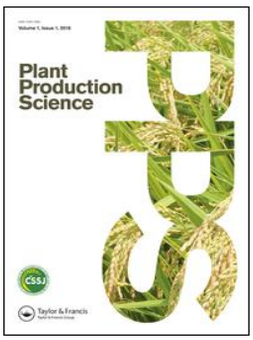

Plant Production Science

ISSN: 1343-943X (Print) 1349-1008 (Online) Journal homepage: https://www.tandfonline.com/loi/tpps20

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To cite this article: Guangwu Zhao & Jianhua Wang (2008) Effect of Gibberellin and Uniconazole on Mesocotyl Elongation of Dark-Grown Maize under Different Seeding Depths, Plant Production Science, 11:4, 423-429, DOI: 10.1626/pps.11.423

To link to this article: https://doi.org/10.1626/pps.11.423

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Published online: 03 Dec 2015.

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Plant Prod. Sci. 11(4) : 423—429 (2008)

Effect of Gibberellin and Uniconazole on Mesocotyl Elongation of Dark-Grown Maize under Different Seeding Depths

Guangwu Zhao and Jianhua Wang

(Department of Seed Science and Technology, China Agricultural University, Yuan Ming Yuan West Road 2, Beijing 100094, P. R. China)

Abstract : Seeds of five maize inbred lines, including 3681-4, were treated with gibberellin A_3 (GA_3) and uniconazole (UCZ) under deep seeding and shallow seeding in order to elucidate the physiological mechanism of maize mesocotyl elongation under different seeding depths. GA_3 was the most effective at 10^{-5} M and the mesocotyl elongation of 3681-4, 178, Zong 3, Huang C, Han 21 was promoted at this concentration by 60.4%, 44.6%, 42.5%, 24.2% and 44.2% under 20 cm seeding depth, respectively. Under 2 cm seeding depth, however, there were no significant differences between mesocotyl length of all inbred lines at any concentration. UCZ treatment at concentrations higher than 10^{-5} M, significantly inhibited mesocotyl elongation in all inbred lines under seeding depths of both 20 cm and 2 cm. Interestingly, mesocotyl elongation of only 3681-4 was significantly inhibited at the concentration of 10^{-7} M. These results suggested that mesocotyl elongation was more sensitive to gibberellin A (GA) under deep seeding than under shallow seeding, and that 3681-4 was more sensitive to GA than the other inbred lines. Endogenous gibberellin A_1 (GA_1) contents in the mesocotyls of 3681-4 and 178 treated with GA_3 and UCZ were accordant with their morphological responses. GA_3 promoted cell elongation rather than cell division, and that UCZ inhibited both cell elongation and cell division in 3681-4 and 178.

Key words : Gibberellin, Maize, Mesocotyl elongation, Uniconazole.

In spring, the arid and semiarid regions often lack rainfall and the top soil is dry, which affects the seed germination and seedling establishment of major crops. Timely seeding is important as delay in seeding results in reduction of both biomass and yield. Deep seeding is an effective measure to ensure seeds absorbing water from deep soil layer and germinate normally in these regions. When seeds are located deep from the soil surface, some organs elongate to reach the soil surface. In wheat and barley, the first internode and coleoptile elongate (Suge et al., 1997; 1998; Schillinger et al., 1998; Takahashi et al., 2001; Matsui et al., 2002; Nishizawa et al., 2002; Rebetzke et al., 2004). In contrast, in rice the mesocotyl and coleoptile elongate (Turner et al., 1982; Mgonja et al., 1994; Zhang et al., 2005).

In maize (*Zea mays* L.), mesocotyl elongation contributes to seedling emergence from the deep soil layer (Troyer, 1997). In fact, however, it is difficult for the seedlings of existing species to emerge and obtain good stands when their seeds are planted deeper than at a normal depth. Therefore, developing maize that is tolerant to deep seeding is an important objective of maize breeding in arid and semi arid regions. Recently, we developed an inbred line called 3681-4 from Hopi Indian corn germplasm, whose mesocotyl can elongate to emerge even when seeds were sown 20–30 cm deep in soil. Much of the research on the mechanism of organ elongation has been focused on hormone regulation, especially on the effect of gibberellin A (GA).

