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Inhibitory Effect of Methyl Jasmonate on Flowering and Elongation Growth in *Pharbitis nil*

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Abstract

The effect of methyl jasmonate (JA-Me) on the floral bud formation and elongation growth in the short-day plant *Pharbitis nil* was investigated. The placing of 4-day-old seedlings of *P. nil* in a solution of JA-Me for a period of 24 h before an inductive (16 h or 14 h of darkness) night led to a dramatic reduction in the number of flower buds formed by the plant. Plants treated with JA-Me also totally lost their capacity to form a generative terminal bud. JA-Me applied after photoinduction does not inhibit flowering. Gibberellic acid (GA_3) partly reverses the inhibitory effect of JA-Me. Plants treated simultaneously with JA-Me and GA_3 formed about 3 flower buds more than plants treated with JA-Me only. JA-Me at a concentration of 10^{-7} M stimulates slightly, but at higher concentrations it inhibits root growth and shoot growth. A distinct lack of correlation between the effect of JA-Me on inhibition of flowering and shoot and root growth was noted. This indicates the independent action of JA-Me in controlling both processes.

Key words: Methyl jasmonate; *Pharbitis nil*; Flowering; Root and shoot growth; Photoperiodic induction; Gibberellic acid

Introduction

Methyl jasmonate (JA-Me) is a naturally occurring substance in plants, produced from linolenic acid (Vick and Zimmerman 1984). This compound belongs to the group of jasmonates (JA) numbered among the endogenous regulators of plant growth and development because of their wide occurrence and their influence on various physiological processes (Parthier 1991; Creelman and Mullet 1997; Saniewski 1987; Koda 1992).

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Data on the effect of exogenous JA on the process of flowering are limited. Jasmonates inhibit flowering of short-day plants: *Nicotiana tabacum* (Barendse and others 1985), *Chenopodium rubrum* (Albrechtová and Ullmann 1994). In plants with distinct photoperiodic requirements – a neutral plant *Spirodela polyrrhiza* (Krajnèiè and Nemec 1995) and a long-short day plant *Wolffia arrhia* (Krajnèiè and Cenciè 2000) -JA in lower concentrations (0.475–47.5 nM/L) promotes flowering.

Little is known about endogenous JA levels in plants during their development. Flowers of dicotyledon plants are known to contain high levels of JA including amino acid conjugates or amides (Miersch and others 1997). JA, JA-Me,

12-oxophydodienoic acid (OPDA), and JA isoleucine conjugate accumulate in tomato flowers to a level of about 20 nM g^{-1} fresh weight, which is two orders of magnitude higher than in leaves. Most interestingly, during flower development, the different tissues exhibited different ratios of these compounds (Hause and others 2000).

Studies carried out on mutants of *Arabidopsis thaliana* provide a great deal of information on the possible participation of JA in flowering. In the mutant *fad3-2 fad 7-2 fad8*, the unique deficiency of linolenic acid in tapetum, the pollen-feeding tissue of flowers, led to male sterility (McConn and Browse 1996). The identified *aim1* mutant of *Arabidopsis* was shown to be deficient in the enoyl-CoA hydratase, an essential enzyme of β-oxidation. As a consequence, abnormal inflorescence development and altered fatty acid composition occurred, which led to the suggestion that lipid-derived signals including JA might be altered in *aim1* (Richmont and Bleecker 2000). Mutants in biosynthesis of JA in *Arabidopsis delayed dehiscence1* inhibit a block in OPR3 (OPDA reductase) and are male-sterile. Exogenous JA application is capable of restoring fertility in the mutant flowers during a specific period of anther development (Sanders and others 2000).

Jasmonates also participate in the control of the elongation growth of plants. In dwarf rice seedlings (cv. Tan-ginbozu), JA reduced the effect of GA_3 on the elongation of the second leaf sheath. In lettuce, JA also diminished the effect of GA_3 on the elongation of hypocotyls (Yamane and others 1981). Exogenously applied JA substantially inhibited IAA-induced elongation of etiolated oat (*Avena sativa* L. cv. Victory) coleoptile segments (Ueda and others 1994). JA also caused a rapid, irreversible inhibition of isolated tomato root growth (Tung and others 1996). Primary root growth of wild-type *Arabidopsis thaliana* seedlings was inhibited by about 50% when seedlings were grown on an agar medium containing JA-Me (Staswick and others 1992).

