020), although Saniewski and Puchalski (1987) reported that 0.5% MeJA inhibited benzyladenine-induced bulblet formation in *Muscari armeniacum* and in lower concentration (0.1% and 0.2%) MeJA delayed development and growth of the bulblets. MeJA decreased bulblet number also in *Tulipa gesneriana*, although in one of the four studied cultivars (P14) MeJA combined with 500 µM Arg increased number of bulblets, their size and weight (Podwyszyńska et al. 2015).

Development of gametophyte and sporophyte

JA may be involved in alternation of generations in ferns by activating the ontogenesis phases. The JA effect on the growth of gametophyte is age-dependent. JA at 0.1–1.0 µM promoted early *Platycerium bifurcatum* gametophyte development and its transition from a filamentous to a spatulate growth. In turn, after 40 days of culture JA inhibited growth

of the gametophyte of this species. Authors proposed that maturation of the gametophytes leads to differences in response to JA (Camloh et al. 1996, 2001). In protoplast culture of a sporophyte 0.01 µM JA stimulated initial divisions of the cells (Camloh et al. 1996). JA, especially in concentration of 10 µM, promoted rhizoids and adventitious shoots development on leaves of this species. Stimulatory effect on rhizoid development was observed even in the presence of 100 µM JA (Camloh et al. 1999). Exogenous JA activated growth of the gametophyte and the further sporophytes development on the thallus surface of *Anemia tomentosa*. It was also observed that JA was able to remain in the gametophyte stage even when sporophytes were already developed (Castilho et al. 2018). However, in horsetail *Equisetum arvense* JA inhibited growth of gametophytic and sporophytic tissues and also suppressed initiation of sporophytic shoots in vitro (Kuriyama et al. 1993).

JAs as a stimulator of secondary metabolism

JAs have been widely used as elicitors to induce secondary metabolite production in a variety of plant in vitro cultures. Increased secondary metabolites accumulation was often associated with decreased explants growth. Treatment of *Calendula officinalis* hairy roots with JA led to slightly decreased growth of the explants, but stimulated secretion of oleanolic acid glycosides into the medium (Alsoufi et al. 2019). Similar correlation was reported for *C. asiatica*. MeJA inhibited shoot, callus and cell suspension culture growth with simultaneous stimulation of asiaticoside (in shoot and callus culture) and asiatic acid (callus culture) biosynthesis (Krishnan et al. 2019). However treatment of adventitious roots of *Ajuga bracteosa* with NAA and MeJA led to increased maximum dry biomass formation and enhanced total phenolic content (Saeed et al. 2017). Similar results were obtained for *Castilleja tenuiflora* thirty-day-old in vitro plants elicited by foliar spraying with MeJA (Rubio-Rodríguez et al. 2021). Effect of jasmonates, as for all growth regulators, strictly depends on the used concentration. Treatment of *Vitis vinifera* with MeJA showed that 100 µM and 50 µM concentrations enhanced and lowered hairy roots biomass and secretion of resveratrol into the culture medium, respectively (Hoseinpanahi et al. 2020). The wider examples of the JAs usage for elicitation under in vitro conditions can be found in other reviews (Giri and Zaheer 2016; Singh and Dwivedi 2018; Ho et al. 2020).

