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ORIGINAL RESEARCH PAPER

Effect of benzyladenine (BA) on auxin-induced stem elongation and thickening in tulip (*Tulipa gesneriana* L.)

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Abstract
It is well known that stem elongation in tulip is induced by the auxin produced in the leaves and gynoecium. Excision of the flower bud and all the leaves in an early stage of tulip growth resulted in almost total inhibition of stem growth, but the inhibition was completely recovered by the exogenous application of auxin to the place from which the flower bud had been removed. Hormonal control of stem thickening in tulip is much less known. Additional application of benzyladenine (BA) to the tulip stem by soaking a cotton wick wrapped around all the internodes only slightly inhibited stem growth induced by IAA at a concentration of 0.1 and 2.0%, but substantially stimulated the thickening of all the internodes. The treatment of the tulip stem with benzyladenine enabled direct contact of the cytokinin with the epidermis, which is an important factor in stem elongation. The experiment conducted in field conditions also showed that BA only slightly inhibited the elongation of the fourth internode induced by IAA, but stimulated the thickening of that internode. IAA applied at a concentration of 2.0% stimulated ethylene production to a much higher extent than IAA at a concentration of 0.1%, and BA affected the auxin-induced ethylene production only to a small extent. Metabolic significance of these findings is discussed.

Keywords
cultivars 'Gudoshnik' and 'Apeldoorn'; stem; growth; thickening; IAA; BA

Introduction

During the development of tulip flowers, three phases can be distinguished: the initiation and formation of a new sprout with flower (at high temperature), the internal preparation for stem elongation (at low temperature), and the rapid elongation of the shoot (at high temperature). Tulip bulbs, with terminal buds containing a complete flower, require a period of 12–16 weeks of low temperature treatment for floral stem elongation [1]. In tulips, the elongation growth of the stem and development of the leaves are almost entirely due to the elongation of the cells produced during earlier developmental stages [2]. The leaves and gynoecium provide auxins which control the elongation of the stem in tulip [3–6]. Excision of the flower bud and all the leaves in an early stage of tulip growth results in almost total inhibition of stem growth, and this inhibition is almost completely recovered by the exogenous application of auxin to the place from which the flower bud has been removed [5,6]. It has also been found that auxin induces the growth of stem segments excised from a growing shoot of cooled tulip bulbs and stem segments excised from cooled and uncooled tulip bulbs [7–9]. In addition, elongation of all the internodes in tulips has been reported to be substantially regulated by the interaction of exogenous auxins with gibberellins [10–13].

Hormonal control of stem thickening in tulip is much less known. It has been found that the growth of tulip stem, which is induced by 0.1% indole-3-acetic acid (IAA) after the cut of flower bud and all leaves, was inhibited by ethephon applied to different internodes, and thickening of the internodes was observed [14]. The inhibitor of ethylene action, i.e., silver thiosulphate (STS) [15], completely turned the inhibitory effect of ethephon on IAA-induced elongation of the stem [14].

Saniewski et al. [16] have shown that higher concentrations of auxin, both IAA and NAA, applied to the place of the removed flower bud and after the excision of all the leaves, promoted internodal growth and thickening to a lesser and greater extent, respectively, than low concentrations of auxin and promoted higher production of ethylene. STS has been found to stimulate the growth of all internodes and to decrease their thickening induced by high concentrations of auxin, without or with a small effect on the production of ethylene in the earlier stages of stem elongation.

It is well known that IAA stimulates ethylene production in many plant organs by inducing the synthesis of 1-aminocyclopropane-1-carboxylic acid (ACC) [17]. Tulips treated with benzyladenine (BA) by injection into the flower bud at the beginning of the greenhouse period, or in a lanolin paste at a concentration of 0.2% applied under the flower bud, become thicker in the last internode [18].

In the present study, we report new data on the stimulatory effect of BA on tulip stem thickening when the stem growth was induced by IAA.

Material and methods

Experiment A: effect of BA on the elongation growth and thickening of the stem induced by IAA in the tulip cvultivars 'Gudoshnik' and 'Apeldoorn'

Tulip 'Gudoshnik' bulbs with a circumference of 10–11 cm were, stored at 18–20°C until transferred on October 20 to 5°C for dry cooling. After the cooling period, starting from January 15, the tunics were removed and bulbs were planted in pots and cultivated at 18–20°C in natural light in a greenhouse. When the length of the stem was about 7 cm above the bulb (two weeks after planting), the following treatments were performed with 0.1 and 2.0% IAA in a lanolin paste in the removed flower bud, and all the internodes were wrapped with a cotton wick and then soaked once or twice with BA at 50 mg/L and 100 mg/L. The length and thickening of different internodes during stem growth were measured, and the documentary photography was made.