Pharbitis nil, the Japanese Morning Glory, has been one of the most intensively studied plants with respect to the conditions that influence its flowering. This plant—especially the Violet strain—has a number of advantages. It initiates flowers at a very early stage of seedling growth (4–6 d after germination), when the plant has only well-developed cotyledons. After photoperiodic induction, flower buds develop rapidly and can be recognized as early as 10 d after induction. *P. nil* is a very sensitive short-day plant (SDP): it initiates flower buds in response to a single short day/long night cycle. This plant is a classical model in studies on the hormonal role in the mechanism of photoperiodic flower induction (Kopcewicz and Tretyn 1998).

Thus, the aim of the experiments presented here was to study the influence of exogenous JA-Me on the flower bud formation and shoot and root growth of *P. nil in vivo*. The interaction of JA-Me with gibberellic acid (GA_3) was also investigated, because it is known that gibberellins take part in the control of both shoot and root growth and flowering of *P. nil* (Kopcewicz and Tretyn 1998).

Materials and Methods

The investigations were conducted on 5-day-old seedlings of *Pharbitis nil* L. Chois (Convolvulus nil L., Ipomoea nil Roth., Convolulaceae), of the Japanese variety Violet (Marutane Seed Co., Kyoto, Japan). Seeds of *P. nil* were scarified and soaked for 24 h in distilled water (25°C ± 1). The swollen seeds were sown in pots filled with a mixture of wet sand and vermiculite (2:1 w/w) and transferred to a growth chamber. Plants were cultivated under controlled temperature (26°C ± 1) and light conditions (130 μmol/m^2/s, cool white light, fluorescent tubes, Polam, Warsaw, Poland) in a growth chamber.

The plants were incubated in 0.05% Tween 20 with JA-Me and the solution penetrated through the roots. The plants were taken out of the pots, rinsed with distilled water, measured, and transferred to erlenmeyer flasks with 0.05% Tween 20/JA-Me solution before, during, and after a 16-h-long night. After a 24-h-long incubation the plants were taken out of the erlenmeyer flasks, rinsed with distilled water, measured, and transferred back to the pots. The control plants were incubated in 0.05% Tween 20 solution only.

In the second experiment, after 24 h of incubation in JA-Me solution (10^{-4} M and 10^{-5} M) the plants were transferred to the pots and grown in a growth chamber under white light for 6 h and then exposed to a 14-h-long night. Gibberellic acid 10^{-3} M (GA_3, Fluca) in 0.05% Tween was applied to the cotyledons using a soft paint brush before (24 h) and at the beginning of the 16-h-long night.

After the completion of treatments the plants were grown in a growth chamber under continuous light at 26°C ± 1 for 14 days. The number of flower buds per plant and the percentage of plants exhibiting terminal flowering were then determined using a dissection microscope. Also at that time, the shoot and root growth of treated plants was measured. 10–15 plants were used in each experiment, which was repeated at least 3 times. The results were presented on diagrams and standard errors were calculated.

