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Effect of Ascorbic Acid on the Gravitropic Response of Primary Roots in Maize

Chung Su Kim[1], Timothy J. Mulkey[2] and Soon Young Kim[1]*

[1]*Department of Biological Sciences, Andong National University, Andong 760-749, Korea*
[2]*Department of Biology, Indiana State University, Terre Haute, IN, 47809, USA*

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Ascorbic acid (AA) is a multifunctional metabolite in plants that is essential for plant development and growth. We examined the effect of AA, an antioxidant, on the gravitropic response of primary roots in maize. The application of 10^{-3} M AA to the elongation zone did not affect the gravitropic response and slightly inhibited the root growth. However, treatment with both 10^{-5} M and 10^{-3} M AA at the root tip increased the gravitropic response and inhibited root growth. Differences in indole-3-acetic acid (IAA) activity between the upper and lower hemispheres of the root resulted in differential elongation along the horizontal root. Roots are extremely sensitive to IAA, and increasing the amount of IAA in the lower hemisphere of the root inhibited elongation. Therefore, we examined the effect of IAA in the presence of AA. The inhibitory effect of AA on the gravitropic response was greater in combination with IAA. To understand the role of AA in the regulation of root growth and the gravitropic response, we measured ethylene production in the presence of AA in the primary roots of maize. AA stimulated ethylene production via the activation of the 1-aminocyclopropane-1-carboxylic acid (ACC) oxidase gene, which regulates the conversion of ACC to ethylene. These results suggest that AA alters the gravitropic response of maize roots through modification of the action of ethylene.

Key words : Ascorbic acid (AA), ACC oxidase, ethylene, gravitropic response

Introduction

Plants detect and respond to external signals from the environment including light and gravity. After perceiving these stimuli, plants respond through various physiological pathways. Gravity is one of the important stimuli involved in the regulation of plant growth and development [5]. In response to gravity, roots exhibit downward growth into the soil permits absorption of water and minerals, and stems grow upright to utilize sunlight for photosynthesis [4]. Gravitropism is a fundamental response required for plants to survive on land. Roots of maize sense gravity in the columella cells of the root tip in which amyloplast sediment based on the gravitational vector. The gravity signal is passed from root cap to the elongation zone where asymmetric auxin distribution is established which induces curvature as a result of differential growth in horizontally-oriented root [3]. Additionally, the gravity signal affects several physiological responses, such as ions concentrations and reactive oxygen species [10, 12, 18]. The signal detection and transduction steps of gravitropic response are not fully understood.

Ascorbic acid (AA) is a multifunctional metabolite in plants that is essential for plant development and growth. Ascorbic acid has been shown to play a role in redox systems as an antioxidant in plants [2]. Ascorbic acid prevents cellular damage associated with ozone exposure in plants due to the ability of AA to scavenge reactive oxygen species (ROS) [6]. Besides its protective role against oxidative damage, it is proposed that AA may be involved in other processes including cell signaling, differentiation, and programmed cell death [7, 9]. The ROS generated in the cell may be a potential signaling molecule in the control of physiological responses, such as gravitropism [12]. Ascorbic acid oxidase (AAO) catalyzes the dioxygen reaction, the reduction of molecular O_2. AAO oxidizes two ascorbic acid molecules and reduces molecular O_2 to two water molecules, yielding two dehydroascorbic acid (DHA) molecules [8].

Ethylene, a gaseous plant hormone, is one of the stress hormones and participates in various plant development and differentiation reactions including seed germination, fruit ripening and senescence [1]. Ethylene synthesis begins

***Corresponding author**
Tel : +82-54-820-5647, Fax : +82-54-820-7705
E-mail : kimsy@andong.ac.kr

from methionine via two major intermediates, S-adenosylmethionine (AdoMet) and 1-aminocycopropane-1-carboxylic acid (ACC), in sequence. The enzyme of ACC synthase (ACS) and ACC oxidase (ACO) regulate the steps from AdoMet to ACC and from ACC to ethylene, respectively. Several factors regulate these two enzymes, especially auxin which stimulates the ethylene production through increasing the expression level of the ACS gene [25]. There are findings that ethylene regulates the root growth and gravitropism via alteration of auxin transport [14, 21], and ethylene is require for root penetration in soil with auxin [22].