The same experiment was repeated for 'Apeldoorn' cultivar, but BA, at the same concentrations of 50 and 100 mg/L, was only used to soak the wicks twice.

Experiment B: effect of the interaction between IAA and BA on elongation growth, thickening, and ethylene production in the fourth internode in decapitated tulips grown naturally in the field

Tulip 'Apeldoorn' bulbs with a circumference of 10–11 cm were, after lifting, stored at 19–22°C, and on October 15 planted in a field. When the length of the fourth internode was about 3.40 cm, the flower bud was removed, and lanolin only (control) or IAA at a concentration of 0.1 and 2.0% were applied to the top of the fourth internode. The same internodes, treated with 0.1 and 2.0% IAA, were wrapped with a cotton wick, which was soaked twice with 100 mg/L BA at a 24 h interval. The growth, thickening, and ethylene production in the fourth internode were measured at different times over the duration of the experiment.

During the experiment, ethylene production was measured in about 1 cm long segments of the middle part of the fourth internode. The segments were placed in 10-mL vials, sealed with a septum. After two hours of incubation, 1 cm^3 gas samples were withdrawn from the vials and analyzed by gas chromatography (Hewlett-Packard model 4890D) for ethylene content. Ethylene production was expressed as nL g^{-1} FW h^{-1}.

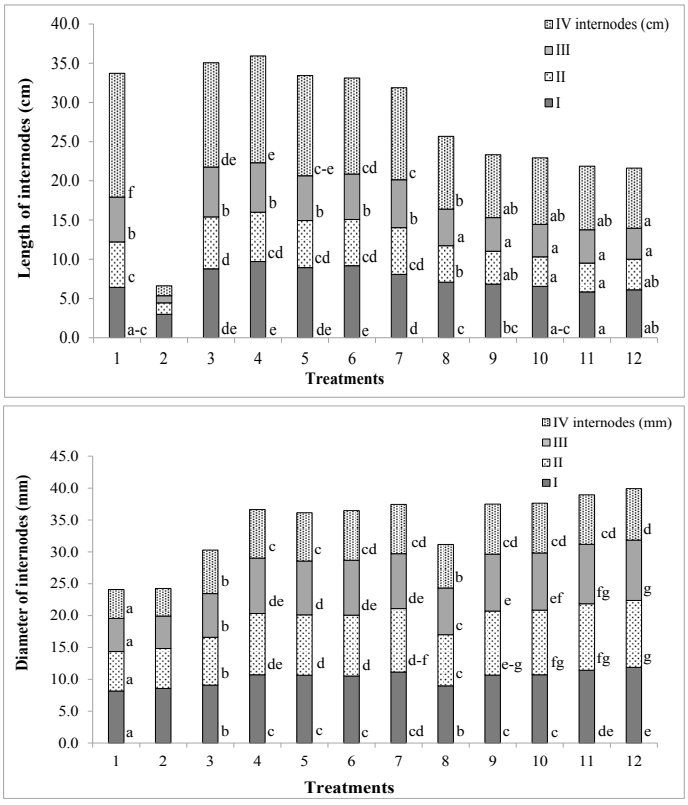
The data were subjected to the analysis of variance and Duncan's test was used to estimate the difference between means, at $p = 0.05$. For each treatment, $n = 7$ plants were used each time for analysis. The results are the mean of two independent replicates.

Results

Excision of the flower bud and all the leaves in an early stage growth of 'Gudoshnik' and 'Apeldoorn' tulip cultivars totally inhibited the stem growth. The application of IAA at concentrations of 0.1 and 2.0%, to the place of the removed flower bud and after the excision of all the leaves, completely recovered inhibition and induced the elongation growth. However, the lower concentration of IAA induced stem growth to a higher degree both in 'Gudoshnik' and 'Apeldoorn' cultivars. The thickening of all the internodes in tulip plants was stimulated by exogenous application of IAA in 0.1 and 2.0%, concentrations (Fig. 1–Fig. 3).

