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Geng, Xing Min
Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University

Sato, Azusa
Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University

Okubo, Hiroshi
Faculty of Agriculture, Kyushu University

Saniewski, Marian
Research Institute of Pomology and Floriculture

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Changes in Carbohydrate and ABA Content during GA–induced Growth of Non–cooled Tulip Bulbs

Xing Min GENG[1]*, Azusa SATO[1], Hiroshi OKUBO and Marian SANIEWSKI[2]

Laboratory of Horticultural Science, Division of Agricultural Botany, Department of Plant Resources,
Faculty of Agriculture, Kyushu University, Fukuoka 812–8581, Japan
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Changes in carbohydrate and ABA content during GA–induced growth of non–cooled tulip bulbs were investigated under the conditions reported previously (Geng *et al*., 2005) that GA_3 promotes the shoot growth and flowering of non–cooled tulip bulbs when planted in December but not in September. Rapid degradation of starch and the increase in soluble carbohydrate content in the floral stalk were observed during GA_3–induced floral stalk elongation in non–cooled bulbs planted in December, but not in those planted in September. The growth of floral stalk promoted by GA_3 application was accompanied by the decrease in ABA content in the shoot of the non–cooled bulbs planted in December.

INTRODUCTION

Exogenously applied gibberellic acid (GA_3) induced shoot growth and flowering of non–cooled tulip bulbs (Hanks, 1982; Saniewski *et al*., 1999b), and the response was higher when the treatment was given later during storage at 20˚C (Geng *et al*., 2005).

Low–temperature treatment of tulip bulbs during storage influences the conversion of starch to soluble sugars, and these soluble constituents are transported to the shoot to be used for elongation growth of the floral stalk after planting at high temperature (Charles–Edwards and Rees, 1974, 1975; Davies and Kempton, 1975; Ohyama *et al*., 1988). After planting, the cold–induced starch breakdown was initially accompanied by an increase in an α–amylase activity in the scales, and flower stalk elongation was accompanied by a decrease in the sucrose content and an increase in the glucose content and invertase activity (Lambrechts *et al*., 1994). Therefore, it is considerable that the similar metabolic changes occur even in non–cooled bulbs when grown with gibberellin.

ABA inhibited the shoot growth of cooled tulip bulbs (Saniewski, *et al*., 1990) or that induced by gibberellin in non pre–cooled derooted bulbs (Saniewski *et al*., 1999a). In the previous report (Geng *et al*., 2007), ABA content in the scales of tulip bulbs decreased during the storage either at 20 or 5˚C and there was no significant difference in the ABA content between the scales at two temperatures at the end of storage.

In this study, changes in carbohydrate and ABA content during GA–induced growth of non–cooled tulip bulbs were investigated.

MATERIALS AND METHODS

Effects of GA_3 on carbohydrate content during GA_3–induced elongation of floral stalk

Plant materials and application of GA_3

Bulbs of tulip (*Tulipa gesneriana* L. cv. Oxford, 10–12 cm in circumference, a product of Niigata Prefecture, Japan), upon arrival at the laboratory on 10 September and 1 October 2004, were disinfected with 1.0% Benlate (Du Pont) for 1 hour and air–dried. They were then stored at 20˚C (non–cooled bulbs). The bulbs were grown on 22 September and 27 December at 15˚C in the phytotron of The Biotron Institute, Kyushu University and transferred to 20˚C in the phytotron on the first day of the next month. The bulbs were put on aluminum trays with distilled water (control) or 200 mgl^{-1} GA_3 solution, and water and GA_3 solutions were renewed every two or three days.

Carbohydrate analysis

Bulbs of September planting were harvested and divided into scales and shoot at 10, 30 and 60 days after planting. Those of December planting were divided into scales, flower, leaves and floral stalk 7, 21 and 35 days after planting, and the floral stalks were further divided into each internode 21 and 35 days after planting.

After fresh weight of all divided organ parts and the length of shoot were measured, they were frozen in liquid nitrogen and kept at −80˚C. Before analyzing, samples were freeze–dried and weighed.

The procedures for carbohydrate analysis were the same as described in the previous report (Geng *et al*., 2007). The experiment was conducted twice, and the data shown here were the average of the twice.

