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DIFFERENT GROWTH OF EXCISED AND INTACT FOURTH INTERNODE AFTER REMOVAL OF THE FLOWER BUD IN GROWING TULIPS: FOCUS ON AUXIN ACTION

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ABSTRACT

The present study is concerned with auxin action in intact and excised 4th internode of tulip shoot after removal of the flower bud in relation to the growth stages. Elongation of the intact 4th internode with or without leaves, after removal of the flower bud, at different stages was very weak. This suggests that the flower bud is always responsible for elongation growth of the 4th internode. Auxin (IAA at 0.1%, w/w in lanolin) exogenously applied to the cut surface of tulip shoot with or without leaves, greatly stimulated the growth of the 4th and lower internodes of tulip shoot. The elongation growth of excised 4th internode of tulip shoot with or without node, after removal of the flower bud was much higher, in comparison with that of intact 4th internode in tulip shoot which was growing and in which the flower bud had been cut. Elongation depended on the initial length of the 4th internode. IAA at 0.1% applied to the cut surface of excised 4th internode, just after removal of flower bud, slightly increased the growth of the 4th internode. The promotion was observed only during the first or second day of the experiment. Finally, auxin did not stimulate, or had no effect on elongation of excised 4th internode with or without node. On the other hand, elongation growth of the excised 4th internode with a flower bud was almost independent of the initial length of the 4th internode. Differences in the growth of excised and intact 4th internode of tulip shoot after removal of the flower bud are discussed in relation to auxin action.

Key words: tulips, stem, internode, growth, auxin

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 tulip plants, elongation growth of stem and development of the leaves are well known to be 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. The leaves and flower bud, mostly gynoecium, 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 flower bud in the early growth stage of tulips, resulted in almost complete inhibition of stem growth. Excision of the flower bud alone (leaves intact) had an inhibitory effect only on the elongation growth of the top and the lower internodes was normal just like in intact plants (Saniewski and de Munk, 1981). Thus, elongation growth of top internode in tulips is only regulated by flower bud. Excision of all leaves in the early growth stage of tulips, when the length of the stem was about 4.0 cm, fully inhibited stem elongation, and flower bud blasting was observed. On the other hand, excision of all leaves when the stem length was about 8.0 cm did not affect the stem growth. In this case, perianth development and pistil growth were significantly higher than those in intact plants (Saniewski, 1986), suggesting that the leaves in the sprouting stage of tulips play an important role in flower bud development. Inhibition of tulip stem growth after excision of all leaves and flower bud, was fully recovered after application of auxin at the cut surface of the top internode (Op den Kelder et al., 1971; Hanks and Rees, 1977; Okubo and Uemoto, 1985; Okubo et al., 1986; Saniewski and de Munk, 1981; Banasik and Saniewski, 1985). The 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). Application of IAA as a lanolin paste, to the cut surface of the top internode of tulip shoot excised from cooled bulbs and/or from growing shoots in cooled bulbs, promoted the extreme growth of all internodes. On the contrary, the growth of all internodes treated only with lanolin in the same way as the IAA application, was very small (Saniewski et al., 2005, 2007).

Rapid elongation of the 4th (top) internode in tulips after earlier elongation of the first, second and third internodes has also been found (Ranwala and Miller, 2008). Dynamic changes in the metabolism of carbohydrates, during flower stalk elongation in tulips, have been reported to be important in the growth of shoot (Lambrechts and Kolloffel, 1993; Lambrechts et al., 1994; Balk and de Boer, 1999; Ranwala and Miller, 2008).

In this study, we report the comparison of the elongation growth of excised and intact 4th internode – with or without node, after removal of flower bud, in various growth stages of tulips. Auxin action in these internodes is also discussed in relation to growth stages.