GA is an essential regulator of many aspects of plant development including organ elongation. It is reported that endogenous GA plays a regulatory role in stem elongation of *Cichorium intybus* and Japanese radish, hypocotyl elongation of Arabidopsis and shoot elongation of tobacco, based on by the effect of uniconazole (UCZ), GA biosynthesis inhibitor (Demeulemeester et al., 1995; Nishijima et al., 1997; Tanaka et al., 2003; Ishida et al., 2004). On the other hand, exogenous GA can strongly stimulate internode elongation in dwarf GA_1-deficient mutants of pea, the first internode elongation of wheat, and mesocotyl and coleoptile elongation of rice (Yang et al., 1996; Chen et al., 2001; Cao et al., 2005; Watanabe et al., 2007). Exogenous GA can promote hypocotyl elongation in light-grown Arabidopsis (Xu et al., 1997), but not in darkness (Cowling and Harberd, 1999).

So far, no study has been reported on how GA regulates mesocotyl elongation of maize seedlings under different seeding depths. In the present study, we examined the effect of GA_3 and UCZ on mesocotyl elongation of dark-grown maize including 3681-4 under the conditions of deep seeding and shallow seeding. Subsequently, the endogenous GA_1 content was measured and the microstructure was observed.

Received 9 January 2008. Accepted 21 April 2008. Corresponding Author: Jianhua Wang (wangjh63@cau.edu.cn, fax+86-10-62732263).
Abbreviations : GA, gibberellin A; GA_1, gibberellin A_1; GA_3, gibberellin A_3; UCZ, uniconazole; HPLC, high performance liquid chromatography.

The aim of our study is to elucidate the physiological mechanism of maize mesocotyl elongation under different seeding depths.

Materials and Methods

1. Plant materials

Five maize inbred lines, including 3681-4 tolerant to deep seeding, developed from Hopi Indian corn germplasm, and four commercial lines 178, Zong 3, Huang C, Han 21, were used in this research. The deep seeding tolerance of different maize inbred lines was examined by sowing seeds reproduced at the same time and place under 25 cm deep soil layer at 25°C under the dark condition in the experimental base of China Agricultural University. The seedlings of 3681-4 emerged at a high rate, but those of 178, Zong 3, Huang C, and Han 21 did not.

2. Application of chemicals and growth measurement

Gibberellin A_3 (GA_3, Beijing Chemical Reagent Company) and uniconazole (UCZ, GA biosynthesis inhibitor) were applied to the seeds in 1000 mL glass tubes, 6.5 cm in diameter and 42.0 cm in length. Three-hundred milliliters of 1.25% agar containing different concentrations of GA_3 and UCZ was placed in a glass tube. Fifty seeds were randomly selected for their uniformity and good health, soaked in 1% NaClO solution for 10 min, and washed with distilled water for three times. Then, they were placed on the surface of the agar and covered with 2 cm and 20 cm of fresh sand, which was passed through a 0.8 mm sieve and sterilized at 180°C for 1 hr. The seeds were incubated for 10 d at 25°C. Finally, thirty seedlings were randomly taken out and mesocotyl length was measured. The average value of the length of thirty mesocotyls was calculated and the experiment was conducted three times.

