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Evidence for a Role of Auxin in the Stem Elongation of Dark-grown Tulips

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ABSTRACT

Shoot growth of fully cooled tulip bulbs cvs. 'Gudoshnik' and 'Apeldoorn' grown in continuous dark conditions was investigated in relation to the role of exogenously applied auxin. Continuous darkness caused much more stem elongation than natural light conditions in the greenhouse. In both cultivars, all internodes were longer in the dark than those in the light. Auxin (indole-3-acetic acid, IAA, applied in the place of a removed flower bud on a stem with no leaves) greatly stimulated the growth of all internodes in the dark in comparison to that in the light whereas almost no growth in all internodes was observed in the absence of exogenously applied auxin both in the dark and in the light. These results confirm that auxin is a major factor responsible for growth of all internodes in etiolated tulip stems. The hormonal control and its metabolic significance during the etiolation of tulips are discussed.

Keywords: IAA, indole-3-acetic acid, Darwin hybrid tulips (*Tulipa gesneriana* × *T. fosteriana*), shoot growth
Abbreviations: IAA, indole-3-acetic acid; **NAA**, naphthalene-3-acetic acid; **morphactin IT 3456**, 2-chloro-9-hydroxyfluorene- 9-carboxylic acid; **NPA**, *N*-(1-naphthyl)phthalamic acid; **TIBA**, 2,3,5-triiodobenzoic acid

INTRODUCTION

Tulip bulbs, with terminal buds containing a complete flower, require a period of 12-16 weeks of low temperature treatment for floral stalk elongation (De Hertogh 1974). In tulips, the elongation growth of stem and development of the leaves are almost entirely due to elongation of cells produced during earlier developmental stages (Gilford and Rees 1973). Auxins are well known to play an important role in the growth and development of tulips. Flower bud, mostly gynoecium, and leaves in tulips have been suggested to provide auxins for inducing stem growth (Op den Kelder *et al*. 1971; Hanks and Rees 1977; Saniewski and de Munk 1981). Excision of all leaves and the flower bud in the early growth stage of tulips results in almost complete inhibition of stem growth. Excision of the flower bud alone (leaves intact) has an inhibitory effect only on the elongation growth of the top internode; conversely, the lower internodes are normal just like in intact plants (Saniewski and de Munk 1981).

Application of IAA in lanolin paste to the cut surface of the top internode of tulip shoots excised from cooled bulbs and/or from growing shoots in cooled bulbs dramatically promotes growth of all internodes (Saniewski *et al*. 2005, 2007). Inhibition of tulip stem growth after excision of all leaves and flower bud was fully reversed after application of auxin at the cut surface of top internode (Op den Kelder *et al*. 1971; Hanks and Rees 1977; Saniewski and de Munk 1981; Banasik and Saniewski 1985; Okubo and Uemoto 1985; Okubo *et al*. 1986). In addition, elongation of all the internodes in tulips has been reported to be substantially regulated by the interaction of exogenous auxins with gibberellins (Okubo and Uemoto 1985; Okubo *et al*. 1986; Saniewski 1989; Saniewski and Kawa-Miszczak 1992; Rietveld *et al*. 2000).

Total darkness (etiolation) enhances shoot growth in many plant species (Kutschera 1992; Miyamoto *et al*. 1992). On the other hand, Okubo and Uemoto (1984a) have shown that final shoot length in tulips (cv. 'Paul Richter') grown in the dark was almost the same as when grown in the light. Dark-grown 'Paul Richter' elongated much earlier than the light-grown plants. The first internode was the longest and the growth of the last internode was much inhibited by the dark treatment, whereas natural light resulted in a long last internode. The elongation of the first internode in the dark was probably due to cell elongation rather than cell division (Okubo and Uemoto 1984a). In addition, the flowering of the plants was much retarded in the dark (Okubo and Uemoto 1984a). Okubo and Uemoto (1984b) concluded that this technique of the dark treatment could be useful for commercial forcing of various cultivars of cut tulips. These facts suggest that response of plants to darkness is different among not only plant species but also tissues and organs in plants.