MATERIAL AND METHODS

Bulbs of tulip (*Tulipa gesneriana* cv. Apeldoorn) with circumference of 10-11 cm, after lifting, were stored at 18-20 °C until transferred on October 15 to 5 °C for dry cooling. The cooling period extended from January until the beginning of March. Then, the tunics were removed and the bulbs were individually planted in pots and cultivated at 18-20 °C in a greenhouse under natural light conditions.

Experiment A

The flower bud and/or all leaves were removed from tulip shoot when the length of the 4th internode was about 27, 60, 90 and 150 mm. Just after removal of the flower bud, lanolin alone (the control) or IAA (0.1%, w/w in lanolin) was applied to the cut surface of the intact 4th internode. The growth of the 4th internode was measured daily until the end of the experiment.

Experiment B

The 4th internodes with or without node were excised from tulip shoots just after removal of the flower bud, when the length of the 4th internode was about 25, 60, 90 and 140 mm. Lanolin alone (the control) or with IAA 0.1% in lanolin, was applied to the cut surface of the 4th internode instead of the flower bud. The basal part of the excised internode was kept in distilled water. The excised 4th internode of about 50, 90 and 150 mm, with intact flower bud, was also included in the experiment as a positive control. The growth of the excised 4th internode was measured daily.

In experiment B, data were subjected to an analysis of variance. The Duncan t-test was introduced to estimate the difference between means at $p = 0.05$. Experiments A and B were made at the same time, and 8 to 10 plants or excised 4th internodes were used in each treatment.

RESULTS AND DISCUSSION

Intact tulip plants with long stalk and good quality of flower has been well known to develop normally. After excision of the flower bud and all leaves at various growth stages of tulip shoot, whose initial length of the 4th internode were ca. 30, 60, 90 and 150 mm, the growth of all internodes almost totally stopped (Tab. 1, Figs. 1-4). When the flower bud was

Table 1. Effect of IAA (0.1%, w/w in lanolin) application to the top of stem, after excision of the flower bud and/or all leaves, at different stages of stem growth, on the 4th internode elongation in tulip cv. Apeldoorn cultivated in a greenhouse

Treatments	Initial length of the 4th internode [mm]	Increase of length of the 4th internode after growth completion [mm]	Total length of the 4th internode; initial + increase of growth [mm]
Flower bud removed (Fig. 1)			
Control (lanolin only)	27.0	3.3	30.3
IAA	28.3	184.0	212.3
Flower bud and all leaves removed (Fig. 1)			
Control (lanolin only)	28.7	3.7	32.4
IAA	25.9	208.6	234.5
Flower bud removed (Fig. 2)			
Control (lanolin only)	58.4	11.8	70.2
IAA	58.8	105.1	163.9
Flower bud and all leaves removed (Fig. 2)			
Control (lanolin only)	61.6	13.1	74.7
IAA	56.9	128.8	185.7
Flower bud removed (Fig. 3)			
Control (lanolin only)	97.3	16.0	113.3
IAA	94.3	78.5	172.8
Flower bud and all leaves removed (Fig. 3)			
Control (lanolin only)	91.1	20.6	111.7
IAA	89.7	82.8	172.5
Flower bud removed (Fig. 4)			
Control (lanolin only)	147.4	14.3	161.7
IAA	142.7	45.1	187.8
Flower bud and all leaves removed (Fig. 4)			
Control (lanolin only)	149.4	16.3	165.7
IAA	153.6	49.9	203.5

removed at each growth stage of tulip shoot, only the growth of the 4th (top) internode was extremely inhibited. An additional effect from removal of all leaves together with the flower bud was not observed (Tab. 1, Figs 1-4). These results suggest that the flower bud is in fact, necessary and responsible for the elongation growth of the 4th internode in tulips.

The application of IAA at 0.1% to the cut surface of the 4th internode just after removal of the flower bud, in the presence or absence of all leaves, resulted in greatly stimulated growth of not only the 4th internode but also lower internodes (Tab. 1, Figs. 1-4). Similar observations have already been reported by Saniewski and de Munk (1981), Banasik and

Saniewski (1985), Saniewski (1989) and others described in the Introduction. This could mean that the lower (the 1st to 3rd) internodes as well as the 4th internode are capable of responding to externally applied auxin in the growth stages of tulip shoots.