JAs under stress conditions

A few studies are available on the effect of JAs on in vitro cultivated plant tissue subjected to stress conditions. Significantly more observations and conclusions were made and reached in pots and fields experiments with foliar application of JAs, e.g. under salinity stress (Manan et al. 2016; Taheri et al. 2020), drought stress (Sadeghipour 2018; Tayyab et al. 2020), heavy metal stress (Ahmad et al. 2017; Ali et al. 2018), heat stress (Lee et al. 2019), cold stress (Connolly and Orrock 2018; Ghanbari et al. 2018) and under biotic stress (Burdziej et al. 2021). Under in vitro conditions JAs were studied under drought, salt and cold stress conditions (Table 3). To simulate drought stress in plants mostly a high molecular weight polyethylene glycol (PEG) has been used as a non-penetrating osmotic agent which lowers the water potential of the medium (Bressan et al. 1981). Improved explants growth under water stress in response to MeJA and JA was reported for *M. acuminata* and *Fragaria*×*ananassa* (Mahmood et al. 2012; Yosefi et al. 2020). Protective role of JAs might be correlated with a mitigation of oxidative stress by increased activity of POD and SOD enzymes (Yosefi et al. 2020), although contradictory effects of JAs in significantly higher concentration (200 µM) were obtained for *Verbascum nudicuale* seedlings (Ghasemlou et al. 2019). Induced activity of antioxidant enzymes was also observed in *T. aestivum* under water stress in presence of a low MeJA concentrations (0.25–2.5 µM) with simultaneous increase in the level of H_2O_2 (Ma et al. 2015), which suggests that JAs might also play role during induction of the oxidative stress. JAs also decreased proline accumulation in *B. napus* and *Saccharum* species under water stress. Increased proline level might indicate high stress level or high stress responsivity (Huguet-Robert et al. 2003; Nieves et al. 2001). Bandurska et al. (2003) indicated that exogenous JA increased endogenous level of ABA in *Hordeum vulgare* and *H. spontaneum* plantlets. ABA is the principal mediator in physiological outcome of drought avoidance, tolerance and resistance. JA and ABA seem to share common targets in a signaling pathway related to drought (de Ollas and Dodd 2016). The linkage of these two phytohormones was also indicated in a cold stress (Wang et al. 2016). In *Malus*×*domestica* cultivated in 8 °C MeJA improved callus growth and increased expression level of the genes involved in cold-signal response (Wang et al. 2019). Encapsulated shoot tips of *Taraxacum pieninicum* in a calcium alginate matrix showed growth inhibition during cold-storage in the presence of JA, although JA limited proline accumulation and oxidative stress by decreased lipid peroxidation (Kamińska et al. 2018). Application of JAs improved explants condition also under salinity stress, e.g. JAs stimulated growth of the *G. max* and *S. tuberosum* explants (Yoon et al. 2009; Efimova et al. 2019) and

Table 2 Effect of jasmonates on storage organ formation under in vitro conditions

Plant species	JAs concentration	Explant	Medium (PGR)	Effect	References
Tuberization					
Dioscoreaceae					
Dioscorea cayenensis—D. rotundata	10 JA	SN	MS	JA increased microtubers number	Ovono et al. (2007)
Discorea rotundata	0.5–50 JA, MeJA	NL	B5	JAs stimulated microtubers formation without effect on its weight (EC_{JA} = 50 µM; EC_{MeJA} = 2 µM)	Jasik and Mantell (2000)
Orchidaceae					
Pterostylis sanguinea	0.1–5 JA	PR	OMA	JA increased microtuber production without effect on microtubers diameter or fresh weight	Debeljak et al. (2002)
Solanaceae					
Solanum tuberosum	2.5 JA	SN	MS	JA induced tuberization under different photoperiod conditions	Pruski et al. (2002)
Bulblet formation					
Amaryllidaceae					
Alium sativum	0.01–10 JA	BP	B5	JA stimulated bulblet development (EC = 10 µM)	Ravnikar et al. (1993)
	1–20 JA	SH	MS (NAA)	JA stimulated bulblet formation and increased number and weights of bulblets (EC = 10 µM)	Kim et al. (2003)
	2.38–23.8 JA	SH	MS	The frequencies of bulblet formation increased with increasing JA concentration till 9.51 µM and then decreased; 9.51 µM JA increased bulblets number, fresh and dry weight	Bekheet (2006)
Allium victorialis	0.048–23.78 MeJA	SH	MS	MeJA increased bulblets formation and its growth (EC = 4.76 µM)	Park et al. (2004)
Narcissus papyraceus	2.23–8.92 MeJA	BS	MS (NAA)	MeJA increased bulblet number and increased its fresh weight (EC = 4.46 µM) but decreased bulblet size (diameter and length)	Hosseini et al. (2013)
Narcissus triandrus	4.76 JA	SH	MS	JA promoted bulblet formation and increased its size	Santos and Salem (2000)
Asparagaceae					
Hyacinthus orientalis	4.76–9.51 JA	E	MS (2iP)	JA with combination with 2iP stimulated bulblet production, increased bulblet diameter and roots number	Doğan et al. (2020)

Medium: *B5* Gamborg's B5 medium, *MS* Murashige and Skoog medium, *OMA* oatmealagar

Plant growth regulators: *2-iP* 6-(γ,γ-dimethylallylamino)purine, *NAA* 1-naphthaleneacetic acid

Explants: *BP* basal plates, *BS* bulb scales, *E* embryos, *NL* nodes with leaves, *PR* protocorms, *SH* shoots, *SN* stem nodes