3. Measurement of endogenous GA_1 content

The endogenous GA_1 content in the mesocotyl treated with GA_3 and UCZ was quantified using gas chromatography/mass spectrometry (GC/MS) according to the method of Nishijima et al. (1997). [17, 17-$^2H_2$] GA_1 was added as an internal standard for quantification of GA_1. Mesocotyls (5.0 g) of 10-day-old seedlings were ground with 80% (v v^{-1}) methanol and then placed into a 10 mL tube. The tube was equably surged and then kept at 4°C for 4 hr. Next, the tube was centrifuged at 1000 *g* for 15 min. The solution in the upper layer was passed through a C-18 solid-phase extraction column and then dried in nitrogen. Finally, the exacted sample was dried and dissolved into 5 mL of methanol, and loaded onto a Bondesil DEA column. The column was eluted with methanol and then with 0.5% acetic acid in methanol. The eluate with 0.5% acetic acid in methanol was evaporated to dryness and further purified by a reverse phase high performance liquid chromatography (HPLC). The HPLC fractions were then derivatized to their methyl or methyl-trimethylsilyl derivatives and subjected to analysis by a GC/MS (Agilent 6890 GC-MSD, USA) equipped with a gas chromatograph and a capillary column. GA_1 was analyzed in selected ion monitoring mode. Then, sample derivatization and GC/MS analysis were conducted. Quantity of endogenous GA_1 was calculated from the ion peak area ratios at 506/508. The experiment was conducted three times.

4. Microscopic observation

To investigate the effects of GA_3 and UCZ on the growth of mesocotyl cells of 3681-4, we anatomically examined the mesocotyls of 10-day-old seedlings. The mesocotyls were fixed with FAA (70% ethanol : acetic acid : formalin, 90 : 5 : 5, V/V/V). According to the method of Tanaka et al. (2003), dehydration treatment, vitrification treatment, wax immersing, embedding, slicing, sticking, expanding, dyeing and enveloping were performed. Cell length and cell number of the mesocotyls were measured and counted under a differential interference microscope (Nikon, Tokyo, Japan).

Results

1. The effect of GA_3 and UCZ on mesocotyl elongation

GA_3 significantly promoted mesocotyl elongation of all inbred lines under 20 cm seeding depth at concentrations higher than 10^{-6} M and the most remarkable promotion occurred at the concentration of 10^{-5} M (Figs. 1A and 2A, C). The results showed that 10^{-5} M GA_3 promoted the mesocotyl elongation by 60.4% in 368-4, but only 44.6% in 178, 42.5% in Zong 3, 24.2% in Huang C and 44.2% in Han 21. Under 2 cm seeding depth, however, there was no significant effect of GA_3 on mesocotyl length at any concentration in any inbred line (Figs. 1B and 2B, D).

Mesocotyl elongation of all inbred lines was significantly inhibited by UCZ treatment under seeding depths of both 20 cm and 2 cm at concentrations higher than 10^{-5} M (Figs. 2 and 3). Mesocotyl elongation of only 3681-4 was significantly inhibited by UCZ at a low concentration of 10^{-7} M. The mesocotyl length of 3681-4 was decreased by 21.4% and 24.4% at the concentration of 10^{-7} M under 20 cm and under 2 cm, respectively.

The above results suggested that mesocotyl elongation was more sensitive to GA under the deep seeding condition than under the shallow seeding condition, and that 3681-4 was more sensitive to GA than the other inbred lines.

2. The effect of GA_3 and UCZ on endogenous GA_1 content

Mesocotyl elongation was markedly affected after the application of GA_3 and UCZ. Therefore, we further analyzed whether endogenous GA_1 contributed to the