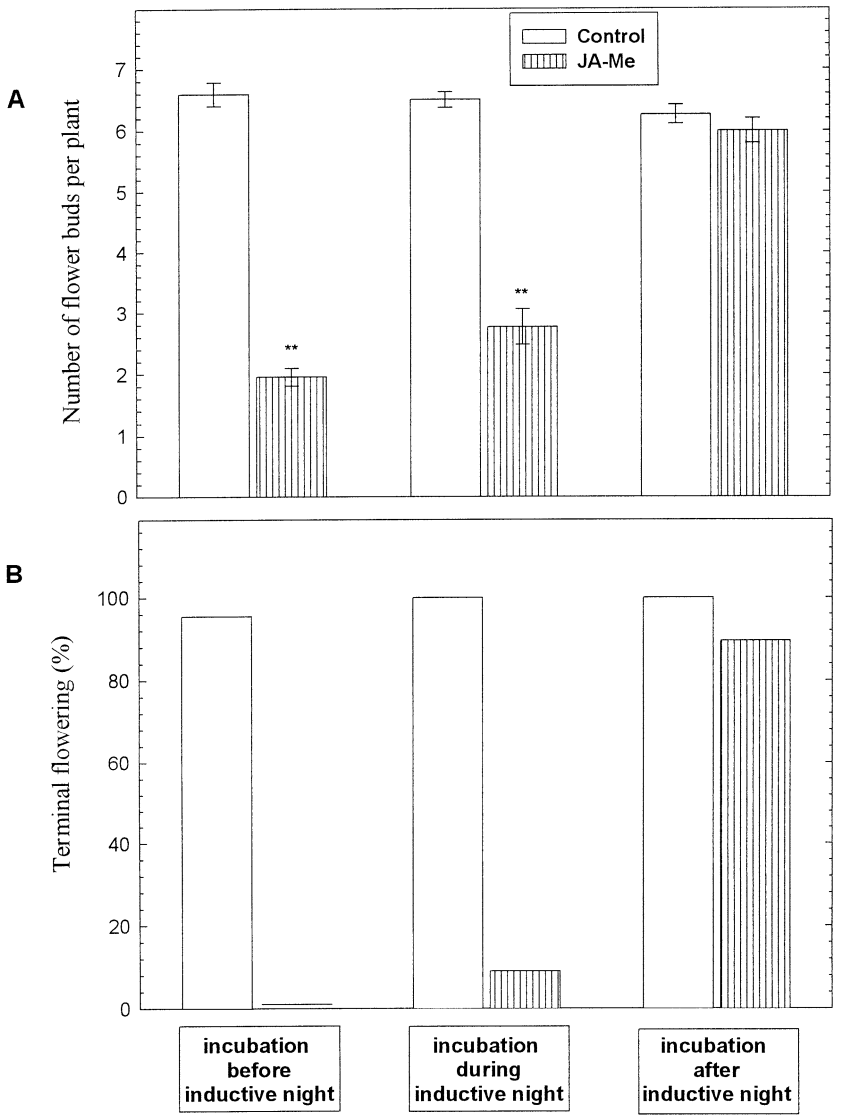

Figure 1. Flowering response of *P. nil* to JA-Me treatment at various times with regard to an inductive night. Plants were incubated with JA-Me (10^{-3} M) for 24 h before, during, or after a 16-h-long night. Control plants were incubated without JA-Me.

Results

Effect of JA-Me on Flower Bud Formation of *P. nil*

JA-Me was applied to 4-day-old seedlings through the roots. Inhibitory activity only took place when JA-Me was applied before and during photoinduction (Figure 1). In such treatments, plants did not form terminal flower buds and had about 3–4 fewer flower buds than control plants. JA-Me applied after photoinduction did not inhibit flowering (Figure 1). Lower concentrations of JA-Me (10^{-5} M and 10^{-4} M) applied before the 14-h-long inductive night inhibited the number of flower buds formed (Figure 2A) and the formation of terminal flower buds (Figure 2B). It was possible to partly reverse the inhibition of flowering caused by JA-Me by applying a solution of 10^{-3} M GA_3 to the cotyledons (Figure 3). Plants treated with both JA-Me and GA_3 formed about 3 generative buds more than those treated with JA-Me alone (Figure 3A).

Effect of JA-Me on Root and Shoot Growth of *P. nil*

Incubation of 4-day-old seedlings in solutions of JA-Me inhibited the growth of the primary root. The higher the concentration of JA-Me, the stronger the inhibition, reaching 83% inhibition in the case of 10^{-3} M. The lowest concentration (10^{-7} M) slightly stimulated root growth (Table 1).