Auxins produced in flower buds have been shown to be transported basipetally to internodes, to promote elongation growth (Op den Kelder et al., 1971; De Munk, 1979). Removal of IAA which had been applied exogenously to the cut surface of tulip shoot without all leaves (instead of the flower bud), at different growth stages of tulips, resulted in an immediate halt in the elongation of each internode of tulip shoot. This result indicates that continuously supplied IAA is required for tulip stem growth as already reported by Saniewski and Węgrzynowicz-Lesiak (1993). Polar auxin transport is a crucial determinant of the initiation, direction and extent of growth throughout plant development (Vieten et al., 2007). There is evidence that only basipetally transported IAA or its metabolites account for the induction of the elongation of tulip stalk (Saniewski et al., 1979; Banasik and Saniewski, 1985).

Figure 1. The effect of IAA (0.1%, w/w in lanolin) application to the top of stem, when the length of the 4th internode was about 28 mm, after excision of the flower bud and/or the all leaves, in tulips cv. Apeldoorn cultivated in a greenhouse:
on left – plants at time of treatment,
on right – plants after completion of extension growth: leaves intact – the control and IAA treatments; all leaves removed – the control and IAA treatments

Figure 2. The effect of IAA 0.1% application to the top of stem, when the length of the 4th internode was about 50 mm, after excision of the flower bud and/or the all leaves, in tulips cv. Apeldoorn cultivated in a greenhouse:
on left – plants at time of treatment,
on right – plants after completion of extension growth: leaves intact – the control and IAA treatments; all leaves removed – the control and IAA treatments

Figure 3. The effect of IAA 0.1% application to the top of stem, when the length of the 4th internode was about 93 mm, after excision of the flower bud and/or the all leaves, in tulips cv. Apeldoorn cultivated in a greenhouse:
on left – plants at time of treatment,
on right – plants after completion of extension growth: leaves intact – the control and IAA treatments; all leaves removed – the control and IAA treatments

Figure 4. The effect of IAA 0.1% application to the top of stem, when the length of the 4th internode was about 148 mm, after excision of the flower bud and/or the all leaves, in tulips cv. Apeldoorn cultivated in a greenhouse:

on left – plants at time of treatment,

on right – plants after completion of extension growth: leaves intact – the control and IAA treatments; all leaves removed – the control and IAA treatments

Figure 5. The effect of IAA 0.1% application to the top of excised the 4th internode with or without node, after removal of the flower bud, when the initial length of the 4th internode was about 137 mm, in tulips cv. Apeldoorn cultivated in a greenhouse; photographed after completion of extension growth:

on left – internode without node, the control and IAA treatments,

on right – internode with node, the control and IAA treatments

As shown in Table 2 and Figure 5, the growth of the excised 4th internode with or without node after removal of flower bud, was much higher in comparison to that in growing tulips after removal of the flower bud. The growth was dependent on the initial length of the 4th internode. IAA at 0.1% applied to the top surface of excised the 4th internode in the place of the removed flower bud, slightly increased the growth of the 4th internode only on the first and second day of the experiment. After the second day, the auxin did not stimulate. Instead, it showed a slight inhibitory effect or no effect, on elongation of the excised 4th internode with or without node (Tab. 3). The mechanism in which auxin slightly inhibits elongation growth for long term incubation is still unclear.

The excised 4th internode with the flower bud at different initial lengths of 53.4, 88.0 and 146.4 mm, substantially elongated up to the length 87.5, 82.3 and 76.6 mm, respectively (Tab. 3). The growth rate of the excised 4th internode with flower bud, was not independent from the initial length of the 4th internode. The results suggest that flower bud is a source of auxin to induce the growth of excised the 4th internode. The ability of the flower bud to supply auxin to the 4th internode was not affected by the initial length of the 4th internode of tulip shoot, or growth stage, in these experimental conditions.