Okubo and Uemoto (1985) also found that 2,3,5-triiodobenzoic acid (TIBA), an inhibitor of polar auxin transport, inhibited dark-induced elongation of the first internode. In further studies in natural light conditions, inhibitors of polar auxin transport (NPA, TIBA and morphactin) inhibit tulip stem growth induced by natural and synthetic auxins (IAA and NAA, respectively), when these auxins were applied in the place of a removed flower bud and after excision of all leaves (Saniewski and Okubo 1988a, 1988b; Saniewski *et al*. 1999). These data also confirmed a crucial role of auxin in tulip stem growth. On the other hand, Okubo *et al*. (1986) reported that elongation of the last internode of tulips (cv. 'Paul Richter') was markedly inhibited under total darkness, but the content of diffusible auxin in the last internode was much lower in the dark than in the light. The relationships between tulip stem growth in the dark and auxin seem to be still unknown.

As described above, the complete mechanism of hor-

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monal control of shoot elongation in tulips grown in darkness is not yet clear. To clarify growth and development of intact tulips grown in the dark as compared to that in the light is very important. In this study, we investigated the effects of auxin applied just after removal of a flower bud and all leaves on tulip stem growth in continuous dark conditions. Inhibitors of polar auxin transport were also introduced for better understanding the role of auxin in growth of tulip stem in darkness.

MATERIALS AND METHODS

Tulip bulbs (cvs. 'Gudoshnik' and 'Apeldoorn') with a circumference of 10-11 cm after lifting were stored at 18-20°C until October 15, and then were dry-cooled at 5°C until planting in February. Before planting, dry scales were removed and the bulbs were planted individually in pots. They were then grown at 18-20°C in natural light conditions in greenhouse or in continuous darkness. The length of internodes and leaves, and their fresh and dry weight were measured during full flowering or a few days after flowering (extension growth was completed). Twenty bulbs were used in each treatment.

Another experiment with cv. 'Apeldoorn' growing in natural light conditions in greenhouse and in continuous darkness was made. When the stem length was about 3 cm, the flower bud and all leaves were removed, and in the place of flower bud, IAA at a concentration 0.1% (w/w in lanolin) was applied. As a control, lanolin paste only was applied. During the experiment, length of different internodes was measured several times, and final length of stem was determined by taking photographs. Eight plants were used in each treatment.

In the third experiment fully cooled tulip bulbs cv. 'Apeldoorn' were planted on January 25 in pots in a room with continuous darkness. When the stem was about 8 cm (February 2), the flower bud and all leaves were removed and IAA at 0.1% (w/w in lanolin) was applied in the place of a removed flower bud. Then lanolin only (control) or NPA, TIBA and morphactin IT 3456 at a concentration of 0.2% (w/w in lanolin) were applied on the middle of 4th (uppermost) internode. Internode length was measured on February 20 and photographed. Four plants were used in each treatment.

Results were expressed as the average values of 20 tulip bulbs. When obvious and/or visual significance were recognized, only the average values were described. In other cases, Duncan's multiple range test was used to determine the significance of difference.

RESULTS AND DISCUSSION

Shoot growth of both cultivars was greatly stimulated in continuous dark conditions in comparison to that in natural light (**Figs. 1, 5**). The flowering was retarded a few days in the dark, but a normally colored perianth developed, similar to light-grown plants. As already reported (Okubo and Uemoto 1984b; Okubo *et al*. 1986), light was not necessary for formation of anthocyanin in perianth of tulips. All internodes were longer in the dark in both cultivars, especially in 'Apeldoorn' (**Figs. 2, 6**). The fresh weight of internodes of cv. 'Gudoshnik' (not measured in cv. 'Apeldoorn') grown in the dark was higher than when grown in the light (**Fig. 2**). Dark-grown leaves were much longer and narrower (**Figs. 3, 7**), but fresh weight of these leaves in cv. 'Gudoshnik' (not measured in cv. 'Apeldoorn') did not differ from those grown in the light (**Fig. 3**). Dry weight of internodes and leaves of tulips grown in the dark was almost the same as those grown in the light (**Fig. 4**). Leaves that sprouted from daughter bulbs were also much longer in the dark (**Fig. 8**), it being very unique. It is an important observation that elongation growth of all internodes was greatly stimulated in both cultivars growing in the dark in comparison to that in the light, mostly in the case of cv. 'Apeldoorn'.