JA-Me also inhibited shoot growth at the two highest concentrations: 10^{-4} M and 10^{-3} M (Tables 1, 2, 3). Inhibition of shoot growth was higher

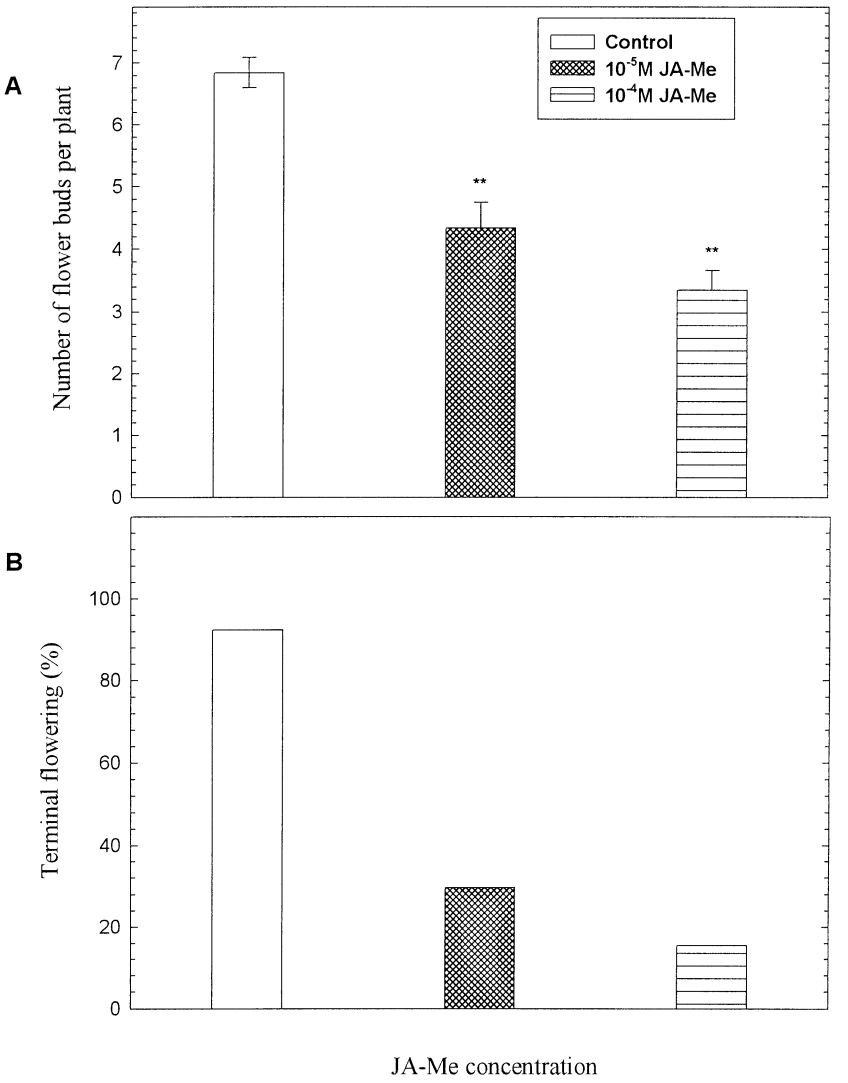

Figure 2. Flowering response of *P. nil* to JA-Me. Plants were incubated with JA-Me (10^{-5} M or 10^{-4} M) for 24 h before a 14-h-long night. Control plants were incubated without JA-Me.

when seedlings were incubated in a solution of JA-Me during the inductive night and after photoinduction (Table 2).

No correlation was found between the inhibitory effect of JA-Me on the growth and flowering of *P. nil*. Plants incubated in a solution of JA-Me before the 16 h inductive night were about 12 cm higher than plants incubated after the inductive night (Table 2). However, they formed, on average, over 4 flower buds fewer than plants treated with JA-Me after the inductive night (Figure 1). At concentrations of 10^{-4} M and 10^{-5} M, JA-Me inhibited the flowering of *P. nil* (Figure 2), but only at the higher concentration (10^{-4} M) did it also inhibit shoot growth (Table 3).