Additional application of BA at a concentration of 50 and 100 mg/L to the tulip stem by soaking, once or twice, cotton wicks wrapped around all the internodes only slightly inhibited the stem growth induced by IAA at a concentration of 0.1% and 2.0%. In contrast, the thickening of all the internodes was substantially stimulated by both concentrations of BA (Fig. 2 and Fig. 3). This kind of treatment of the tulip stem with benzyladenine enabled direct contact between the cytokinin and the epidermis.

The results of the experiment conducted in field conditions also demonstrated that BA slightly inhibited the IAA-induced elongation of the fourth internode of tulip 'Apeldoorn'. On the other hand, the addition of BA together with IAA stimulated the thickening of the fourth internode in field-grown tulips (Tab. 1).



'Gudoshnik'

Treatments

1.Intact plants

All leaves and flower bud were removed.

2. Control (lanolin only)

3. IAA 0.1%

4. IAA 0.1% + BA 50 mg/L cotton wick soaked 1×

5. IAA 0.1% + BA 50 mg/L cotton wick soaked 2×

6. IAA 0.1% + BA 100 mg/L cotton wick soaked 1×

7. IAA 0.1% + BA 100 mg/L cotton wick soaked 2×

8. IAA 2.0%

9. IAA 2.0% + BA 50 mg/L cotton wick soaked 1×

10. IAA 2.0% + BA 50 mg/L cotton wick soaked 2×

11. IAA 2.0% + BA 100 mg/L cotton wick soaked 1×

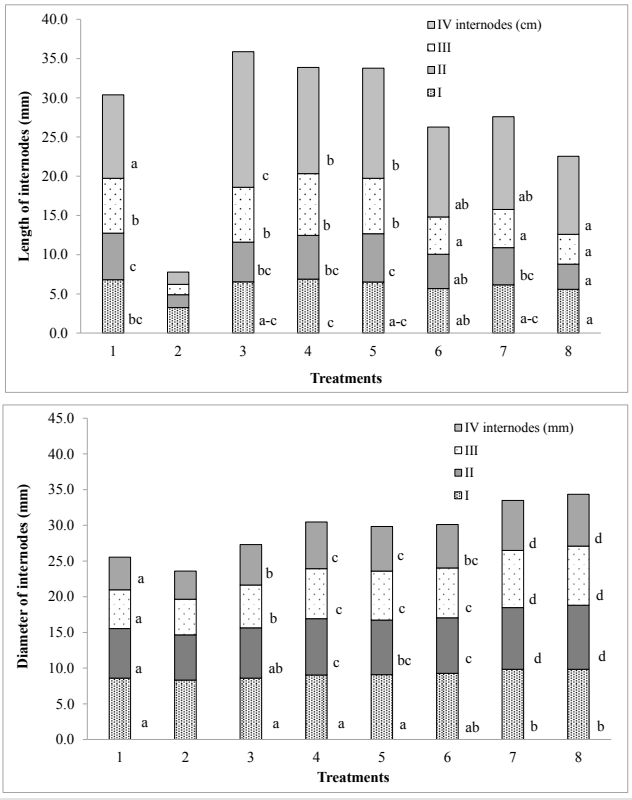
12. IAA 2.0% + BA 100 mg/L cotton wick soaked 2×

Fig. 1 The effects of BA on the elongation growth and thickening of the stem induced by IAA in tulip 'Gudoshnik'; IAA was applied to the place of the removed flower bud, and BA in a soaked cotton wick around the stem, after excision of all the leaves (experiment A). Values are calculated separately for each internodes. Means followed by the same letter are not significantly different at $p = 0.05$ according to Duncan's test.

Treatments

1. Intact plants
2. Control (lanolin only)
3. IAA 0.1%
4. IAA 0.1% + BA 50 mg/L cotton wick soaked 2×
5. IAA 0.1% + BA 100 mg/L cotton wick soaked 2×
6. IAA 2.0%
7. IAA 2.0% + BA 50 mg/L cotton wick soaked 2×
8. IAA 2.0% + BA 100 mg/L cotton wick soaked 2×

Fig. 2 The effect of the interaction between IAA and BA on the elongation and thickening of the stem induced by IAA in tulip 'Apeldoorn'; IAA was applied to the place of the removed flower bud and the internode was wrapped with a cotton wick soaked with BA after excised of all leaves (experiment A). See Fig. 3.



