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Methyl Jasmonate Induces Gum and Inhibits Stem Growth Promoted by Auxin in Uncooled Tulip Bulbs

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Methyl jasmonate (JA–Me) induced strong gummosis when it was applied at a concentration of 1.0% in lanolin paste in the middle of the fourth internode of the stem promoted by indole–3–acetic acid (0.1% IAA) of uncooled derooted and cooled derooted tulip bulbs of ‘Apeldoorn’ and ‘Gudoshnik’. In addition, JA–Me inhibited growth of the internode of tulip stem induced by 0.1% IAA in lanolin paste when it was applied to the cut surface of the top internode of the same tulip stems. The possible inhibitory action of JA–Me on stem elongation induced by IAA in uncooled and cooled tulip bulbs is also discussed.

INTRODUCTION

It is well known that formation of gums in tulip bulbs is induced by ethylene produced by tulip bulbs infected by *Fusarium oxysporum* f. sp. *tulipae* (Swart and Kamerbeek, 1975, 1977) and by exogenously applied ethylene or ethylene–releasing compound, ethephon (Kamerbeek *et al.*, 1971; Kamerbeek and De Munk, 1976; De Hertogh *et al.*, 1980). The occurrence and severity of gummosis are dependent on the stage of the bulbs; maximal gummosis takes place 2–4 weeks after lifting, and after about 4 months it disappears (Kamerbeek and De Munk, 1976). Ethylene is a common factor involved in the induction of gummosis of stone–fruit trees (apricot, cherry, peach, plum) and other fruits (Boothby, 1983). Jasmonates including methyl jasmonate (JA–Me) have also been shown to have a promoting effect of the induction and/or production of gums in stone–fruit trees (Saniewski *et al.*, 1998b, c, 2000, 2001) and in tulips (Saniewski and Puchalski, 1988; Saniewski *et al.*, 1998a, d; Saniewski, 1989; Saniewski and Wegrzynowicz–Lesiak, 1994, 1995). JA–Me exogenously applied as a lanolin paste induced gummosis in bulbs, all internodes of stem and basal part of leaves of intact tulips (Saniewski and Puchalski, 1988). JA–Me also induced strong gummosis in all internodes when applied on fully elongated stem induced by indole–3–acetic acid (IAA) after excision of flower bud and all leaves in fully cooled tulip bulbs (Saniewski, 1989). In

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addition, JA-Me applied in the middle of the second or fourth internodes, partially inhibited stem growth induced by IAA when it was applied in place of the removed flower bud and after excision of all leaves in sprouted cooled tulip bulbs. In this case, JA-Me also induced strong gummosis in the treated internodes and the inhibition of growth was observed mainly in the internodes (Saniewski, 1989). Saniewski and Okubo (1997) showed that treatment with IAA in lanolin paste to the cut surface of the top internode of uncooled and cooled derooted bulbs of tulip after decapitation promoted the entire stem elongation. These results suggest that auxin has an important role in stem elongation of uncooled bulbs as well as of cooled bulbs.

The aim of the present work was to study the effect of JA-Me on gum induction in stem promoted by auxin in uncooled tulip bulbs. The effect of JA-Me on stem growth is also documented.

MATERIALS AND METHODS

Plant materials

Two cultivars of tulip (*Tulipa gesneriana* L.) bulbs, 'Apeldoorn' and 'Gudoshnik' were used in the study.

Experiments with uncooled derooted tulip bulbs

Bulbs of 'Apeldoorn' and 'Gudoshnik', after flower bud formation, were kept at 17°C until use. On January 9, the bulbs were derooted and upper part of the scales together with flower bud was removed. Then the flower bud was replaced by plain lanolin (control) or 0.1% IAA in lanolin paste. The bulbs were placed in water in plastic trays and incubated in a greenhouse at 17–20°C. On January 16, when the total length of the stem treated with IAA was 44.0 mm (last internode–26.3 mm) in 'Apeldoorn' and 34.5 mm (last internode–20.1 mm) in 'Gudoshnik', additional treatment was made in the middle of the last internode with plain lanolin or 1.0% JA-Me in lanolin paste. The bulbs were kept in the same conditions as before to incubate. Measurements of the stems took place on January 20 and 25 for 'Apeldoorn' and on January 20, 25 and 30 for 'Gudoshnik'. Photographs were taken on January 26 for both cultivars.

