チューリップ花茎の最上節間の伸長制御要因

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Factors Controlling Elongation of the Last Internode in Tulip Flower Stalk[1]

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Summary

Elongation of the last internode of intact tulips was inhibited by dark or ancymidol treatment. More diffusible auxin was obtained from the last internode of light- than dark- or ancymidol-treated plants. GA_3 application recovered the ancymidol-mediated reduction in elongation and content of diffusible auxin. Decapitation reduced elongation of the last internode. IAA recovered the reduction in elongation, but GA_3 alone did not. The effect of IAA with ancymidol or with dark treatment on elongation of the last internode was less than that of IAA+GA_3. It is suggested that elongation of the last internode is controlled by auxin and gibberellin, as was previously shown with the first internode.

Introduction

Dark treatment during the most active period of shoot growth of tulip induced rapid elongation of the first internode, and this treatment has been shown to be potentially usefull for obtaining taller tulips for commercial cut flower production(12, 13). Okubo and Uemoto(14) showed that the dark-induced elongation of the first internode of tulip is promoted by auxin, and that auxin transport from the upper organs into the first internode is stimulated by the dark-induced increase in free gibberellin. However, elongation of the last internode is markedly inhibited in the dark(12).

It is important to clarify the mechanism controlling elongation of the last internode as well as the first in order to obtain tulips of adequate stem length. Control of elongation of the last internode after harvest must also be considered, because elongation of the last internode causes the stem to bend in the vase. It has been shown that elongation of the last internode of tulip is mainly promoted by auxin(6, 16, 17). However, Okubo and Uemoto(15) showed that two different gibberellins are independently involved in controlling the elongation of the lower and upper internodes. The fact that ancymidol (α-cyclopropyl-α-(*p*-methoxyphenyl)-5-pyrimidine methyl alcohol), an inhibitor of gibberellin biosynthesis(1), reduced the elongation of the last internode(2), as well as the first internode(6, 21), indicates the involvement of gibberellin in controlling elongation of the last internode.

The purpose of the present study was to clarify the factors controlling elongation of the last internode of tulip flower stalk.

Materials and methods

Plant materials and growing conditions

Tulip bulbs (*Tulipa gesneriana* L. cv. Paul Richter) from the 1978 and 1984 harvests, with a circumference of 11-12 cm, were stored at 25°C from their arrival in July until August 31, then at 15°C for 20 days, and finally at 5°C until November 9. On November 10, after removal of the tunics, they were planted in sand in wooden flats (45×22×12 cm) in 1978 or in plastic flats (46×33×10 cm) in 1984. They were grown at 20°C under natural light in the phytotron or in the dark room of the Biotron Institute, Kyushu University.

Experimental treatments

Ancymidol, 25 ppm in aqueous solution, was applied as a 1,000 ml soil drench once per flat on December 11, 1984. In experi-

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ments with intact plants, gibberellin A_3 (GA_3), 1 ml of 400 ppm, was applied to the flower bud of growing tulips in the form of drops on December 14, 1984. Decapitation was performed at the base of the flower bud, at the top end of the last internode, on December 14, 1984, and immediately the cut surfaces received a single application of plain lanolin or lanolin containing 0.1% indole-3-acetic acid (IAA), GA_3 or a combination of these.

Diffusible auxin

Auxin activity was assayed on December 13 or 15, 1984 by the *Avena* curvature test. The last internode of tulips was replaced by blocks of 1.5% aqueous agar, 2×2×2 mm, on the cut end of the flower bud. Diffusible materials were allowed to move from the flower buds into the agar blocks in a moist chamber for 3 hours at 25°C. Seeds of dehusked oat (*Avena sativa* L. cv. Victory) were incubated for 24 hours at 25°C under continuous light. They were then placed in coarse sand in plastic cases and incubated at 25°C in the dark. The top 1 mm of selected straight coleoptiles of uniform height (15-20 mm) was cut off and, 2 hours after the decapitation, the uppermost 5 mm of the remaining coleoptiles was cut off and the primary leaf inside the coleoptile cylinder was pulled upward. Each agar block which received diffusible material was applied to one side of the upper cut surface of the coleoptile. The coleoptiles were then incubated for 1.5 hours at 25°C in the dark, and the curvature of each coleoptile was measured.

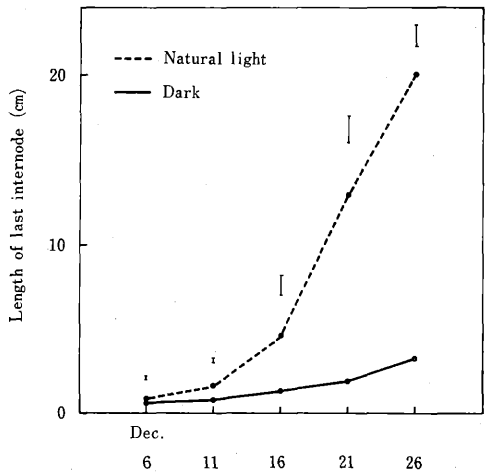

Fig. 1. Effect of light on elongation of the last internode. Vertical bars are LSD's (p=0.05).