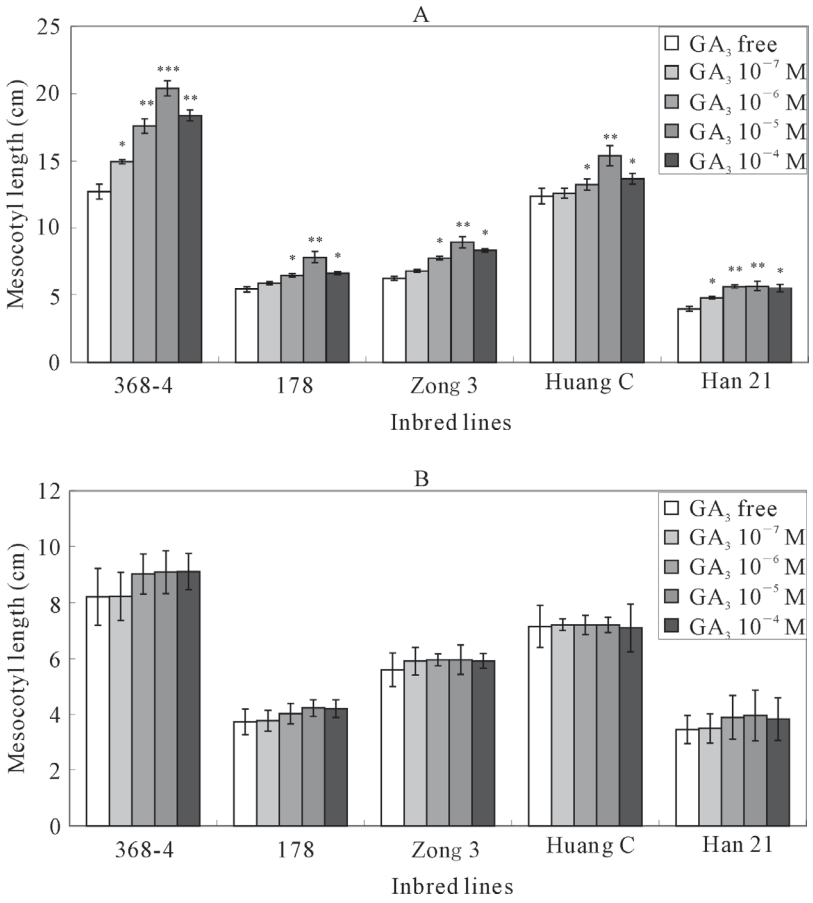

Fig. 1 The effect of GA_3 on mesocotyl elongation in darkness of five inbred lines. Maize seedlings were grown for 10 d under the seeding depth of 20 cm (A) or 2 cm (B). Values represent a mean of 30 mesocotyls with SE. Duncan's LSR test : * $p<0.05$, ** $p<0.01$, *** $p<0.001$ shows significance level of difference from GA_3-free control.

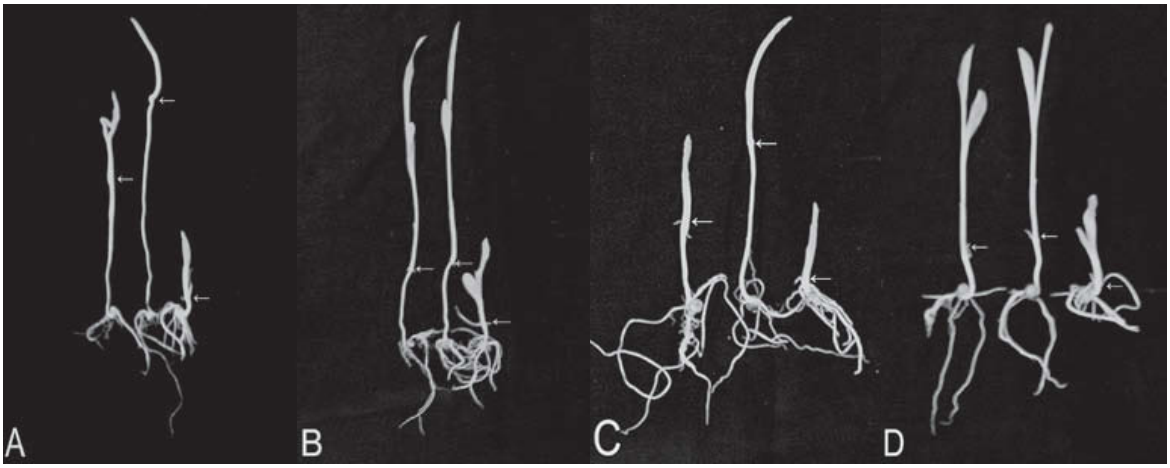

Fig. 2 Morphological observation of maize seedlings treated with GA_3 and UCZ. Photographs show the seedlings of maize inbred lines 3681-4 (A, B) and 178 (C, D) grown in the presence of GA_3 or UCZ for 10 days under 20 cm seeding depth (A, C) and 2 cm seeding depth (B, D). In each panel, treatments from left to right are control, GA_3 (10^{-5} M), UCZ (10^{-5} M). Arrows indicate the position of coleoptile node.