As shown in **Fig. 9**, IAA applied in the place of a removed flower bud and after excision of all leaves greatly stimulated the growth of all internodes in the dark as well as in the light. The dynamics of the growth of all internodes is shown in **Fig. 10**. These results together with the fact that

Fig. 1 The effect of natural light conditions in greehouses (left) and in continuous dark conditions (right) on shoot growth of tulips (cv. 'Gudoshnik'). Fully cooled bulbs were planted on February 27 and grown at about 20°C. Photograph was taken on March 21.

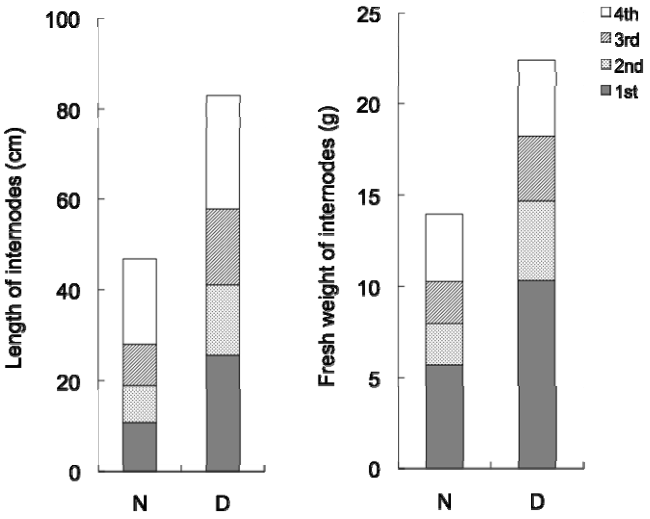

Fig. 2 Length and fresh weight of tulip internodes in fully cooled bulbs cv. 'Gudoshnik' grown in natural light in greenhouse (N) or continuous dark conditions (D) at about 20°C. Bulbs were planted on February 27. Measurements were made on March 21 at the stage of full flowering. Results were expressed as the average values of 20 tulip bulbs.

exogenously applied auxin induced growth of tulip stem in natural light conditions (Saniewski 1989) suggest that auxin induces cell elongation of tulip internodes not only in the light but also in the dark. Polar transported auxin is very important in stem growth of tulips as suggested by Kramer and Bennett (2006), Vieten *et al*. (2007) and, Roberts and Friml (2009). This observation was confirmed by the results described in **Table 1**. NPA, TIBA and morphactin IT 3456 applied in the middle of 4th internode substantially inhibited stem growth in darkness induced by IAA applied in the place of a removal flower bud and after removal of all leaves; lowest inhibitory effect was caused by NPA, and strongest by morphactin IT 3456 (**Table 1**). Judging from the data presented here, growth processes in intact tulips grown in continuous dark conditions seem to mimic the

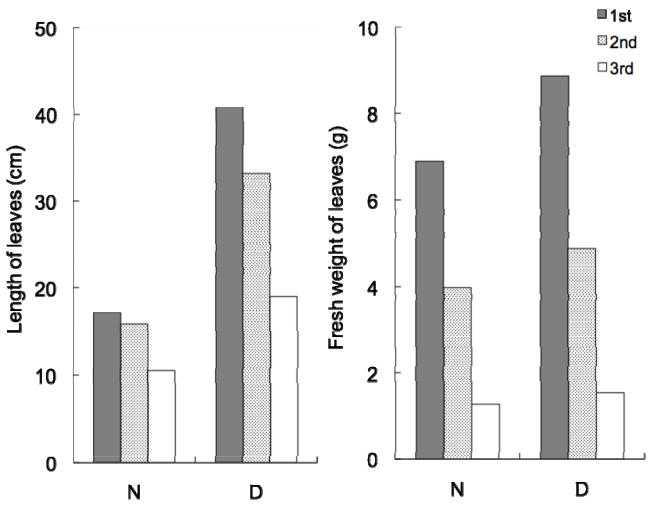

Fig. 3 Length and fresh weight of tulip leaves of fully cooled bulbs cv. 'Gudoshnik' grown in natural light conditions in greenhouse (N) or in continuous dark conditions (D) at about 20°C. Bulbs were planted on February 27. Measurements were made on March 21 in the stage of full flowering. Results were expressed as the average values of 20 tulip bulbs.