Experiments with cooled derooted tulip bulbs

Bulbs of 'Apeldoorn' and 'Gudoshnik', after flower bud formation, were cooled at 5°C from October 25 until use. On January 19, after the bulbs were derooted and upper part of the scales together with flower bud was removed, the flower bud was replaced by plain lanolin or 0.1% IAA in lanolin. The bulbs were incubated in the same manner as above. When the total length of the stem of IAA-treated 'Apeldoorn' and 'Gudoshnik' was 44.3 mm (last internode–20.4 mm) and 39.5 mm (last internode–17.6 mm), respectively, on January 25 additional treatment with plain lanolin or 1.0% JA-Me was made in the middle of the last internode. Measurements of the stems were made on January 28, 31 and February 3. Photographs were taken on February 3.

RESULTS AND DISCUSSION

JA-Me applied in the middle of the fourth internode partially inhibited the stem growth induced by IAA applied in the place of removed flower bud and after excision of all leaves in uncooled derooted tulip bulbs of both cultivars (Tables 1-2, Fig. 1). Growth

Table 1. Effect of JA-Me on stem elongation (mm) induced by IAA in uncooled derooted bulbs of tulips 'Apeldoorn'; treatment with IAA made on January 9 and treatment with JA-Me in the middle of the 4th internode on January 16 when the length of the stem was 44.0 mm.

Treatment	Total length of stem on Jan. 20	Length of internodes on January 25					Total
		1st	2nd	3rd	4th		
Control	0	0	0	0	0	0	
IAA	99.7c	32.1b	26.7b	39.6b	87.3b	185.7b	
IAA+lanolin	79.5b	28.0b	22.8b	35.9b	79.7b	166.4b	
IAA+JA-Me	66.2a	18.8a	16.9a	28.6a	41.9a*	106.2a	

* Gums were extruded on stem surface on January 23.

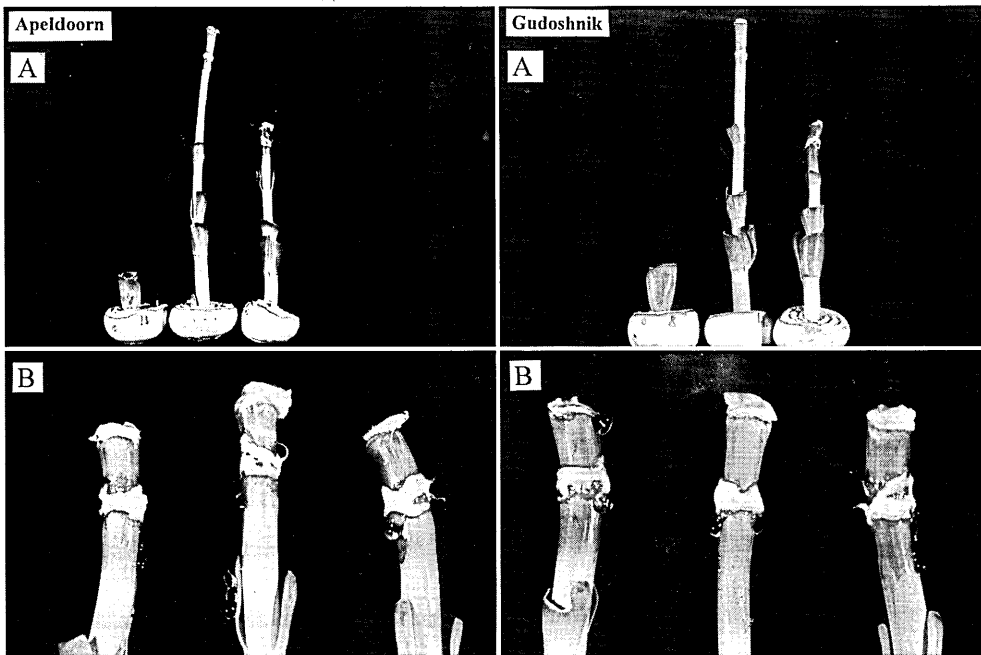


Fig. 1. Inhibitory effect of JA-Me on stem elongation induced by IAA in uncooled derooted tulip bulbs of 'Apeldoorn' and 'Gudoshnik' and induction of gums formation by JA-Me. A) left: control—flower bud replaced by lanolin only; middle: flower bud replaced by 0.1% IAA; right: flower bud replaced by 0.1% IAA and seven days later additionally treated with 1.0% JA-Me in the middle of 4th internode—induction of gum on the 4th internode can be observed. B) induction of gums on the 4th internode by JA-Me—see Fig. 1A (higher magnification).