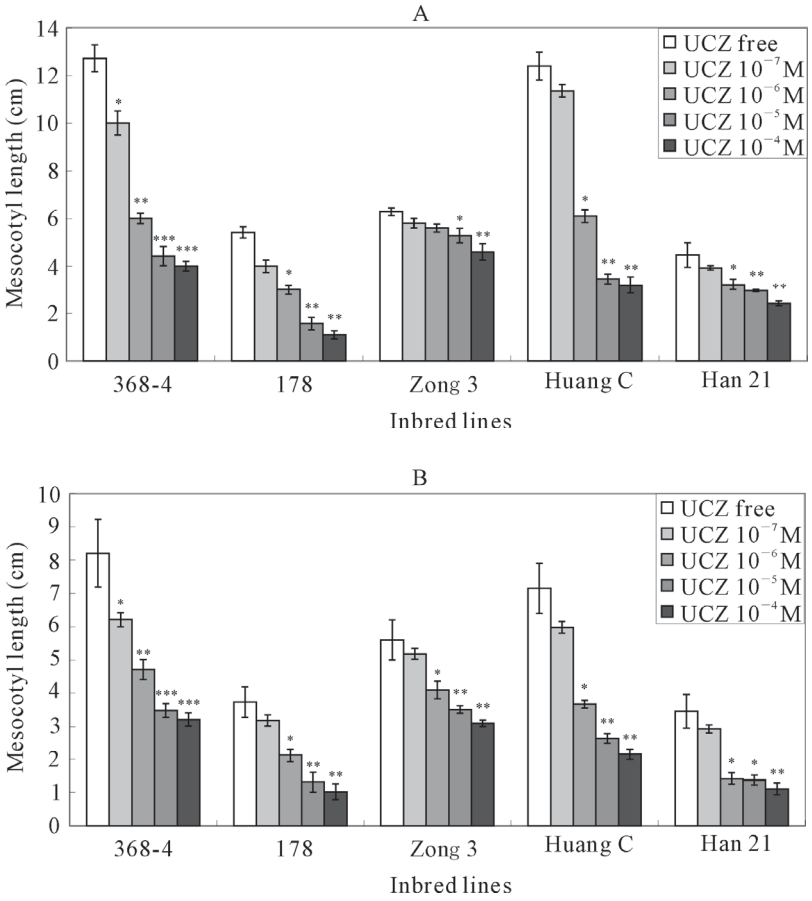

Fig. 3 The effect of UCZ on mesocotyl elongation in darkness of five inbred lines of maize. Maize seedlings were grown for 10 d under the seeding depth of 20 cm (A) and 2 cm (B). Values represent a mean of 30 mesocotyls with SE. Duncan's LSR test : * $p<0.05$, ** $p<0.01$, *** $p<0.001$ shows significance level of difference from control.

change of mesocotyl elongation.

GA_3 treatment increased endogenous GA_1 content of 3681-4 and 178 by 25.1% and 39.2%, respectively, under 20 cm seeding depth, respectively (Fig. 4), but not under 2 cm seeding depth. UCZ greatly decreased the endogenous GA_1 content of 3681-4 and 178 under seeding depths of both 20 cm and 2 cm (Fig. 4). Under 20 cm seeding depth, endogenous GA_1 content of 3681-4 and 178 was decreased by 28.4% and 18.0%, respectively. Under 2 cm seeding depth, endogenous GA_1 content of 3681-4 and 178 was decreased by 23.2% and 9.5%, respectively.

The above results suggested that the changes in endogenous GA_1 content of the mesocotyls of 3681-4 and 178 under different treatments were in accordance to their morphological ones.