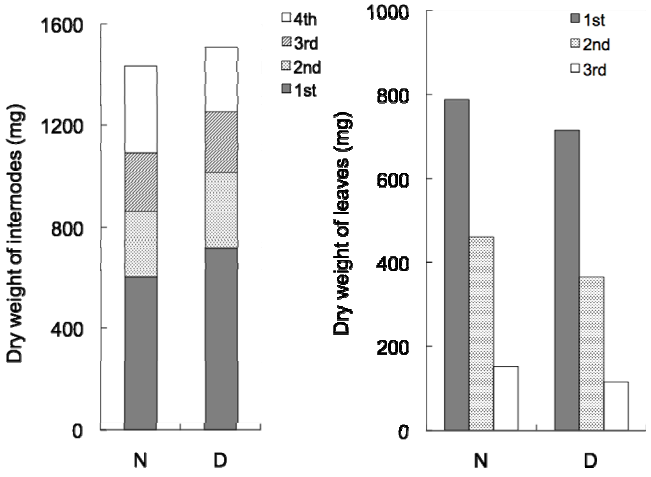

Fig. 4 Internode and leaf dry weight from fully cooled tulip cv. 'Gudoshnik' grown in natural light conditions in greenhouse (N) or in continuous dark conditions (D) at about 20°C. Bulbs were planted on February 27. Measurements were made on March 21 in the stage of full flowering. Results were expressed as the average values of 20 tulip bulbs.

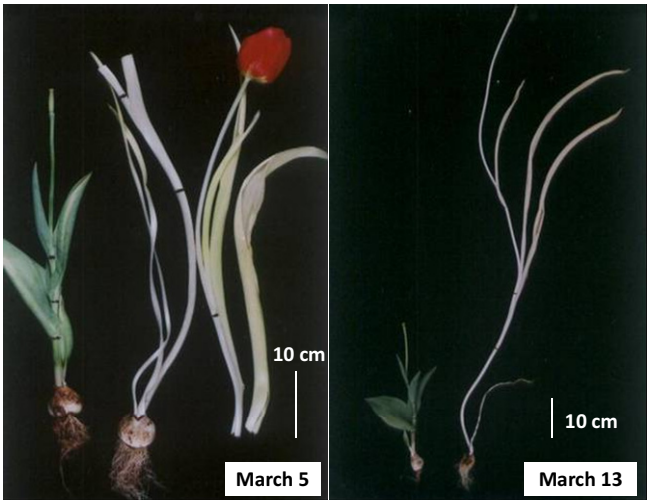

Fig. 5 Appearance of 'Apeldoorn' tulips grown in natural light conditions in the greenhouse (left) or in complete darkness (right) at about 20°C. Fully cooled bulbs were planted on February 6 and grown at about 20°C. Photographs were made on March 5 (left picture) and 13 (right picture), respectively.

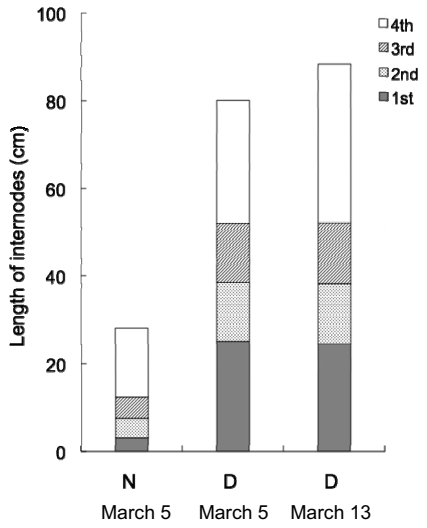

Fig. 6 Internode length of fully cooled cv. 'Apeldoorn' grown in natural light conditions in greenhouse (N) and in continuous dark conditions (D) at about 20°C. Bulbs were planted on February 6. Measurements were made on March 5 and 13. Results were expressed as the average values of 20 tulip bulbs.

tulip growth induced by the application of auxin in the place of a removed flower bud and after excision of all leaves in the dark. In addition, basipetal auxin transport also seems to take place in tulip stem even in continuous dark conditions.