Effects of GA_3 application on endogenous ABA content

Plant materials and application of GA_3

The bulbs (non–cooled bulbs) prepared in the same

[1] Laboratory of Horticultural Science, Division of Agricultural Botany, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University, Fukuoka 812–8581, Japan
[2] Research Institute of Pomology and Floriculture, Pomologiczna 18, 96–100 Skierniewice, Poland
* Present address: Department of Landscape Architecture, College of Landscape Architecture, Nanjing Forestry University, Lonpan Road, Nanjing, Jiangsu Province 210037, P. R. China
* Corresponding author (e–mail: xmgeng@njfu.edu.cn)

manner as above were grown on 9 September and 8 December in the same conditions as described above.

ABA analysis

The samples for ABA analysis were collected when the length of floral stalk was about 1.3 cm. All the procedures thereafter were the same as previously reported (Geng *et al.*, 2007).

RESULTS AND DISCUSSION

Effects of GA_3 on carbohydrate content during GA_3–induced elongation of floral stalk

Shoot growth of the non–cooled bulbs with GA_3 was not different from that without GA_3 (control) up to 60 days after planting when the culture started in September (Fig. 1A). GA_3 application promoted the floral stalk elongation in December planting (Fig. 1B), and 100% of the bulbs reached anthesis 35 days after planting (data not shown). The results indicates that the response to GA_3 treatment varies by the time of planting (=GA_3 application time); the response increases as when the bulbs are planted with GA_3, in accordance with the previous results (Geng *et al.*, 2005).

Starch content in the scales was still high and the breakdown rate of starch in the scales of the control (grown on water) and GA_3–treatment bulbs was only 7.2 and 12.4%, respectively when the bulbs were planted in September (Fig. 2A). Starch content in the shoot slightly increased 30 days after plating with a little difference between the treatments; a little higher in the control than in the GA_3–treated shoot. Scales in the bulbs for September planting contained a little higher amount of starch than those for December planting at the beginning of the culture (Figs. 2A and 3A). During the GA_3–induced growth and flowering in December planted bulbs, the starch breakdown proceeded and its breakdown rate was 21.8% in the scales and 58.8% in the floral stalk at anthesis (35 days after planting) (Fig. 3A), but no such a starch breakdown was observed in the scales and shoots in September planting (Fig. 2A).

In September planting, sucrose content in the shoot gradually increased when the bulbs were grown either with or without GA_3, but the content in the scales decreased in the GA_3–treated bulbs (Fig. 2B). Sucrose content in the shoot increased without significant difference between the treatments in September planting. Effects of GA_3 on sucrose content in the scales were not observed in December planting, but GA_3 application increased the sucrose content in the first internode noticeably (Fig. 3B).

Increase in glucose and fructose content was notable in the first internode of GA_3–treated bulbs planted in December, whereas there was small fluctuation of the content in the shoot of September planted bulbs even with GA_3 (Figs. 2C, 2D, 3C and 3D). No clear changes and differences in glucose and fructose content were observed in the scales irrespective of the planting time and of the GA_3 treatment.

Similar tendency of the changes in these carbohydrates in GA_3–treated vs. control bulbs were observed in cooled vs. non–cooled bulbs as reported by Lambrechts *et al.* (1994), although some data were out of accordance with their report. α–amylase induces breakdown of starch and sucrose is produced. Sucrose is metabolized into glucose and fructose by invertase when floral stalk elongates. Gibberellins induce a–amylase in cereal seeds (Choi *et al.*, 1996; Fincher, 1989). Elongation of inflorescence stalk in non–cooled hyacinth bulbs treated with GA was correlated with a sharp increase in invertase activity in the stalk (Nowak and Rudnicki, 1976). An increase in acid invertase activity in response to gibberellin was observed in the stem of *Phaseolus vulgaris* L. (Morris and Arthur, 1985) and the elongating dwarf pea shoots (Wu *et al.*, 1993). It is, therefore, considerable that GA_3 plays a role similarly to that of low temperature in the growth of tulip flower stalk after planting.