3. The effect of GA_3 and UCZ on cell growth of 3681-4 mesocotyl

Mesocotyl elongation was markedly affected by the application of GA_3 and UCZ. Therefore, we further analyzed whether cell division, cell elongation, or both contributed to the change in mesocotyl growth.

Under 20 cm seeding depth, as shown in Table 1 and Fig. 5, cell length along the longitudinal axe was increased dramatically by GA_3 treatment. The average length of GA_3-treated cells in the mesocotyl of 3681-4 and 178 was approximately 1.8 and 1.5 times longer than that of the control, respectively. The number of individual cells in each cell file along the longitudinal axe of the mesocotyl was not significantly influenced by GA_3 treatment in 3681-4 and 178. However, cell length along the longitudinal axe was dramatically decreased by UCZ treatment. The average length of UCZ-treated cells in the mesocotyls of 3681-4 and 178 was approximately 71.4 and 54.5% of the control, respectively. The cell number in both 3681-4 and 178 was significantly decreased by UCZ and TIBA treatment. By UCZ treatment, the cell number in 3681-4 and 178 was decreased by 45.3% and 51.1%, respectively.

Under 2 cm seeding depth, as shown in Table 1, there were no significant changes in the cell length in both 3681-4 and 178 after GA_3 treatment. However, the cell length in both 3681-4 and 178 significantly decreased after UCZ treatment. The average length of UCZ-treated cells in the mesocotyl of 3681-4 and

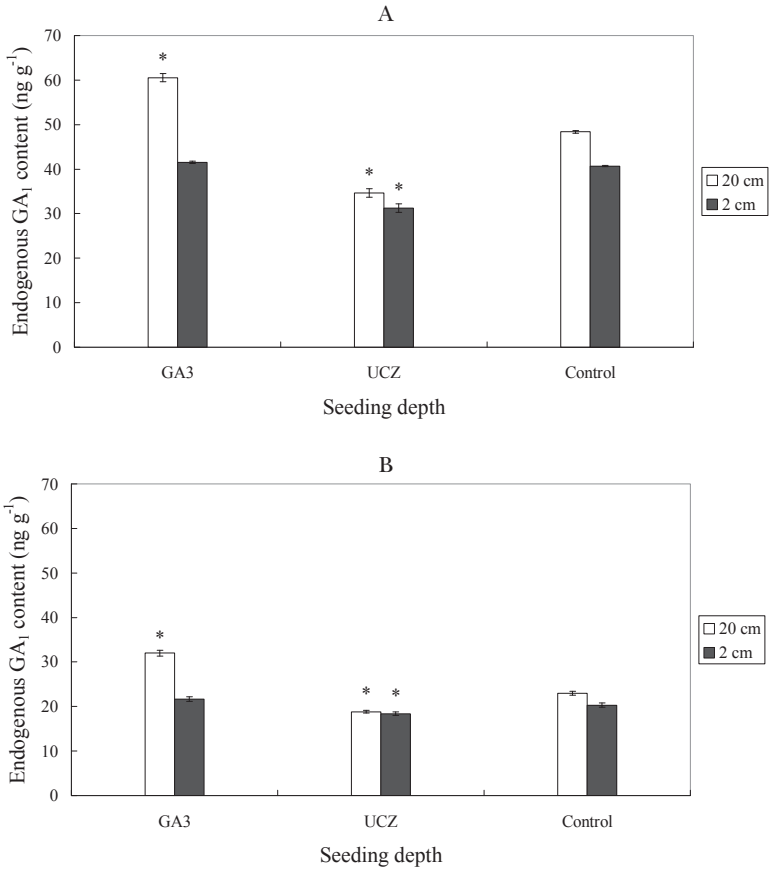

Fig. 4 The changes of endogenous GA_1 content in the mesocotyls of 3681-4 and 178 under different treatments. Endogenous GA_1 content was measured in the mesocotyls of 3681-4 (A) or 178 (B). Duncan's LSR test : * $p<0.05$ shows significance level of difference from control.