As described above, tulip stem growth was extremely promoted in continuous dark conditions, it being explained by the role of endogenous auxin and its polar transport affecting the mechanical properties of the cell wall. Etiolation is well known to be connected with higher elongation of cells, and the process is affected by the cell wall mechanical properties including cell wall extensibility and cell wall accumulation (Miyamoto *et al.* 1992; Kutschera 1992). Auxin moves between plant cells through a combination of diffusion and carrier-mediated transport. Different internal and external signals have been shown to modulate both auxin biosynthesis and polar auxin transport (Kramer and Bennett 2006; Roberts and Friml 2009). Many theories concern the mechanism of cellular and molecular aspects of auxin transport and its regulation in plants (Zazimalova and Napier 2003; Kramer and Bennett 2006; Vieten *et al*. 2007; Kuppusamy *et al*. 2009; Roberts and Friml 2009). Endogenous auxin (IAA) has been reported to be transported basipetally from cell to cell in shoots towards the roots in a process referred to as polar auxin transport. It is generally accepted that polar auxin transport is involved in the growth of seedlings growing in the light and inhibitors of polar auxin transport (NPA, TIBA) inhibit IAA transport (Haga and Iino 1998). There are some papers reporting basipetal transport of auxin in etiolated plant tissues such as lupin hypocotyls and epidermal cells of maize shoots. In these cases, NPA and/or TIBA were effective to inhibit basipetal auxin transport (Jones 1990; Botía *et al*. 1992; López-Nicolás *et al*. 2004).

Polar auxin transport in plant tissues grown in the dark seems to be complicated. In dark-grown *Arabidopsis*, auxin transport is not required for hypocotyl elongation (Jensen *et al*. 1998). Negligible inhibition of hypocotyl elongation with concentrations up to 5.0 μM NPA in dark-grown seedlings was observed. On the other hand, hypocotyl elongation in light-grown seedlings was strongly inhibited by approximately 0.5 μM NPA. Finally, Jensen *et al.* (1998) suggest that basipetal auxin transport is not important for

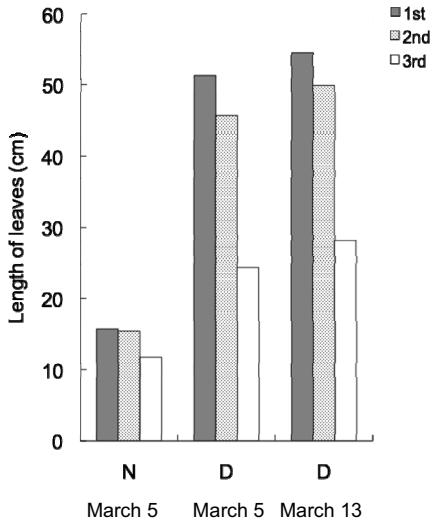

Fig. 7 Leaf length fully cooled cv. 'Apeldoorn' grown in natural light conditions in greenhouse (N) and in continuous dark conditions (D) at about 20°C. Bulbs were planted on February 6. Measurements were made on March 5 and 13. Results were expressed as the average values of 20 tulip bulbs.

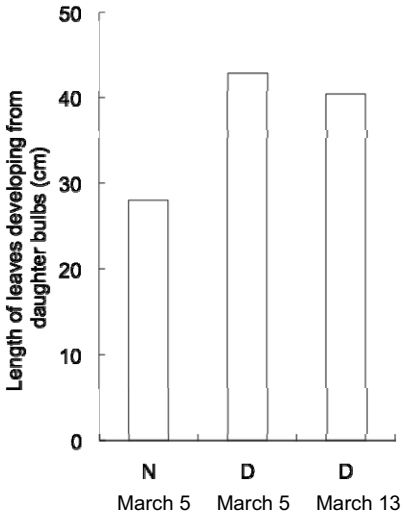

Fig. 8 The length of leaves developing from daughter bulbs in fully cooled bulbs cv. 'Apeldoorn' grown in natural light conditions in greenhouse (N) and in continuous dark conditions (D). Bulbs were planted on February 6. Measurements were made on March 5 and 13. Results were expressed as the average values of 20 tulip bulbs.