Results

The growth curves of the last internode of intact tulips grown under natural light or darkness are presented in Fig. 1. Elongation of the last internode was markedly inhibited under total darkness. However, there was no difference in the appearence of anthocyanin pigments in the perianth and in the size of the flower of light- and dark-grown tulips. Epidermal layers of the last internode in the light and dark are shown in Fig. 2. It appears that the reduction in elongation of the last internode was probably due to a reduction in cell elongation rather than cell division.

Table 1 shows the effect of ancymidol and

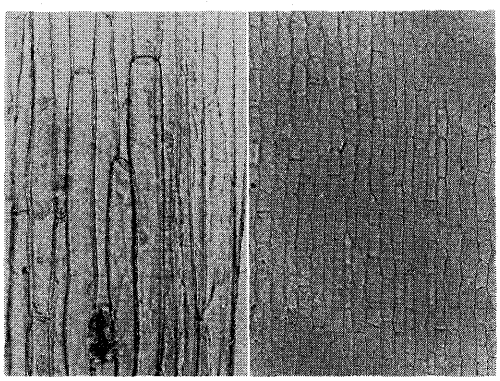

Fig. 2. Longitudinal sections of the epidermis of the last internode. Left ; Natural light, Right ; Dark. Length of the last internode was 14.5 cm in the light and 1.3 cm in the dark.

Table 1. Effects of ancymidol and GA_3 on elongation of the last internode. Length of the last internode was 2.9 cm in the light and 1.2 cm in the dark at the time of ancymidol treatment, and was measured 9 days after ancymidol treatment (7 days after GA_3 treatment).

Treatment	Length of last internode (cm)		LSD (p=0.05)
	Light	Dark	
Control	22.1	3.1	1.55
Ancymidol	11.1	2.3	1.31
Ancymidol+GA_3	21.1	—	—
LSD (p=0.05)	2.31	0.71	

Table 2. Effects of ancymidol and GA_3 on yield of diffusible auxin from the flower bud into the last internode. Diffusible auxin was measured 2 days after ancymidol or GA_3 treatment.

Treatment	Curvature (°)		LSD (p=0.05)
	Light	Dark	
Control	26.6	6.9	7.2
Ancymidol	5.8	1.8	NS
Ancymidol+GA_3	20.0	—	—
LSD (p=0.05)	6.69	NS	

Table 3. Effects of decapitation and application of growth regulators on elongation of the last internode in the light. Length of the last internode was 3.5 cm at the time of ancymidol treatment, and was measured 9 days after ancymidol treatment (7 days after hormone treatment).

Treatment	Length of last internode (cm)		LSD (p=0.05)
	−Ancymidol	+Ancymidol	
Control	4.7	3.7	0.54
GA_3	6.9	3.9	0.60
IAA	17.1	5.0	0.54
GA_3+IAA	17.1	11.8	0.66
LSD(p=0.05)	0.64	0.67	

GA_3 treatments on elongation of the last internode of intact plants. Since in the dark all leaves remained folded until flowering, GA_3 application in the form of drops to the flower bud of the dark-grown tulips was impossible without surgical treatment. Ancymidol reduced the elongation of the last internode by 50% in the light, but when followed by GA_3 treatment, the ancymidol-mediated reduction in elongation was recovered to the level in the controls. Ancymidol was also effective in reducing elongation of the last internode in the dark. As shown in Table 2, without ancymidol the content of diffusible auxin in the last internode due to transport from the flower bud was much higher in the light than in the dark. There was a large reduction in diffusible auxin content in the ancymidol-treated last internode both in the light and the dark. In the light, the reduction in diffusible auxin content due to ancymidol application was recovered by GA_3 treatment.

Effects of decapitation and application of growth regulators on elongation of the last internode are shown in Table 3. Comparison of data from Tables 1 and 3 shows that decapitation reduced the length of the last internode considerably, and that there was norecovery of elongation with application of GA_3, with or without ancymidol treatment. IAA alone gave a large growth response, but its effect was reduced by ancymidol treatment Application of IAA with GA_3 caused elongation of the last internode, with or without ancymidol treatment. Without ancymidol there was no significant difference between the effects of IAA alone and IAA+GA_3 on the length of the last internode, but with ancymidol, the effect of IAA alone was much smaller than that of IAA+GA_3.

Table 4. Effects of decapitation and application of growth regulators on elongation of the last internode in the dark. Length of the last internode was 1.2 cm at the time of ancymidol treatment, and was measured 9 days after ancymidol treatment (7 days after hormone treatment).