Discussion

Data on the effect of JA on the process of flowering are limited. The first paper suggesting the possible participation of JA in flowering control appeared in the 80s (Barendse and others 1985). It was found then that JA at a concentration of 10^{-6} M and higher inhibited the formation of flower buds in thin-layer explants of *Nicotiana tabacum* cv. Samsun. The inhibitory effect of JA-Me on flowering was also demonstrated by Albrechtowá and Ullmann (1994). It follows from their research that seedlings of the short-day plant *Chenopodium rubrum* treated for 12 or 24 h with a solution of JA-Me (5×10^{-5} M) form 30% and 50%, respectively, fewer flower buds than control plants. No effect of JA-Me application on ethylene formation was observed. Because plants treated with JA-Me were also characterized by inhibited root and shoot growth, the conclusion was drawn that both of these processes are causally linked. The results presented in this paper indicate, however, that although JA-Me has an inhibitory effect on

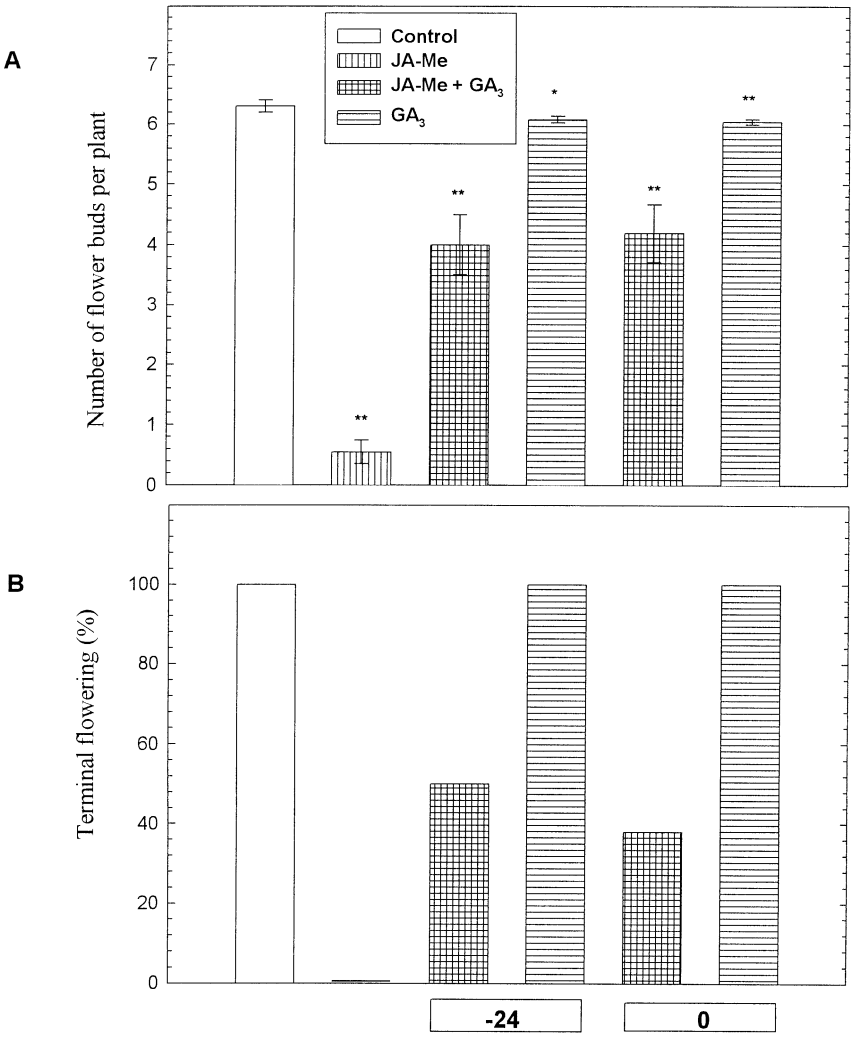

Figure 3. Flowering response of *P. nil* to JA-Me and GA_3 treatment. Plants were incubated with JA-Me (10^{-3} M) for 24 h before a 16-h-long inductive night. GA_3 (10^{-3} M) was applied to cotyledons 24 h before (−24) and at the beginning (0) of an inductive night. Control plants were incubated without JA-Me.