Table 2. Effect of JA-Me on stem elongation (mm) induced by IAA in uncooled derooted bulbs of tulips 'Gudoshnik'; treatment with IAA made on January 9 and treatment with JA-Me in the middle of the 4th internode on January 16 when the length of the stem was 34.5 mm.

Treatment	Total length of stem on		Length of internodes on January 30					Total
	Jan. 20	Jan. 25	1st	2nd	3rd	4th		
Control	0	0	0	0	0	0	0	
IAA	62.1a	126.4b	32.6b	29.6b	33.9a	73.6b	169.7b	
IAA + lanolin	66.9a	142.9c	33.4b	32.2b	36.2a	79.3b	181.1b	
IAA + JA-Me	57.9a	103.1a	20.8a	23.3a	32.1a	33.9a*	110.1a	

* Gums were extruded on stem surface on January 23.

inhibition of all internodes was observed, especially in the treated 4th internode with JA-Me. JA-Me also induced strong gummosis in the internode (Tables 1–2, Fig. 1). In case of the cooled derooted bulbs of both cultivars, treated in the same way as uncooled bulbs, JA-Me inhibited only the 4th internode growth induced by IAA and induced gummosis in that internode (Tables 3–4, Fig. 2). It is interesting to know that JA-Me induced gummosis in the stem of uncooled tulip bulbs induced by auxin samely as in the stem promoted by auxin in cooled tulip bulbs. The reason(s) of inhibitory effect of JA-Me on the 4th internode elongation induced by IAA both in uncooled derooted and cooled derooted tulip bulbs has not known yet, but one possibility is that the inhibition was caused by the disturbing the effect of IAA due to gummosis induced by JA-Me. It should be mentioned that in uncooled tulip bulbs after flower bud formation it is impossible to induce gums in tulip scales by JA-Me. In an earlier work, Yamane *et al.* (1981) reported that jasmonic acid (JA) inhibited the elongation of gibberellic acid (GA)-sensitive rice seedling leaf sheaths and lettuce hypocotyls but failed to find an effect on IAA-stimulated *Avena* coleoptile growth. Partial evidence for physiological action of jasmonates was reported in the study on the inhibitory effect of JA on IAA-induced elongation of oat coleoptile segments (Ueda *et al.*, 1994, 1995; Miyamoto *et al.*, 1997). JA does not appear to interact directly with IAA but rather to inhibit some physiological processes required for IAA-induced cell elongation. Some parameters of controlling cell elongation such as oxygen consumption, ATP levels, osmotic properties represented by the amount of osmotica, and mechanical property of cell walls were not affected by the simultaneous application of jasmonates with IAA, but an increase in the amount of the cell wall polysaccharides was largely prevented. Further study using [¹⁴C] glucose showed that JA really interfered with sugar metabolism of cell wall polysaccharides, especially it affected their biosynthesis, and then inhibited IAA-induced elongation of oat coleoptile segments (Ueda *et al.*, 1994, 1995; Miyamoto *et al.*, 1997). Simultaneous application of sucrose, glucose or fructose nullified the inhibition of the growth of oat coleoptile segments induced by JA (Ueda *et al.*, 1995). JA and JA-Me treatments also resulted in an increase in cytosolic pH and inhibited the growth of maize coleoptile segments in the presence or absence of IAA (Irving *et al.*, 1999). The similar explanations will be possible in the case of the inhibition of tulip stem growth induced by the application of JA-Me in IAA-applied internodes.

Moreover, simultaneous application of JA partially inhibited IAA-promoting elon-

Table 3. Effect of JA-Me on stem elongation (mm) induced by IAA in cooled derooted bulbs of tulips 'Apeldoorn'; treatment with IAA made on January 19 and treatment with JA-Me in the middle of the 4th internode on January 25 when the length of the stem was 44.3 mm.

Treatment	Total length of stem on		Length of internodes on February 3				
	Jan. 28	Jan. 31	1st	2nd	3rd	4th	Total
Control	0	0	0	0	0	0	0
IAA	94.4a	170.4a	53.1a	32.2a	38.7a	71.7b	195.8a
IAA+lanolin	91.2a	160.8a	50.2a	30.4a	36.6a	67.4b	184.6a
IAA+JA-Me	93.3a	157.3a	53.2a	33.1a	39.7a	45.6a*	171.6a

* Gums were extruded on stem surface on January 31.