Here, the main question is why the growth of the excised 4th internode, independently of the length - with or without node, is much higher than that in tulips which are growing after removal of the flower bud? One possible explanation is that endogenous auxin in the 4th internode in growing tulip shoot after removal of the flower bud, is easily transported basipetally to lower internodes. This transport takes place because there is interaction between the growth of each internode in intact tulip shoot. Lack of endogenous auxin would then cause a limitation on the growth of the 4th internode.

As described above, Saniewski and Węgrzynowicz-Lesiak (1993) have reported that a continuous supply of auxin is necessary for tulip stem growth. Xu et al. (2008) examined diffusible IAA, from various parts of tulips, during rapid elongation of the flower stalk using gas chromatography-mass spectrometry (GC-MS). The amount of diffusible IAA from different organs followed the order of that of the internodes>flower organs>leaves at that time. The 4th internode exported higher quantity of IAA than did the flower during most of the rapid elongation period, except of the beginning of the rapid elongation stage and on one day after flowering. They also suggested, that the top (the 4th internode) was probably more important than the flower, in the production of IAA accountable for rapid elongation of the flower stalk. Xu et al. (2008) also described that it is possible that before the beginning of the rapid elongation stage, the flower exudes higher levels of IAA than does each internode, acting as the major source of auxins.

Table 2. Growth of the excised 4th internode with or without node at different stages of tulip development after application of lanolin (the control) or IAA 0.1% in the place of the removed flower bud (the basal part was kept in water)

Treatments	Initial length of the 4th internode [mm]	Length increase [mm] of the 4th internode after days						
		1	2	3	5	7	9	11
Excised 4th internode without node								
Control	20.7	-	5.9a	10.9a	15.4a	18.4a	21.4a	22.0a
IAA	22.7	-	11.6b	12.1a	15.0a	19.9a	22.0a	22.3a
Excised 4th internode with node								
Control	26.6	-	5.1a	16.6a	25.4a	31.3a	32.6a	33.0a
IAA	26.1	-	14.7b	18.3a	22.3a	26.4a	27.4a	27.7a
Excised 4th internode without node								
Control	58.9	11.3a	21.3a	31.5a	38.6a	41.6a	43.5b	44.9b
IAA	52.9	19.0b	28.9b	31.1a	33.6a	34.5a	36.3a	37.0a
Excised 4th internode with node								
Control	55.9	10.3a	21.8a	31.3a	37.9b	39.9b	41.0b	42.1b
IAA	54.4	14.3a	24.5a	27.0a	28.5a	29.6a	30.3a	31.0a
Excised 4th internode without node								
Control	81.9	16.6a	28.1a	33.7a	38.3a	39.3a	42.1a	-
IAA	83.6	30.4b	35.1b	36.1a	37.9a	38.3a	38.7a	-
Excised 4th internode with node								
Control	89.4	19.0a	38.9a	46.4a	54.1b	54.9b	56.3b	-
IAA	90.6	24.9b	38.1a	39.9a	41.1a	41.1a	41.7a	-
Excised 4th internode without node								
Control	133.3	26.1a	43.7a	54.6a	60.1b	63.1b	-	-
IAA	132.3	37.0b	47.7a	49.9a	50.0a	49.7a	-	-
Excised 4th internode with node								
Control	142.9	27.4a	46.0a	56.6a	62.1b	68.0b	-	-
IAA	141.9	37.0b	48.0a	50.1a	50.3a	50.3a	-	-

Table 3. Growth of the excised 4th internode with node and the intact flower bud at different stages of tulip development

Length of excised 4th internode with node and the intact flower bud [mm]	Length increase [mm] of the 4th internode after days				
	1	3	5	7	9
53.4	22.4	59.0	75.0	83.3	87.5
88.0	30.4	61.6	72.0	77.6	82.3
146.4	31.6	64.8	71.8	76.4	76.6