In this research, we examine the effect of AA on the gravitropic response since ROS is suggested as one of the signal to regulate cellular responses, including gravitropism in roots. According to Joo et al. [12], ROS stimulated gravitropic curvature and antioxidants, such as N-acetylcyctein, inhibited gravitropism. Recently, Lee et al. [16] suggested that AA stimulated the gravitropic curvature in Arabidopsis root, and Jiang et al. [11] suggested that exogenously applied H_2O_2 inhibits the root curvature during germination in grass pea (*Lathyrus sativus* L.). Based on these reports, we examined the role of ascorbic acid on the gravitropic response in maize root. An agar block system was used to apply the chemicals to specific regions such as root tip or elongation zone in maize root. Further, we investigated the possibility that ascorbic acid plays a role in gravitropic response via ethylene production.

Material and Methods

Plant Material

Maize seeds (*Zea mays* L., Golden × Bantam 70) were soaked in aerated tap water for 12 hr and then placed on wet paper towels held between opaque plastics trays in a vertical position. The trays were kept in the incubator at 27 ℃. The seedlings were used when the primary roots were approximately 1.5 cm long (42 hr after planting).

Measurement of Ethylene Production

Ethylene production was measured in 10 mm root segments excised from the tips of maize roots. The root tips were placed in 25 ml, silicon-capped vials containing 0.5 ml of potassium phosphate buffer (50 mM, pH 6.8) containing the test compounds. The vials were shaken in the dark at 27℃ in an incubator. After incubation, 1-ml of gas sample was withdrawn from the vial with a syringe and injected to the gas chromatograph (HP5890 Series II; Hewlett-Packard, USA) equipped with an alumina column (80/100 Porapak-Q; 1.8-m × 2.1-mm).

Determination of root growth and gravitropic curvature

Chemicals to be tested were incorporated into agar blocks (0.6% agar; 1 mm^3). The agar blocks were applied to the root tip and the seedling oriented horizontal or vertical in a chamber with near saturating humidity (>98%). Growth rate and curvature were monitored using a camera (Rexsa, DS-400 PC-camera) and time-interval software (SupervisionCam ver. 3.2.2.4; http://supervisioncam.com). Images were recorded at 15 min intervals. The images were analyzed using UTHSCSA Image Tool Program (ver. 3.0; http://comdent.uthscsa.edu/dig/itdes.html).

Assay of *in vivo* ACC oxidase (ACO) activity

The analysis of ACO activity was performed in vivo as described by Wang and Woodson (1989). Root segments were incubated in a 50 mM potassium phosphate buffer (pH 6.8) containing 0.1 mM aminoethoxyvinylglicine (AVG). After 1 hr incubation, the root segments were washed with distilled water, and infiltrated for 2 hr with 1 mM ACC at 27℃ in the dark. After the infiltration of ACC, roots are completely washed with distilled water, and ethylene production was performed using the prior procedure in potassium phosphate buffer, without ACC or other chemicals. The ethylene production is regarded as *in vivo* ACO activity.

Extraction of Total RNA and RT-PCR

Tissue samples were ground into a powder with a mortar and pestle under liquid nitrogen. The powder was suspended with an RNA extraction buffer [0.1 M Tris-HCl (pH 9.0), 0.1 M NaCl, and 1% SDS]. A volume of phenol: chloroform: isoamylalcohol (25:24:1; v:v:v) equal to the volume of the buffer was added and the mixture incubated for 10 min at 50℃. The reaction mixture was centrifuged at 13,000 rpm for 15 min at 4℃; the supernatant was transferred into new tubes and incubated with 2.5 M LiCl for 30 min at -20℃. The mixture was centrifuged for 15 min at 13,000 rpm (4℃); the pellet was washed with 70% ethanol and dissolved in DEPC-treated water. Total RNA was quantified at 260/280 using a microplate reader (Microplate Reader Infinite® 200, Tecan Group Ltd, Morrisville, NC, USA).