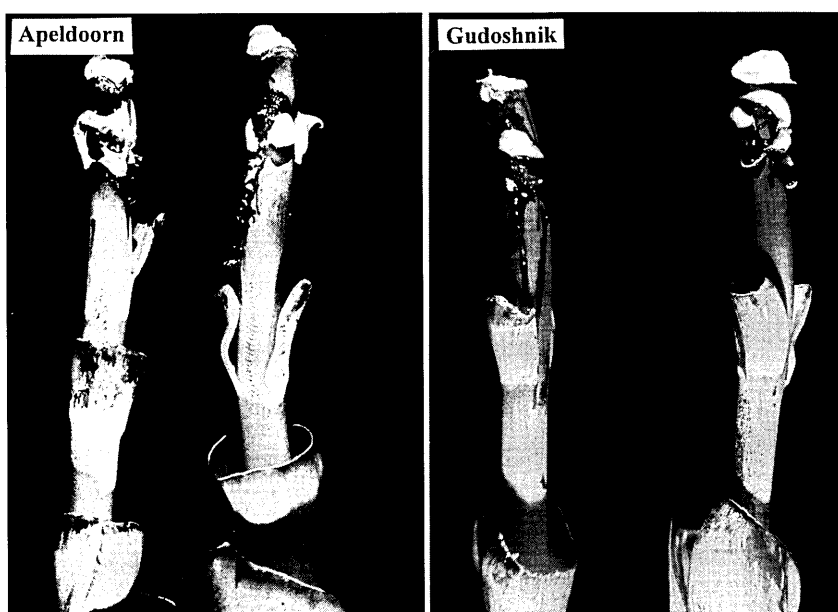


Fig. 2. Induction of gums by JA-Me in 4th internode of stem induced by IAA in cooled derooted tulip bulbs 'Apeldoorn' and 'Gudoshnik'.

gation of the pulvinal tissues of oat stem segments cut from the next-to-last internode of 45-day-old plants (so as to contain the internodal intercalary meristem, the node below it, the encircling leaf sheaths and the leaf sheaths pulvinus) (Montague, 1997). When the segments were pretreated with JA prior to transfer to IAA+JA, however, the stimulatory effect of IAA on pulvinal elongation was completely blocked. JA also inhibited fusicocin-induced elongation of oat pulvinal tissues. On the other hand, JA promoted elongation of oat internodal tissues of the segments, but inhibited GA-induced elongation (Montague, 1997). JA-Me also inhibited elongation and radial growth promoted in petioles of *Ranunculus scleratus* by IAA and ethylene, respectively (Smulders and Horton,

Table 4. Effect of JA-Me on stem elongation (mm) induced by IAA in cooled derooted bulbs of tulips 'Gudoshnik'; treatment with IAA made on January 19 and treatment with JA-Me in the middle of the 4th internode on January 25 when the length of the stem was 39.5 mm.

Treatment	Total length of stem on		Length of internodes on February 3				
	Jan. 28	Jan. 31	1st	2nd	3rd	4th	Total
Control	0	0	0	0	0	0	0
IAA	67.5a	162.0a	60.0a	38.6a	42.4a	73.7b	214.7a
IAA+ lanolin	65.1a	149.0a	57.1a	34.1a	35.1a	57.5b	183.8a
IAA+ JA-Me	78.6a	155.8a	60.9a	41.6a	42.2a	40.1a*	184.8a

* Gums were extruded on stem surface on January 31.

1991). Recently, it was found that IAA stimulated elongation growth of petiole and induced epinasty of intact *Bryophyllum calycinum* plants, and JA-Me greatly inhibited both processes (M. Saniewski and J. Ueda, unpublished results). The outcome of the interactions between JA and other hormones seems to be quite different among plant tissues including tulip stems.

What kind of carbohydrates (precursors) participate in gum formation induced by JA-Me in leaves, stems and bulbs of tulip and biosynthesis pathway(s) of polysaccharides consisting gums induced by JA-Me are unknown. Histological studies of tulip stem in different stages in gum formation induced by JA-Me suggest that the degradation products of cell walls and protoplasts contribute to the gum exudates (Saniewski and Dyki, 1997; Saniewski *et al.*, 1998a).

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