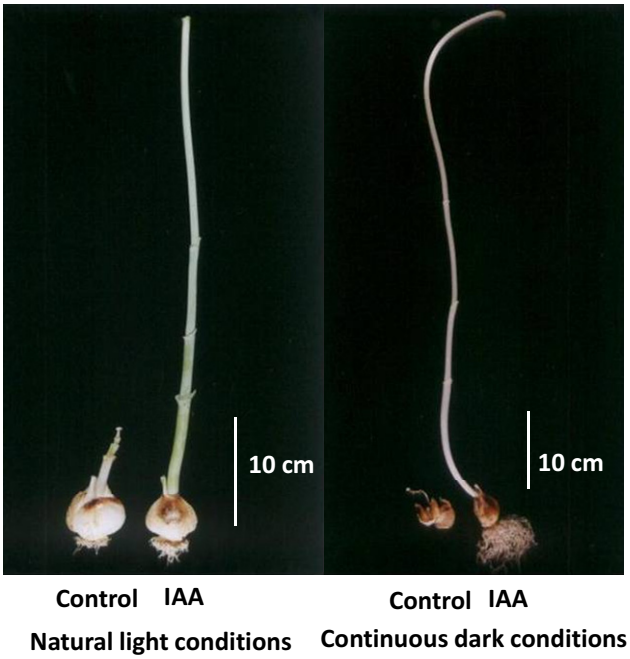

Fig. 9 The effect of 0.1% IAA applied in the place of a removed flower bud and after excision of all leaves on the stem growth of tulips (cv. 'Apeldoorn') grown in natural light conditions in greenhouse (left) and in continuous dark conditions (right). Fully cooled bulbs were planted on February 2 and grown at about 20°C. Photograph was taken on March 1. Right picture is lower magnification than left picture.

Table 1 The effects of NPA, TIBA and morphactin IT 3456 on tulip stem growth.

Treatments	Length of internodes (mm)				Total length
	1st	2nd	3rd	4th	(mm)
IAA	163 c	96 b	121 c	307 c	687 d
IAA + NPA	126 b	72 b	81 b	259 bc	538 c
IAA + TIBA	56 a	34 a	34 a	214 b	338 b
IAA + morphactin IT 3456	35 a	10 a	5 a	158 a	208 a

After excision of all leaves, NPA, TIBA and morphactin IT 3456 (0.2%) were applied on the middle of the 4th internode on tulip stem grown in continuous dark conditions in the presence of IAA (0.1%) in the place of a removed flower bud. Initial length of stem was about 80 mm on February 2 and length of internode was measured on February 20. Duncan's multiple range test was used to determine significant differences between means ($P = 0.05$). n = 4

hypocotyl elongation in dark-grown seedlings. This implies either that auxin is synthesized in elongating tissue and does not need to be transported, or that auxin is not important for elongation during skotomorphogenesis. Polar auxin transport in cucumber hypocotyls grown for 4 days in red light showed as much as 3-fold higher than in dark controls (Shinkle 1996). NPA and TIBA at the concentration of 3×10^{-6} M substantially caused an 80% inhibition of auxin transport in the hypocotyl of dark-grown cucumber seedlings. In red-light-grown cucumber seedlings, NPA causes 80% inhibition of auxin transport, while TIBA causes 60% inhibition (Shinkle 1996).

Gibberellins are another important factor inducing tulip stem growth. The elongation of internodes in tulips grown in natural light conditions is controlled by auxin and gibberellins (Saniewski 1989; Saniewski *et al*. 2000). While endogenous levels of gibberellins might not be a suitable indicator for properly cold-treated tulip bulbs (Rebers et al. 1996), Hanks and Rees (1980) have substantially found two peaks of activity of gibberellins-like substances in tulips sampled at intervals from October (planting time) until the following April (flowering time). The first peak occurred in December samples or in early-January ones, before the cold requirement was completed, and the second peak occurred around the time of rapid shoot extension and flowering found in roots, scales, leaves, stem, daughter bulbs and flowers. Saniewski (1989) also suggested that together with auxin, a pool of gibberellins synthesized during shoot growth contributes to tulip stem elongation as well.