Table 1. Effect of Methyl Jasmonate (JA-Me) on Root and Shoot Growth of *P. nil*

JA-Me Concentration	Main Root Increment for 24 h Incubation (cm)	Shoot Length (cm)
0 (Control)	2.01 ± 0.05	41.3 ± 1.3
10^{-7} M	2.23 ± 0.06	43.9 ± 1.5
10^{-6} M	1.55 ± 0.05	44.4 ± 1.7
10^{-5} M	1.42 ± 0.04	44.2 ± 1.5
10^{-4} M	1.17 ± 0.04	36.8 ± 1.7
10^{-3} M	0.34 ± 0.05	28.3 ± 1.2

Plants were incubated with JA-Me (10^{-7} M–10^{-3} M) for 24 h before a 16-h-long night. Control plants were incubated without JA-Me.

both flowering and growth, there is no direct correlation. The influence of JA-Me on the flowering process depends on photoperiodic conditions (Figures 1, 2), whereas the influence on the shoot growth is dependent on the concentration of the substance applied (Tables 2, 3). Placing 4-day-old seedlings of *P. nil* in a solution of JA-Me for a period of 24 h before a 16 h inductive night led to a dramatic reduction in the number of flower buds formed by the plant. Plants treated with JA also totally lost their capacity to form a generative terminal bud (Figures 1, 2). It was possible to partially reverse the inhibitory effect of JA-Me by applying gibberellins to the cotyledons (Figure 3). Plants

Table 2. Effect of Methyl Jasmonate (JA-Me) Application at Different Times on *P. nil* Shoot Growth

	Shoot Legth (cm) Sedling Incubation		
JA-Me Concentration	Before Inductive Night	During Inductive Night	After Inductive Night
0 (Control)	39.9 ± 1.5	38.0 ± 2.2	40.7 ± 2.0
10^{-3} M	29.4 ± 1.7	25.2 ± 2.0	17.2 ± 1.5

Plants were incubated with JA-Me (10^{-3} M) for 24 h before, during, or after a 16-h-long night. Control plants were incubated without JA-Me.

Table 3. Effect of Methyl Jasmonate (JA-Me) on Shoot Growth in *P. nil* Plants Exposed to a 14-h-long Inductive Darkness

JA-Me Concentration	Shoot Length (cm)
0 (Control)	44.6 ± 1.6
10^{-5} M	44.2 ± 2.0
10^{-4} M	36.6 ± 1.5

Plants were incubated with JA-Me (10^{-5} M or 10^{-4} M) for 24 h before a 14-h-long night. Control plants were incubated without JA-Me.

treated simultaneously with JA-Me and GA_3 formed about 3 flower buds more than plants treated with JA-Me only. The role of gibberellins in the flowering of *P. nil* is widely known (Ogawa 1981; Galoch and others 1995; Kulikowska-Gulewska and others 2000). The cotyledons in induced plants contain about 20% more gibberellins than non-induced ones (Kulikowska-Gulewska and others 2000). Exogenous GA_3 does not act if there is no photoperiodic induction (continuous light, 8-h-long night) or if the induction is strong. However, application of GA_3 to cotyledons over suboptimal photoperiods (12- or 14-h-long night) increases flowering. Light, acting through phytochromes, may disturb the biosynthesis or the transport of gibberellins, leading to the inhibition of flowering (Kulikowska-Gulewska and others 2000). The effect of JA-Me and GA_3 on the flowering of *Pharbitis nil* is therefore antagonistic.

Krajnèiè and Nemec (1995) analyzed the influence of JA on the flowering of *Spirodela polyrrhiza* (L.) Schleiden, a photoperiodically neutral plant. Under both short-day (SD) and long-day (LD) conditions JA (0.475–47.5 nM/L) enhances flowering in this plant. The higher concentrations (237.5 and 475 nM/L) prevent flowering. Similar results were obtained by Krajnèiè and Cenciè (2000). JA in lower concentrations (0.475–47.5 nM/L) promotes flowering of *Wolffia arrhiza*, a long-short day plant (LSDP), under both LD and SD conditions. Divergent results from the research concerning the influence of jasmonates on the flowering of short-day plants (*Chenopodium rubrum, Nicotiana tabacum, Pharbitis nil*) and plants with distinct photoperiodic requirements—a neutral plant (*Spirodela polyrrhiza*) and a long-short day plant (*Wolffia arrhiza*)—may be caused by differing mechanisms of JA action in these plants.