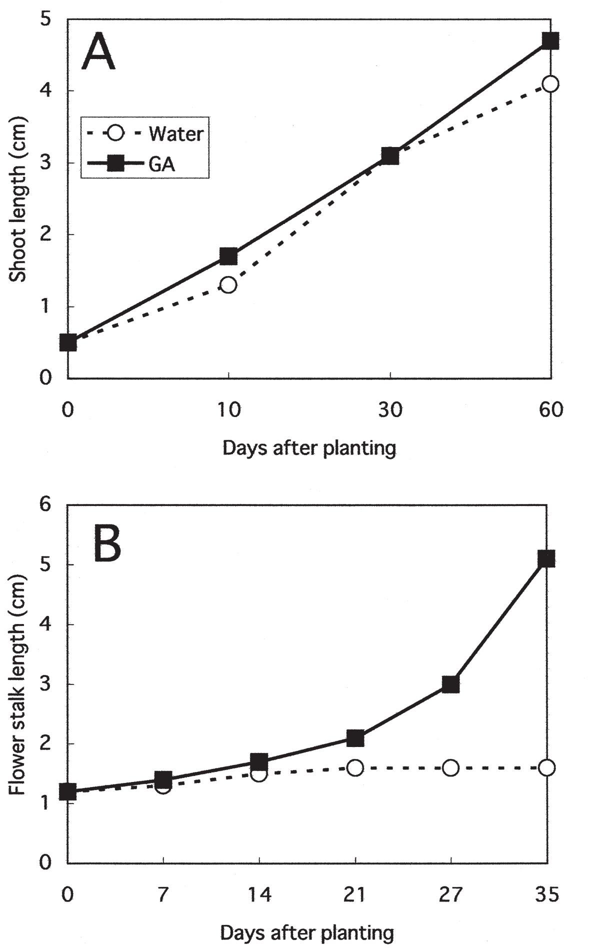

Fig. 1. Effects of GA_3 on shoot growth of non–cooled bulbs. Shoot length was measured in September planting (A), whereas the floral stalk length was measured in December planting (B).

Effects of GA_3 application on endogenous ABA content in shoot

ABA content in the shoots of the non–cooled bulbs planted in September and in December was not different when grown on water (Table 1). Application of GA_3 lowered the ABA content in the shoot of the bulbs grown in September to a half amount of that grown in December.

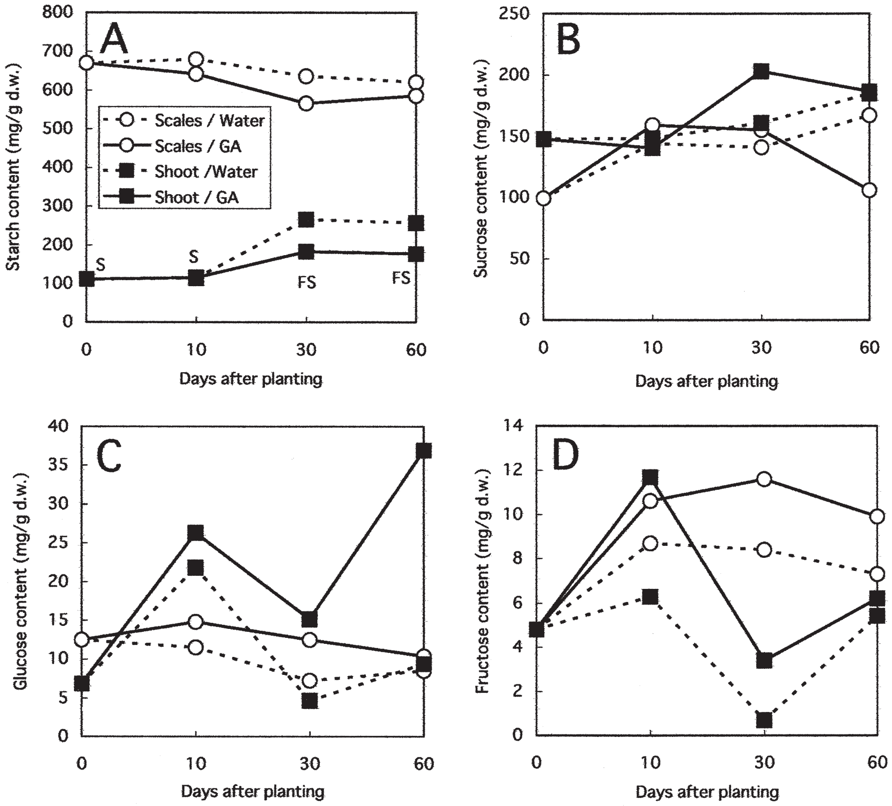

Fig. 2. Effects of GA_3 on carbohydrate contents in the non–cooled bulbs of September planting. A; starch, B; sucrose, C; glucose and D; fructose. Water; grown on water, GA; grown on GA_3 solution. Shoot; whole shoot was used for the analyses on the day 0 and 10 (indicated as S), whereas flower stalk was on the day 30 and 60 (indicated as FS). S and FS are also applicable to B–D.