Treatment	Length of last internode (cm)		LSD (p=0.05)
	−Ancymidol	+Ancymidol	
Control	2.1	1.9	NS
GA_3	2.2	2.4	NS
IAA	12.5	7.4	2.04
GA_3+IAA	16.5	11.6	2.25
LSD(p=0.05)	1.40	1.34	

A similar experiment was carried out with tulips grown under total darkness, which reduces elongation of the last internode even without ancymidol treatment. As shown in Table 4, results were similar to those of experiments carried out in the light (Table 3). IAA alone also caused elongation of the last internode, but when combined with ancymidol, the effect was small. Elongation was greater in plants treated with IAA+GA_3 than with IAA alone, both with and without ancymidol treatment.

Discussion

Light seems to be required for sufficient elongation of the last internode, but not for flowering and full coloration of the perianth. Reduction in length of the last internode in the dark seems to be due to a reduction in cell length.

Shoub and De Hertogh(21) showed that

ancymidol was most effective in reducing the length of the first internode, but in our experiments, ancymidol was equally effective in reducing elongation of the last internode. Einert(2) also showed that ancymidol was effective in controlling elongation of the last internode. Since elongation of flower stalk in tulip begins in the first internode and progresses in acropetal order, whether or not lower or upper internodes respond to ancymidol may depend on the time of application. Shoub and De Hertogh(21) showed that GA_{4+7} completely reversed the effect of ancymidol, but that GA_3 was ineffective. However, in our experiments, the ancymidol-mediated reduction in elongation of the last internode was recovered by GA_3 treatment to the level of the controls. Reduction in elongation of the first internode by ancymidol was also recovered by an application of GA_3(14).

The amount of auxin in the last internode of light-grown tulips which was transported from the flower bud was reduced by ancymidol, and was recovered by GA_3, as with the first internode(14). In non-ancymidol treated plants, more diffusible auxin was obtained from light- than dark-grown last internode. This is in accordance with results of Guttenberg and Zetsche(3) and Scott and Briggs (19), and may indicate the involvement of auxin in controlling elongation of the last internode.

Elongation of the upper internodes in tulip is more dependent on an auxin- rather than a gibberellin-mediated system(6, 16, 17). However, Okubo and Uemoto(15) showed that the amount of non-polar, free gibberellin activity detected in the upper internodes, which has a specific relationship with elongation of the last internode, was higher in the light than in the dark and they suggested that elongation of the last internode, as well as that of the first, is controlled by gibberellin.

Decapitation reduced elongation of the last internode, and in this case a very small promotion of elongation of the last internode by GA_3 was only observed in the light without ancymidol. IAA alone restored elongation in decapitated tulips in the light without ancymidol. These findings are in agreement with those of Op den Kelder *et al.* (16), Hanks and Rees(6) and Saniewski and De Munk(17). However, the effect of IAA in the light with ancymidol, or in the dark either with or without ancymidol, was smaller than its effect in the light without ancymidol. Ancymidol inhibits gibberellin biosynthesis (1). Endogenous gibberellin activity in the last internode is lower in the dark than in the light(15). When endogenous gibberellin activity in the last internode was reduced by ancymidol or dark treatment, the effect of IAA alone on elongation of the last internode was smaller, buta an pplication of IAA together with GA_3 caused the greatest stimulation of elongation. This may indicate that GA_3 applied exogenously supplies the low level of gibberellins in the last internode needed for normal elongation in the presence of auxin, but that exogenous administration of GA_3 is not needed when plants are grown in the light without ancymidol.

From these results, it is conceivable that elongation of the last internode is under direct control of auxin, but that the content of auxin which is transported from the flower bud into the last internode is controlled by gibberellin. There is evidence that gibberellin increases diffusible auxin in some plants (10, 11, 22). There is also a possibility that gibberellin increases auxin levels by enhancement of auxin biosynthesis in the last internode or that gibberellin sensitizes cells of the last internode to the influence of auxin, as reported by Katsumi and Kazama(9), Jindal and Hemberg(8) and Sastry and Muir(18). In either case, it is possible that elongation of the last internode is controlled by both gibberellin and auxin, as was shown to be the case with the first internode(14).

The main pigments of the flowers of red cultivars of tulips are pelargonidin, cyanidin and delphinidin 3-glucosides and 3-rhamnoglucosides(4, 5, 20). It is well known that light is necessary for the full development of anthocyanin color in most garden flowers(7). It should be noted that, in tulip, full development of flower color was observed in plants grown in the dark.