EC the most effective concentration

Table 3 Effect of jasmonates on explants conditions under abiotic stress

Plant species	Jas concentration	Explant	Stress conditions	Effect	References
Water stress					
Brassicaceae					
Brassica napus	50–600 µM MeJA	LD	178–350 g·L^{-1} PEG	MeJA decreased Pro accumulation	Huguet-Robert et al. (2003)
Musaceae					
Musa acuminata	5–160 µM MeJA	ST	30 g·L^{-1} PEG	MeJA above 5 µM increased proliferation rate and vigour of shoots, FW, relative water and Pro content	Mahmood et al. (2012)
Poaceae					
Hordeum vulgare *Hordeum spontaneum*	5–15 µM JA	PL	− 1.5 MPa PEG	JA increased ABA but decreased spermidine content	Bandurska et al. (2003)
Saccharum sp. hybrid	4.7 µM JA	ESE	0.5 M sucrose, silicagel	JA decreased embryos survival, soluble proteins and free Pro content, increased starch, total phenolics and polyamines content	Nieves et al. (2001)
Triticum aestivum	0.25–2.5 µM MeJA	C	− 1.25 MPa PEG	MeJA increased LOX activity, endogenous JA and H_2O_2 content, induced antioxidant enzymes, decreased MDA level and improved cell viability	Ma et al. (2015)
Rosaceae					
Fragaria×*ananassa*	10–50 µM JA	HC	5–7% PEG	JA improved plantlets growth, increased Chl and carotenoids content, enhanced activity of POD and SOD enzyme	Yosefi et al. (2020)
Scrophulariaceae					
Verbascum nudicuale	200 µM MeJA	SD	− 0.3 and − 0.6 Mpa PEG	MeJA decreased shoot FW and DW, photosynthetic pigments contents, increased total phenol, flavonoid, H_2O_2 and MDA content, decreased SOD and PPO activity, increased POD activity	Ghasemlou et al. (2019)
Cold stress					
Asteraceae					
Taraxacum pieninicum	24–96 µM JA	ST	4 °C	JA inhibited explants growth, reduced accumulation of Pro and TBARS	Kamińska et al. (2018)
Rosaceae					
Malus×*domestica*	10–1000 µM MeJA	C	8 °C	MeJA improved calli growth and increased expression level of the cold-signal response genes	Wang et al. (2019)
Salt stress					
Fabaceae					
Glycine max	20 µM MeJA	SD	60 mM NaCl	MeJA alleviated the detrimental effect of salt stress (growth parameters, Chl and Pro content, photosynthesis and transpiration rate)	Yoon et al. (2009)
Solanaceae					
Solanum melongena	10–20 µM JA	E	100 mM NaCl	Pretreatment with 10 µM JA reduced salt stress affecting embryos development	Manar et al. (2013)
Solanum tuberosum	0.001–10 µM JA	PL	100 mM NaCl	JA stimulated stem growth, number of tiers and leaves, FW, increased Chl and carotenoids content	Efimova et al. (2019)

Explants: *C* callus, *E* embryos, *ESE* encapsulated somatic embryos, *HC* herbaceous cuttings, *LD* leaf discs, *PL* plantlets, *SD* seedlings, *ST* shoot tips

Chl chlorophyll, *DW* dry weight, *FW* fresh weight, *LOX* lipoxygenase, *MDA* malondialdehyde, *PEG* polyethylene glycol, *POD* peroxidase, *PPO* polyphenol oxidase, *Pro* proline, *SOD* superoxide dismutase, *TBARS* thiobarbituric acid reactive substances

development of *S. melongena* embryos (Manar et al. 2013) treated with 60–100 mM NaCl (Table 3). At molecular level it was reported that JA-inducible salt stress related genes were not activated in presence of ABA in *O. sativa* roots, although some evidence of a crosstalk between these phytohormones for regulating salt stress was proposed (Ryu and Cho 2015).

Conclusions

Jasmonates can differentially affect explants growth under optimal and stress conditions. More detailed works are needed to determine what mechanisms decide about physiological effect of JAs. JA is best studied as an elicitor and undoubtedly plays an important role in a secondary metabolite biosynthesis. The detailed role of JAs in a whole plant or explants growth is still unknown. JAs are often described as a growth retardant during defense related to biotic stresses, however they have also stimulatory effect on explants growth, especially microtubers and bulblets. The crosstalks between JAs and other phytohormone (mainly cytokinins, auxins and gibberellins) seems to be crucial for shoot proliferation, rooting and embryogenesis efficiency of different species. Particularly interaction linking JAs responses with gibberellins signaling pathway is a key factor determining explant growth and tuberization process. Knowledge about the mechanism of JA action in explants will provide useful information, especially important for species with problematic propagation and microprapagation system.

Declarations

Conflict of interest The authors declare that they have no relevant conflict of interest.

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