The purified total RNA was used for first-strand complementary DNA synthesis in a AccuPower® RT Premix (Bioneer, Korea). Polymerase chain reaction (PCR) conditions included 30 cycles of denaturing at 95℃ for 5 min, annealing at 55℃ for 20 s, and extension at 72℃ for 5 min; and, a final elongation step at 72℃ for 10 min. The gene-specific primers were used as listed in Table 1. ZmACO31 and ZmACS7 are primers for ACC oxidase and ACC synthase gene in maize, respectively. The gels were analyzed using Gel Image Analysis System (Core, i-MAX-D500, Korea). The band density was measured and normalized with that of the GAPDH gene expression.

Statistical Analysis

All experiments were conducted at least three times, with no fewer than 40 primary roots each. To test for significance at p values of <0.05, the data mean values were calculated according to Student's t-test.

Results and Discussion

Effects of AA on the growth and gravitropic response in the elongation zone

Agar blocks (0.6% agar; 1 mm^3) containing each concentration of ascorbic acid provided point application of the compound to the maize roots. The gravitropic response could be mediated by alteration of the sensory mechanism in the tip of the root and/or by effects in the elongation zone. To examine the effect of ascorbic acid on the root growth, the point applications of agar blocks containing AA were made to the elongation zone of root. Root growth was slightly inhibited at 10^{-3} M AA application, whereas it was not inhibited at 10^{-5} M AA. Gravitropic curvature was not significantly inhibited nor stimulated by AA application to the elongation zone (Fig. 1). These data suggest that AA applied to the elongation zone did not alter differential elongation to result in gravitropic curvature, but AA application did slightly inhibited growth. Based on this result, we suggested that the high concentration of AA could inhibit root growth. The gravity signal is passed from root cap to the elongation zone where asymmetric auxin distribution is established which induces curvature as a result of differential growth in horizontally-oriented root [3]. To examine the possibility of the role of AA in the gravitropic response, we applied the AA to the root tip which may affect the IAA redistribution in the elongation zone when roots perceive gravity.

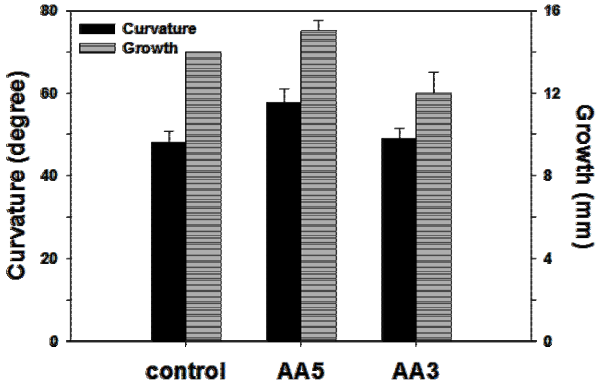

Fig. 1. Effect of ascorbic acid (AA) on the gravitropic curvature and growth in the elongation zone for 4 hr. AA was applied to the root tip using an agar block (0.6%, 1 mm^3). The gravitropic curvature and growth was measured at 4 hr after treatment. Bars are mean values ± SE from 9 independent experiments.

Effects of AA on the growth and gravitropic response in the root tip

Application of AA to the tip region of the root stimulated the gravitropic response at concentrations of 10^{-5} M and 10^{-3} M after 4 hr while inhibiting root growth (Fig. 2). Especially, the gravitropic response was stimulated 16% and 50% of control by the treatment of 10^{-5} M and 10^{-3} M AA respectively. The root growth was inhibited about 20% of control by the treatment of both 10^{-5} M and 10^{-3} M AA. Dehydroascorbic acid (DHA), a fully oxidized form of AA, did not affect the both gravitropic response and root growth (data not shown).

The curvature of roots in response to gravity results from differential growth along opposing sides of the organ. The gravitational signal recognized in the root cap is transduced

Table 1. Gene-specific primers used for RT-PCR experiments

Gene (accession no.)	Forward (5′ to 3′)	Reverse (5′ to 3′)
ZmACO31 (HM_001111764)	CTGTTCAGGACGACAAGGT	GCCTGGAACTTCTGCTTGAC
ZmACS7 (HM_001152929)	GTTGGACCTGATCGAGCAAT	AGCTTCACTCCTGACCTCCA
GAPDH	CTGGTTTCTACCGACTTCCTTC	CGGCATACACAAGCAGCAAC

ZmACO31 and *ZmACS7* are primers for the ACC oxidase and ACC synthase gene from maize (*Zea mays* L.), respectively.