'Apeldoorn'

Treatments

1. Intact plants

All leaves and flower bud were removed

2. Control (lanolin only)
3. IAA 0.1%
4. IAA 0.1% + BA 50 mg/L cotton wick soaked 2×
5. IAA 0.1% + BA 100 mg/L cotton wick soaked 2×
6. IAA 2.0%
7. IAA 2.0% + BA 50 mg/L cotton wick soaked 2×
8. IAA 2.0% + BA 100 mg/L cotton wick soaked 2×

Fig. 3 The effects of BA on the elongation growth and thickening of the stem induced by IAA in tulip 'Apeldoorn'; IAA was applied to the place of the removed flower bud, and BA in a soaked cotton wick around the stem, after excision of all the leaves (experiment A). Values are calculated separately for each internodes. Means followed by the same letter are not significantly different at $p = 0.05$, according to Duncan's test.

Tab. 1 The effect of interaction between IAA and BA on elongation growth, thickening and ethylene production in the fourth internode in decapitated tulips 'Apeldoorn' naturally-grown in the field; the initial length of the fourth internode was about 3.40 cm (experiment B). Means and ±*SD* are given ($n = 7$).

Treatment of 4th internode	Length of 4th internode (cm)		Diameter of 4th internode (mm)						Ethylene production (nL/g × h)	
	after days		after days						after days	
	4	9	7		9				4	9
			center	bottom	center	bottom				
Control	3.41a ±0.47	3.86a ±0.54	6.22a ±0.35	5.82a ±0.49	6.41a ±0.25	5.85a ±0.30			0.42a ±0.13	0.37a ±0.07
IAA 0.1%	6.61c ±1.00	9.54c ±0.56	6.93b ±0.52	6.56b ±0.55	7.24b ±0.32	6.85bc ±0.30			2.26ab ±0.71	5.18b ±1.31
IAA 0.1% + BA 100 mg/L	5.67b ±0.65	7.20b ±1.25	7.24b ±0.52	6.80b ±0.47	7.67bc ±0.54	7.31cd ±0.48			3.43b ±1.18	4.12b ±1.31
IAA 2.0%	6.87c ±0.66	11.20d ±1.31	6.92b ±0.52	6.57b ±0.53	7.23b ±0.47	6.63b ±0.34			13.03c ±1.13	12.31c ±2.81
IAA 2.0% + BA 100 mg/L	6.44bc ±0.73	10.60cd ±1.24	7.33b ±0.39	6.87b ±0.46	8.15c ±0.21	7.69d ±0.38			15.67d ±2.82	12.80c ±2.60

Values are calculated separately for each day. Means followed by the same letter are not significantly different at $p = 0.05$ according to Duncan's test.

Application of IAA to field-grown bulbs of 'Apeldoorn' cultivar induced ethylene production. The stimulating effect of IAA on ethylene production was much greater after adding IAA at a concentration of 2.0% than at a concentration of 0.1% (Tab. 1). The addition of BA affected the auxin-induced ethylene production only to a small degree.

Discussion

The stimulatory effect of IAA on tulip stem growth has been documented well in previous studies [16]. A high concentration of IAA greatly stimulates ethylene production in the tulip stem in comparison with a low concentration of IAA, and ethylene is responsible for the inhibition of tulip stem growth [16]. It is evident that ethylene in conjunction with auxins plays a major role in determining the rate, extent and orientation of cellular growth [19]. Ridge [20] has suggested that the physiological role of ethylene-induced swelling is regulated chiefly by the balance between auxins and ethylene, i.e., swelling occurs as ethylene levels rise and auxin levels fall, although a certain amount of auxins must be present for growth to occur.

The epidermis cell growth and cell division is a necessary factor for the growth of the stem. Auxin-mediated cell elongation is related to changes in the outer epidermal cell wall [21,22]. It has been known that the removal of the epidermis of an internode of a tulip plant inhibited the elongation in that internode [8].

It has been found that gibberellins (GA_3 and GA_{4+7}) applied in a soaked cotton wick wrapped around all the internodes of the tulip stem, after the excision of all the leaves and the flower bud, evidently induced stem elongation [23]. In the present studies, BA applied in a soaked cotton wick around the tulip stem evidently stimulated the thickening of all the internodes when the growth was induced by IAA. Niklas and Paolillo [24] have concluded that in the tulip stem the epidermis acts as a tension-stiffening agent. Katsumi [25] has found that stem sections excised from the third internode of etiolated pea seedlings became relatively thick due to the effect of kinetin, and more so in the presence of IAA, NAA or 2,4-D in the dark. However, all these auxins did not indicate a synergistic effect with kinetin on the thickening of pea stem sections. The effect was additive or less than additive. The thickening effect of kinetin was not observed in sections from the second internode. The thickening effect of kinetin has also been demonstrated with hypocotyls and cotyledons of cucumber seedlings [25].