Under short-day conditions, there is an increase in the level of tuberonic acid, whose chemical structure is very similar to JA (Koda and Okazawa 1988). As long as 30 years ago, Oelze-Karow and coworkers (1970) reported that phytochrome P_{fr} rapidly inhibits synthesis of lipoxygenase, an enzyme from the JA biosynthesis pathway. It is possible that the concentration of JA and its derivatives is dependent on the state of phytochrome and the length of the photoperiod.

In this paper the influence of exogenous JA-Me on the growth of the root and shoot of *P. nil* was also studied. After 24 h of incubation of 4-day-old seedlings in solutions of JA-Me at concentrations of 10^{-6} M–10^{-3} M, strong inhibition of primary root growth took place, according to the concentration used (Table 1). Similar results were obtained by Staswick and others (1992). When plants of wild-type *Arabidopsis thaliana* were cultivated on a medium containing 0.1 μM JA-Me, inhibition of about 50% of primary root growth was observed. These results enabled a mutant *jar1* (jasmonic resistant) *Arabidopsis* insensitive to high concentrations of JA (0.1 μM) to be isolated. The influence of JA on the growth, morphology, and development of isolated roots of *Lycopersicon esculentum* Mill. cv. Bush Beefsteak *in vitro*, has also been studied (Tung and others 1996). JA at a concentration of 10^{-7} M caused a rapid, irreversible root growth inhibition. Higher concentrations of JA showed increased cellular vacuolation, root tip swelling, and decreased cell elongation. JA at low concentrations of 10^{-9} M and 10^{-8} M promoted lateral root initiation and lateral root elongation but had little effect on the elongation of the main axis. In this paper, the stimulating

effect of JA-Me on the increment of root length was also noted (Table 1) at the low concentration (10^{-7} M). Such a double effect of activity according to concentration is characteristic for plant hormones.

The influence of jasmonates on the elongation growth of roots may be the result of the reorganization of the root meristem, a reduction in cell division, inhibition of cell elongation, and premature cell maturation (Tung and others 1996). The inhibitory effect of JA-Me (10^{-4} and 10^{-5} M) on shoot growth of *P. nil* was also found in this paper (Table 2). Similar results were obtained by Yamane and others (1981). JA isolated from immature seeds of *Phaseolus vulgaris* L. inhibited the growth of rice seedlings and lettuce hypocotyls induced by GA_3.

Many reactions of plants to JA are similar to the effects caused by ABA. Miyamoto and coworkers (1997) suggest, however, that these two compounds act in different ways. The inhibitory effect of JA was observed only in monocotyledons, but that of ABA was observed in both mono- and dicotyledons. Furthermore, the inhibitory effect of JA can be reversed by adding sucrose, which was not possible in the case of ABA.

It has been demonstrated several times that JA-Me stimulates the production of ethylene (Saniewski and others 1987; Saniewski and others 1998). Tung and coworkers (1996) noted that isolated tomato roots cultivated *in vitro* treated with the ethylene precursor ACC showed morphological changes similar to the JA-treated roots. However, roots treated with JA produced an amount ethylene similar to the control plants. Inhibitors of synthesis and the action of ethylene did not inhibit the effects of JA. Tung and coworkers (1996) thus suppose that the mechanisms of the action of JA and ethylene on the growth and differentiation of roots are different.

The results presented in this paper testify to the fact that JA-Me inhibits the flowering of *P. nil* and that this effect depends above all on the photoperiodic conditions applied. In other short-day plants, the inhibitory effect of JA on flowering was also found (Albrechtowá and Ullmann 1994; Barendse and others 1985; Krajnèiè and Cenciè 2000). It may be assumed that JA-Me plays the role of an inhibitor in the flowering of short-day plants. JA-Me also acts antagonistically with gibberellins because the inhibitory effect of JA-Me was partially reversed by applying GA_3 to the plants. Thus, the endogenous balance of gibberellins and jasmonates may decide the direction of differentiation. JA-Me also inhibited the root and shoot growth of *P. nil*. However, a distinct lack of correlation between growth inhibition and flowering was noted, indicating the independent activity of JA-Me in controlling both of these processes. This may also testify to the fact that inhibition of flowering by JA-Me has a specific character, and that jasmonates are natural factors controlling the process of generative differentiation in short-day plants.

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