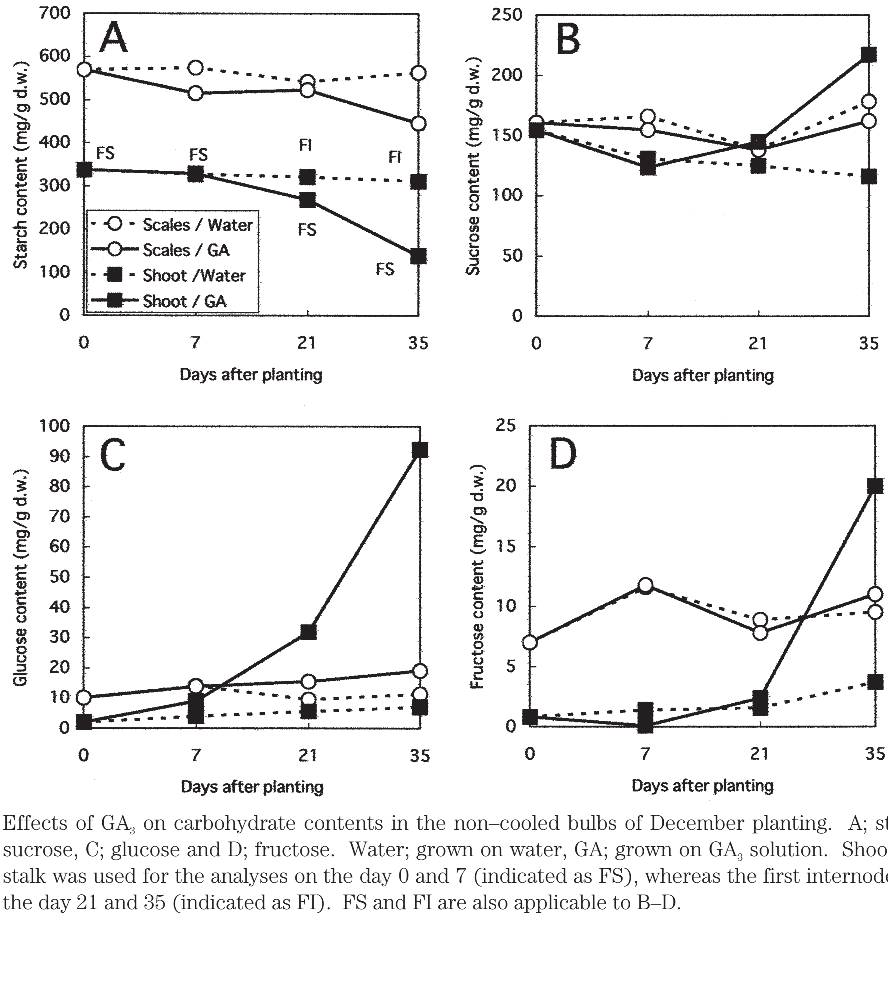

Fig. 3. Effects of GA_3 on carbohydrate contents in the non–cooled bulbs of December planting. A; starch, B; sucrose, C; glucose and D; fructose. Water; grown on water, GA; grown on GA_3 solution. Shoot; flower stalk was used for the analyses on the day 0 and 7 (indicated as FS), whereas the first internode was on the day 21 and 35 (indicated as FI). FS and FI are also applicable to B–D.

Table 1. Effects of application time of GA_3 on ABA content (pmol/g F.W.) in the shoot

Planted on	Grown on	
	water	GA_3
9 Sept.	57	66
8 Dec.	59	33

ABA content was measured when the shoot length was 1.3 cm.

Antagonism of gibberellin and ABA is known in non–cooled tulip bulbs; ABA inhibited the gibberellin–induced shoot growth of non–cooled tulip bulbs (Saniewski *et al*., 1999a). It is suggested by Terry *et al.* (1982) that the lack of elongation growth of the floral shoot in non–cooled bulbs might be related to its high ABA content. Natural decrease in ABA content in the scales, which is temperature–independent, occurring during bulbs storage may increase the response of the bulbs to gibberellin after planting (Geng *et al*., 2007). After planting it is considerable that gibberellin decreases ABA content to promote the response to the gibberellin.

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