178 was approximately 78.1% and 82.0% of the control, respectively. Furthermore, in each cell file along with longitudinal axe of the mesocotyl, there was no significant change in the cell number after GA_3 treatment in either 3681-4 or 178. However, there was a significant change in the cell number after UCZ treatment in both 3681-4 and 178. UCZ treatment decreased the cell number by 46.4% and 56.5%, in 3681-4 and 178, respectively.

The above results strongly suggested that GA_3 promoted mesocotyl elongation via cell elongation rather than cell division, and that UCZ inhibited mesocotyl elongation via the inhibition of both cell elongation and cell division.

Discussion

The GA response of maize mesocotyl is cultivar dependent. Our results showed that mesocotyl elongation of 3681-4 was more significantly promoted by GA_3 than that of the other four maize inbred lines under the deep seeding condition. Similar phenomena have been observed in rice and wheat. GA_3 promote mesocotyl elongation of rice varieties with longer mesocotyl more remarkably than that with short mesocotyl (Cao et al., 2005). GA_3 can significantly promote the first internode elongation of Hong Mang Mai, a variety tolerant to deep seeding, whereas it has no effect on other wheat varieties (Chen et al., 2001).

To further examine the effect of GA on mesocotyl elongation, we applied a GA biosynthesis inhibitor. Mesocotyl elongation of all maize inbred lines was significantly inhibited by UCZ under the conditions of both deep seeding and shallow seeding. The similar results occurred in stem elongation of radish (Nishijima et al., 1997). These data also suggest that endogenous GA play an important role in organ elongation. Interestingly, mesocotyl elongation of only 3681-4 was significantly inhibited by UCZ at the concentration of 10^{-7} M under the conditions of both deep seeding and shallow seeding. The results again suggested that mesocotyl elongation of 3681-4 tolerant to deep seeding was more sensitive to GA than that of the other inbred lines.

However, mesocotyl elongation of all maize inbred lines was insensitive to GA_3 under the shallow seeding condition. The possible explanation is that the endogenous hormone level is optimal and the additional hormone has no effect on mesocotyl elongation

Table 1 The mean cell length and cell number in the mesocotyls of 3681-4 and 178 under various treatments.

Seeding depth	Treatment	Cell length (μm)		Cell number per mesocotyl	
		3681-4	178	3681-4	178
2 cm	GA_3	126.7±11.6 a	105.2±7.3 a	741.1±15.6 a	417.3±10.6 a
	UCZ	80.7±5.1 b	78.4±2.8 b	427.5±14.3 b	169.6±8.5 b
	Control	103.3±5.8 a	95.6±6.6 a	797.7±16.6 a	390.2±8.0 a
20 cm	GA_3	256.7±6.8 a	183.3±11.5 a	786.7±10.6 a	404.8±20.2 a
	UCZ	100.0±5.3 c	65.0±5.0 c	440.9±16.8 b	232.3±17.5 b
	Control	140.0±5.0 b	119.3±5.1 b	806.6±20.1 a	475.3±24.6 ab

Values represent a mean of 30 mesocotyl cells with SE. Means of different treatments of the same inbred lines followed by the same letters are not significantly different at the 0.01 probability level according to Duncan's LSR.