The higher growth of the excised 4th internode, in comparison to that in growing tulips after removal of the flower bud, is possibly caused by weaker and/or slow flow of auxin into water. Consequently, relative higher levels of endogenous auxin are still present in the 4th internode, which accounts for the elongation. It is possible to limit elongation growth of the excised 4th internode, both untreated (the control) and treated with IAA at 0.1%. Such limiting can be done by an endogenous level of sucrose and hexoses that can be readily utilized in elongating cells. This process is known, because the importance of dynamic changes in carbohydrates metabolism for flower stalk elongation in tulips has been reported (Lambrechts and Kolloffel, 1993; Lambrechts et al., 1994; Balk and de Boer, 1999; Ranwala and Miller, 2008).

In addition, endogenous auxin, indole-3-acetic acid, has been shown to promote the biosynthesis of active gibberellin A_1 in elongating internodes of pea, and inhibited GA_1 deactivation (Ross et al., 2003). In the case of tulips the growth of all internodes is substantially regulated by interaction of auxin and gibberellins (Okubo and Uemoto, 1985; Okubo et al., 1986; Saniewski, 1989; Rietveld et al., 2000). These facts suggest that not only auxin but also gibberellin are responsible for the growth of internodes in tulip shoots. Further studies on the growth of tulip shoots will be focused on the important role of auxin and gibberellin.

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ZRÓŻNICOWANY WZROST ODCIĘTEGO I NIENARUSZONEGO CZWARTEGO MIĘDZYWĘŹLA PO USUNIĘCIU PĄKA KWIATOWEGO U ROSNĄCYCH TULIPANÓW: ROLA AUKSYN W TYM PROCESIE

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STRESZCZENIE

Badania dotyczyły działania auksyny (IAA) na wzrost nienaruszonego i odciętego czwartego międzywęźla pędu tulipana po usunięciu pąka kwiatowego, w zależności od etapu wzrostu. Wzrost nienaruszonego czwartego międzywęźla, w różnych etapach wzrostu roślin, w obecności liści lub po ich usunięciu, i po odcięciu pąka kwiatowego, był bardzo mały, co sugeruje, że pąk kwiatowy jest zawsze odpowiedzialny za wzrost wydłużeniowy czwartego międzywęźla. Auksyna (IAA 0,1% w paście lanolinowej) podana w miejsce usuniętego pąka kwiatowego, w obecności liści lub po ich odcięciu, silnie stymulowała wzrost czwartego i wszystkich niższych międzywęźli pędu tulipana. Wzrost wydłużeniowy odciętego czwartego międzywęźla pędu tulipana, z węzłem lub bez węzła, po usunięciu pąka kwiatowego, był dużo większy w porównaniu ze wzrostem czwartego nienaruszonego międzywęźla roślin rosnących w obecności liści lub po ich usunięciu, i zależał od długości początkowej czwartego międzywęźla. IAA w stężeniu 0,1% podany w miejsce usuniętego pąka kwiatowego w odciętym czwartym międzywęźlu w niewielkim stopniu stymuluje wzrost wydłużeniowy jedynie w pierwszym lub drugim dniu po traktowaniu. Ostatecznie auksyna nie stymulowała lub nie miała większego wpływu na wzrost odciętego czwartego międzywęźla z węzłem lub bez węzła. Z drugiej strony, wzrost wydłużeniowy odciętego czwartego międzywęźla z pąkiem kwiatowym był prawie niezależny od początkowej długości tego międzywęźla. Różnice we wzroście odciętego i nienaruszonego czwartego międzywęźla pędu tulipana po usunięciu pąka kwiatowego są dyskutowane w kontekście działania auksyny.

Słowa kluczowe: tulipany, łodyga, międzywęźle, wzrost, auksyna