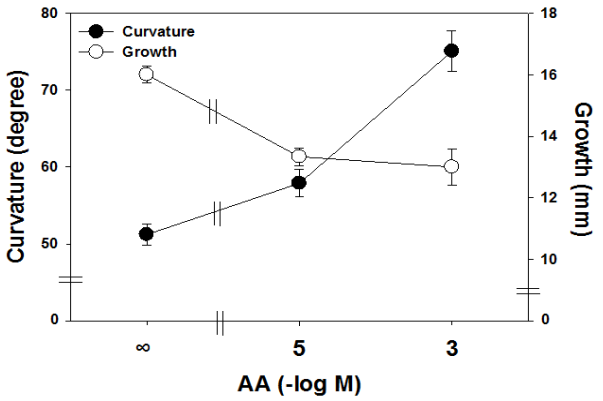

Fig. 2. Effect of ascorbic acid (AA) on the gravitropic curvature and growth in the root tip for 4 hr. AA was applied to the root tip using an agar block (0.6%, 1 mm^3). The gravitropic curvature and growth was measured at 4 hr after treatment. Symbols are mean values ± SE from 9 independent experiments.

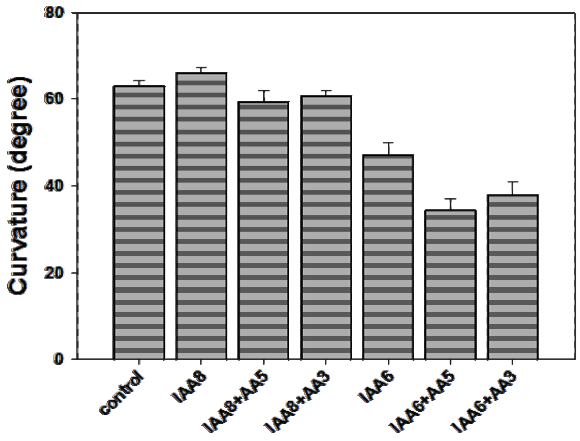

Fig. 3. Effect of ascorbic acid (AA) and IAA on the gravitropic curvature in the root tip for 4 hr. AA and IAA was applied to the root tip using an agar block (0.6%, 1 mm3). The gravitropic curvature was measured at 4 hr after treatment. IAA8: 10^{-8} M IAA; IAA6: 10^{-6} M IAA; AA5: 10^{-5} M AA; AA3: 10^{-3} M AA. Bars are mean values ± SE from 9 independent experiments.

from the tip to the elongation zone resulting in differential growth. It is widely accepted that differences in indole-3-acetic acid (IAA) activity between the upper and lower hemispheres of the root results in the differential elongation along the horizontal root [20]. Roots are extremely sensitive to IAA and increasing the amount of IAA in the lower hemisphere of the root results in inhibition of elongation [19]. Therefore, IAA is one of the major factors to induce the differential elongation during the gravitropism curvature [18]. Ascorbic acid might induce transport of IAA to the elongation zone, resulting in the inhibition of growth; ascorbic acid also may play a role of redistribution of IAA in the elongation zone between upper and lower side of the root and result in stimulation of gravitropic curvature. The findings of Lee et al. [16] suggest that AA can alter the auxin transport system in Arabidopsis roots. They reported that AA stimulated gravitropic response over a range of concentrations from 10 μM to 1 mM in Arabidopsis root. In those studies, an AA biosynthesis mutant of Arabidopsis exhibiting a greatly reduced level of AA, showed the suppression of root elongation and gravitropic response [16]. These data suggests that AA may act on the IAA redistribution in the elongation zone when the root perceived the gravity in the root cap.

In order to determine the relationship between AA and IAA, we measured the curvature of roots treated with IAA and AA. Roots were pretreated with the solution containing both IAA and AA for 30 min in vertical position, and measured the gravitropic response in horizontal roots. When 10^{-8} M IAA was applied to the root, the gravicurvature did not change compared to the control (Fig. 3). And the treatment of 10^{-8} M IAA with AA to the root also did not have a significant effect on the inhibition of curvature (Fig. 3). However, gravicurvature was inhibited about 25% of control by the treatment of 10^{-6} M IAA alone. However, AA exerted the inhibition of gravitropic curvature in the presence of 10^{-6} M IAA, even though 10^{-3} M AA stimulated the curvature without IAA, as shown in Fig. 2 (Fig. 3). These data suggested that AA may have an effect on lateral transport of IAA from the upper to the lower side when root tip perceive the gravity.