Hashimoto [26] has reported the effect of kinetin on the primary thickening of light-grown pea stem segments, and the author found a synergistic effect of IAA and kinetin on the primary thickening of pea stem segments. Bartell et al. [27] have documented the fact that ACC and BA treatment synergistically increased the swelling of pea roots caused by auxin, and that auxin and ethylene acted synergistically in the process. Lau and Yang [28] and Lau and Yung [29] have shown that kinetin has a significant synergistic effect on IAA-induced ethylene production in hypocotyl sections of etiolated mungbean (*Phaseolus mungo*) seedlings. The

authors suggest that it is possible that kinetin suppresses the formation of enzymes which catalyze the breakdown of "metabolic intermediates" induced by IAA, or alternatively, kinetin may prevent IAA from forming any inactive complexes.

Vanderhoef et al. [30] and Victor and Vanderhoef [31] have shown that cytokinins – isopentyladenine, kinetin, zeatin, and benzyladenine, inhibited auxin-induced hypocotyl elongation in hypocotyl segments excised from 3-day-old soybean seedlings and promoted radial enlargement. The authors suggest that the cytokinin-induced radial growth may be a secondary effect of cytokinin inhibition of auxin-promoted elongation. The levels of ethylene produced in the presence of auxin plus cytokinins indicated that ethylene was not involved in the auxin–cytokinin interaction in the system [30]. Shibaoka [32] has documented the fact that IAA-induced elongation of light-grown epicotyl segments of azuki bean (*Azukia angularis* = *Vagina angularis*) was inhibited by kinetin, but stem thickening was increased. Electron-microscopic examination revealed that wall microtubules in the cells treated with kinetin together with IAA ran parallel to the cell axis, while wall microtubules in the cells treated with IAA were randomly oriented.

The mechanism of the stimulatory effect of BA on stem thickening in IAA-induced tulip stem growth is as yet unknown, but it seems that ethylene is not involved in the process of thickening.

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Streszczenie

Wpływ benzyloadeniny na wzrost łodygi tulipana (*Tulipa gesneriana* L.) indukowany przez auksynę

Dotychczasowe wyniki wskazują, że po chłodzeniu cebul wzrost pędu jest regulowany przez współdziałanie auksyny (produkowanej w liściach i pąku kwiatowym) i giberelin produkowanych w łodydze. Wysokie stężenie egzogennej auksyny (IAA), podanej po obcięciu wszystkich liści i pąka kwiatowego, powoduje słabszy wzrost wydłużeniowy, zwiększenie grubości łodygi i zwiększoną produkcje etylenu, w przeciwieństwie do niskiego stężenia auksyny.

Obecne badania wykazały stymulujący wpływ benzyloadeniny (BA) na grubość łodygi tulipana indukowanej przez auksynę (IAA) zarówno w niskim jak i wysokim stężeniu. IAA w stężeniu 0.1% i 2.0% w paście lanolinowej nakładano w miejsce usuniętego pąka kwiatowego i po usunięciu wszystkich liści, a benzyloadeninę w stężeniu 50 i 100 mg/L podano w tym samym czasie wokół łodygi poprzez nasączenie ligniny. Ten sposób traktowania zapewnił kontakt komórek epidermy z benzyloadeniną. Epiderma odgrywa ważną rolę we wzroście łodygi, a auksyna jest odpowiedzialna za wydłużanie komórek. Stwierdzono hamujący wpływ benzyloadeniny na wydłużanie łodygi, indukowane przez auksynę. Auksyna stymulowała produkcję etylenu we wszystkich międzywęźlach, ale najbardziej po zastosowaniu wysokiego stężenia IAA, a benzyloadenina w niewielkim stopniu wzmagała produkcję etylenu indukowaną przez auksynę. W pracy dyskutowano możliwy mechanizm stymulującego działania benzyloadeniny na grubość łodygi, a hamującego na wzrost wydłużeniowy (po indukcji przez auksynę).