Literature cited

1. COOLBAUGH, R. C. and R. HAMILTON. 1976. Inhibition of *ent*-kaurene oxidation and growth by α-cyclopropyl-α-(*p*-methoxyphenyl)-5-pyrimidine methyl alcohol. Plant Physiol. 57 : 245—248.
2. EINERT, A. E. 1971. Reduction in the last internode elongation of cut tulips by growth retardants. HortScience 6 : 459—460.
3. GUTTENBERG, H. V. und K. ZETSCHE. 1956. Der Einfluss des Lichtes auf die Auxinbildung und den Auxintransport. Planta 48 : 99—134.
4. HALEVY, A. H. 1962. Anthocyanins in petals of tulip var. President Eisenhower. Biochem. J. 83 : 637—639.
5. HALEVY, A. H. and S. ASEN. 1959. Identification of the anthocyanins in petals of tulip varieties Smiling Queen and Pride of Haarlem. Plant Physiol. 34 : 494—499.
6. HANKS, G. R. and A. R. REES. 1977. Stem elongation in tulip and narcissus : The influence of floral organs and growth regulators. New Phytol. 78 : 579—591.
7. HARBORNE, J. B. 1967. Comparative biochemistry of the flavonoids. p. 273—275. Academic Press, London.
8. JINDAL, K. K. and T. HEMBERG. 1976. Influence of gibberellic acid on growth and endogenous auxin levels in epicotyl and hypocotyl tissues of normal and dwarf bean plants. Physiol. Plant. 38 : 78—82.
9. KATSUMI, M. and H. KAZAMA. 1978. Gibberellin control of cell elongation in cucumber hypocotyl sections. Bot. Mag. Tokyo Special Issue 1 : 141—158.
10. KURAISHI, S. and R. M. MUIR. 1962. Increase in diffusible auxin after treatment with gibberellin. Science 137 : 760—761.
11. KURAISHI, S. and R. M. MUIR. 1964. The relationship of gibberellin and auxin in plant growth. Plant & Cell Physiol. 5 : 61—69.
12. OKUBO, H. and S. UEMOTO. 1984. Effect of darkness on stem elongation in tulip. Scientia Hortic. 23 : 391—397.
13. OKUBO, H. and S. UEMOTO. 1984. The application of dark treatment for cut-tulip production. Scientia Hortic. 24 : 75—81.
14. OKUBO, H. and S. UEMOTO. 1985. Changes in endogenous gibberellin and auxin activities during first internode elongation in tulip flower stalk. Plant & Cell Physiol. 26 : 709—719.
15. OKUBO, H. and S. UEMOTO. 1986. Changes in endogenous gibberellins during internode elongation of tulip flower stalk as affected by light conditions. J. Japan. Soc. Hort. Sci. 55 : 215—220.
16. OP DEN KELDER, P., M. BENSCHOP and A. A. DE HERTOGH. 1971. Factors affecting floral stalk elongation of flowering tulips. J. Amer. Soc. Hort. Sci. 96 : 603—605.
17. SANIEWSKI, M. and W. J. DE MUNK. 1981. Hormonal control of shoot elongation in tulips. Scientia Hortic. 15 : 363—372.
18. SASTRY, K. S. K. and R. M. MUIR. 1965. Effects of gibberellic acid on utilization of auxin precursors by apical segments of the avena coleoptile. Plant Physiol. 40 : 294—298.
19. SCOTT, T. K. and W. R. BRIGGS. 1960. Auxin relationship in the Alaska pea (*Pisum sativum*). Amer. J. Bot. 47 : 492—499.
20. SHIBATA, M. and N. ISHIKURA. 1960. Paper chromatographic survey of anthocyanin in tulip-flower, I. Jap. Jour. Bot. 17 : 230—238.
21. SHOUB, J. and A. A. DE HERTOGH. 1974. Effect of ancymidol and gibberellin A_3 and A_{4+7} on *Tulipa gesneriana* L. cv. Paul Richter during development in the greenhouse. Scientia Hortic. 2 : 55—67.
22. SKYTT ANDERSEN, A. and R. M. MUIR. 1969. Gibberellin induced changes in diffusible auxin from savoy cabbage. Physiol. Plant. 23 : 354—363.

チューリップ花茎の最上節間の伸長制御要因

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摘 要

暗黒処理もしくはアンシミドール処理によりチューリップ花茎の最上節間の伸長は抑えられ，花蕾から最上節間への拡散性オーキシン量も減少した．GA_3処理は暗黒及びアンシミドール処理による最上節間の伸長抑制並びに拡散性オーキシンの減少を回復した．花蕾の切除もまた最上節間の伸長を抑制した．IAA は切除処理による伸長抑制を回復したが GA_3 は効果がなかった．あらかじめ暗黒処理もしくはアンシミドール処理をしておくと，花蕾切除後の IAA 処理による伸長回復効果は認められなかったが，IAA＋GA_3処理により効果が認められた．以上のことから，最上節間の伸長もまた，最下節間の場合と同様，ジベレリン及びオーキシンの双方によって制御されていることが示唆された．