It has been reported that ethylene inhibits the elongation of stem and roots [23]. Inhibition of root elongation by IAA can be reversed by the treatment of the tissue with ethylene antagonists [13]. Lee et al. [15] suggested ethylene may modify positive curvature in the primary roots of maize by affecting gravity induced-lateral auxin transport. Kim et al. [14] suggested that an optimal concentration of ethylene might be required for the regulation of gravitropism in maize roots. Based on these results, AA may affect the gravity induced-lateral IAA transport in maize root resulting in the inhibition of curvature by AA in the presence of IAA. In an attempt to explain the effect of AA, we measured modification of ethylene production in the presence of AA. These data may provide insight into the inhibition of growth and gravicurvature in the elongation zone by AA.

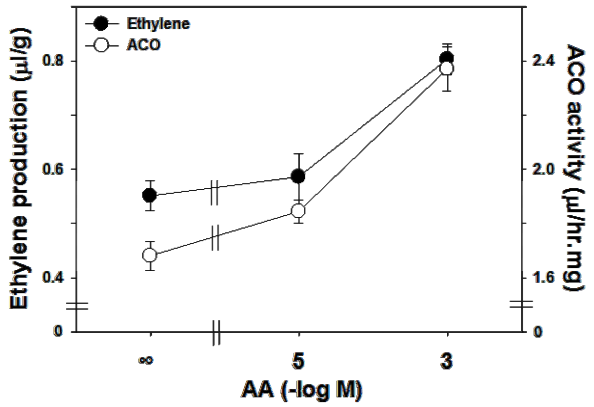

Fig. 4. Effect of ascorbic acid (AA) on the ethylene production and ACO activity in the root segments for 4 hr. Root segments were incubated for 4 hr in solution containing 10^{-5} M and 10^{-3} M AA. At 4 hr, 1 ml of gas sample was withdrawn from the vials for measuring ethylene production. ACO activity was assayed with intact root segments incubated for 4 hr in solution containing 0.1 mM AVG with AA as described in Material and Methods. AA5: 10^{-5} M AA; AA3: 10^{-3} M AA. Symbols are mean values ± SE from 9 independent experiments.

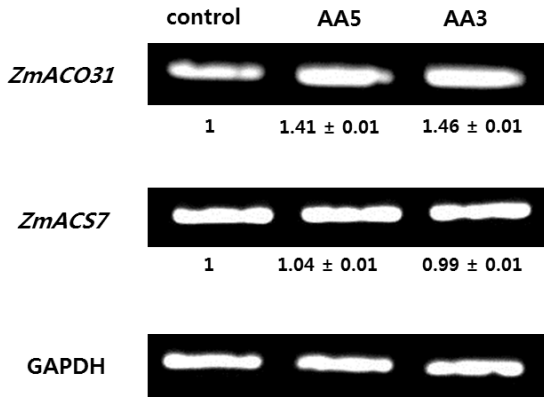

Fig. 5. Effect of ascorbic acid on gene expression levels for ACC oxidase and ACC synthase. Root segments were incubated for 4 hr in solution containing potassium phosphate buffer (50 mM, pH 6.8) with AA. Total RNAs were extracted and used for RT-PCR as described in Material and Methods. AA5: 10^{-5} M AA; AA3: 10^{-3} M AA; *ZmACO31*: ACC oxidase gene; *ZmACS7*: ACC synthase gene; *GAPDH*: control. Gel image shows results with consistent patterns from 6 independent experiments. The values of band density are mean values ± SE from 6 independent experiments.