Tulip shoot growth in the dark has also shown to be regulated not only by auxin but also by gibberellins. Okubo and Uemoto (1985, 1986) showed that endogenous free-form gibberellin and diffusible auxin in the first internode of tulip shoot increased while bound-form gibberellin decreased after the dark treatment. The rapid first internode elongation caused by the dark treatment was quickly suppressed whenever the dark treatment was stopped but restored when it was resumed (Okubo and Uemoto 1985). The activity of free-form gibberellin and diffusible auxin increased while the plants were kept in the dark but decreased in the light (Okubo and Uemoto 1985). Elongation of the last internode of non-cold-treated tulips was more promoted than that of the first internode in the dark (Okubo and Uemoto 1990). Partial substitution for cold requirement by dark, and promotive effect of dark on the elongation of the last internode, may be explained by increased level of endo-

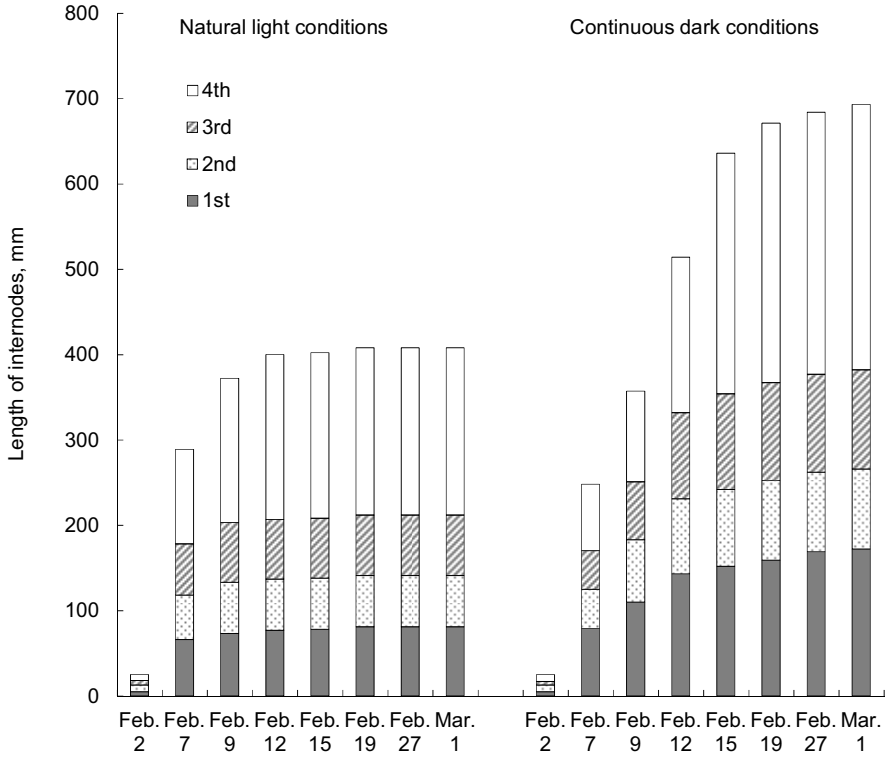

Fig. 10 Dynamics of stem growth induced by 0.1% IAA applied in the place of a removed flower bud and after excision of all leaves in tulips (cv. 'Apeldoorn') grown under natural light conditions in greenhouse and in continuous dark conditions. Fully cooled bulbs were planted on February 2 and grown at about 20°C. Results were expressed as the average values of 20 tulip bulbs.

genous gibberellins (Okubo and Uemoto 1990). According to the facts described above, auxin seems to be responsible for growth of all internodes, probably through the interaction with endogenous gibberellins in etiolated tulips. Further studies concerning the interaction of auxin and gibberellins in etiolated tulip shoot growth will be required, especially in the focus on the effect of gibberellins on polar auxin transport in etiolated tulips.

From the results obtained in this study, it can be concluded that auxin is one of main factors responsible for growth of all internodes in etiolated tulip stems.

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