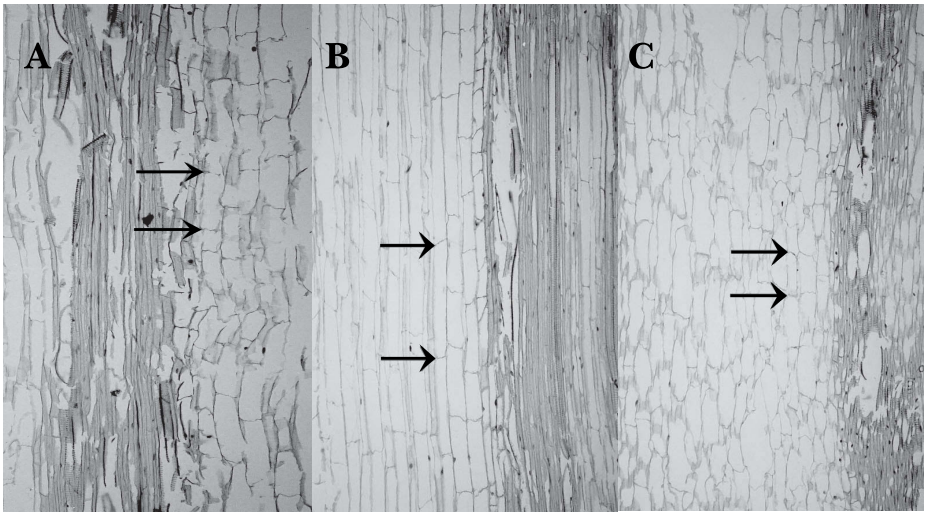

Fig. 5 Longitudinal section of mesocotyl cells of 3681-4 treated with GA_3 and UCZ under 20 cm seeding depth. A, control; B, GA_3 treatment; C, UCZ treatment. Arrows indicate the length of mesocotyl cells.

and seedling emergence from the shallow layer of sand. This suggestion may be supported by a previous report that the endogenous hormone level is optimal for hypocotyl elongation of wild-type Arabidopsis and the additional hormone has no effect (Collett et al., 2000).

From the comparison between shallow seeding and deep seeding, we further found that deep seeding contributed to the sensitivity of mesocotyl elongation to GA_3. Similarly, the first internode elongation of Hong Mang Mai was more sensitive to GA_3 under the deep seeding condition than under the shallow seeding condition (Chen et al., 2003). Furthermore, we also found that there existed possible interaction between deep seeding and GA. In our study, endogenous GA content was higher under the deep seeding condition than under the shallow seeding condition. Deep seeding possibly promotes GA biosynthesis, which need to be verified by further experimentation.

In addition, the changes of endogenous GA content were in accordance with the morphological responses to the application of GA_3 and UCZ, indicating that mesocotyl elongation was closely correlated with endogenous GA level. Consistent results were reported by Nishijima et al. (1997) and Chen et al. (2001). Their results showed that the GA level was lowered by application of UCZ, which strongly inhibited stem elongation of *Raphanus sativus* and that the GA content of the first internode of Hong Mang Mai was doubled by GA treatment. According to Zhou and Leul (1998), UCZ-treated plants had lower endogenous GA content and higher abscisic acid (ABA) content. The recent studies showed that UCZ inhibited the activity of ABA 8´-hydroxylase, a major ABA catabolic enzyme and *ent*-kaurene oxidase activity (Saito et al., 2006; Sawada et al., 2008). These results suggested that UCZ inhibited GA biosynthesis as well as ABA catabolism.

GA influences cell elongation and cell division (Tanaka et al., 2003). To examine whether cell division, cell elongation, or both contributed to the changes of mesocotyl growth induced by GA and its inhibitor, we conducted microscopic observation. Our results suggested that GA_3 promoted mesocotyl elongation via cell elongation rather than cell division. Consistent results were reported by Cowling and Harberd (1999) and Chen et al. (2003). Their studies showed that the application of GA_3 dramatically promoted the elongation of Arabidopsis hypocotyl and the first internode of Hong Mang Mai via cell elongation. In contrast, UCZ suppressed mesocotyl elongation via inhibition of both

cell elongation and cell division. The results obtained here are comparable with those obtained by Tanaka et al. (2003). Their result showed that Brassinosteroid biosynthesis inhibitor suppressed cell elongation of Arabidopsis hypocotyls but had no effect on cell division.

Acknowledgments

We thank Dr. Dong Xuehui (China Agricultural University) for his kind gift of uniconazole. We also thank Dr. Wang Baoming (China Agricultural University) for the measurement of endogenous GA_1 content. This work is supported by the Natural Science Foundation of China (30730063).

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