Effect of AA on the ethylene production

External application of AA stimulated the ethylene production in the concentration of 10^{-5} M and 10^{-3} M AA for 4 hr (Fig. 4). The treatment of 10^{-3} M AA increased about 60% of control at 4 hr. Typically, ethylene affects the growth pattern of plants by reducing the rate of elongation and increasing lateral expansion, leading to swelling of the tissue and modifying the gravitropic response [1]. Thus, the slight inhibition of growth by AA in the elongation zone (Fig. 1) may be due to the increasing ethylene production by AA treatment. Additionally, the inhibition of gravitropic response by in combination with IAA (Fig. 3) could be related to the modification of gravity-induced lateral auxin transport in the root by ethylene. Ruzicka et al. [21] reported that ethylene stimulated auxin biosynthesis and increased the capacity of auxin transport by regulating the transcription of auxin transport components such as AUX1 and PIN2. The increase in auxin production due to ethylene could alter redistribution of auxin, by polar auxin transport, from root cap to the elongation zone via outer cell layer, to the elongation zone where auxin could inhibit cell elongation. Recently, Ma and Ren [17] reported during the germination of flax, the gravitropic response of the flax root becomes weaker due to a decrease in auxin sensitivity and decrease in auxin transport regulated by ethylene. Therefore, stimulation of ethylene production by AA treatment could regulate auxin movement and/or lateral auxin transport in horizontal roots. To confirm the action of AA on ethylene production (Fig. 4), we measured the activity of ACC oxidase (ACO). ACO is involved in the conversion of ACC into ethylene. ACO activity was increased depending on the AA concentrations at 4 hr in the same pattern as the ethylene production (Fig. 4). Therefore in this system, AA stimulates ethylene production via the activation of ACO.

To confirm this result, we determined whether AA activates the expression of the ACO and ACS gene through conducting RT-PCR. The expression level of *ACO31* was increased about 1.41 and 1.46 fold by 10^{-5} M AA and 10^{-3} M AA, respectively (Fig. 5). However, AA had no apparent influence on the ACS gene. ACS is the enzyme catalyzing the step from AdoMet to ACC in the ethylene production in plants.

Conclusion

In these studies, AA stimulated gravitropic curvature of maize roots and increased the ethylene production via activation of ACO when AA was applied to the root tip. However, AA applied to the elongation zone of the root did not stimulate the gravitropic response, and root growth slightly was inhibited. The increased ethylene may regulate

the auxin transport and/or lateral auxin transport from root tip to elongation zone resulting in differential growth in the elongation zone and lateral transport of auxin from upper to the lower side in horizontal position. These data suggested that redox environment in soil in which AA involved might affect the root growth and gravitropism.

Acknowledgement

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초록 : 옥수수 일차뿌리에서 Ascorbic acid가 굴중성 반응에 미치는 효과

김충수[1] · Timothy J. Mulkey[2] · 김순영[1]*
([1]안동대학교 생명과학과, [2]인디애나 주립대학교 생물학과)

Ascorbic acid (AA)는 식물 발달과 생장에 필수적인 다기능성 대사산물이다. 본 연구에서는 항산화제인 AA가 옥수수 일차 뿌리에서 굴중성 반응에 미치는 효과를 조사하였다. 10^{-3} M AA를 신장대에 처리하면 뿌리 굴중성 반응은 영향을 받지 않고 뿌리 생장은 약간 억제되었다. 그러나 10^{-5} M과 10^{-3} M AA를 뿌리 끝에 처리하였을 때, 뿌리 굴중성 반응은 촉진된 반면, 뿌리 생장은 억제되었다. 수평으로 놓인 뿌리의 윗면과 아랫면에서 IAA함량의 차이는 차등 생장을 유발한다. 뿌리는 IAA에 대하여 매우 민감하여 아랫면에 증가된 IAA는 뿌리 생장을 억제한다. 그러므로 본 연구에서 AA가 존재할 때 IAA의 효과를 조사하였다. AA는 IAA와 함께 처리하면 굴중성 반응을 더욱 억제시켰다. 뿌리 생장과 굴중성 반응의 조절에 관여하는 AA의 작용을 알아보기 위하여, AA를 처리한 후 에틸렌 생성을 측정하였다. AA는 ACC가 에틸렌으로 전환되는 단계를 조절하는 ACC oxidase gene을 활성화시켜 에틸렌 생성을 촉진하였다. 이 결과는 AA가 에틸렌 작용의 조절을 통하여 옥수수 뿌리에서 굴중성 반응에 영향을 준다는 것을 제시한다.