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Physiological and morphological responses induced by α-particle radiation on *Arabidopsis thaliana* embryos

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ABSTRACT. Alpha (α)-particle radiation has been thoroughly studied in the occupational and residential environments, but biological mechanisms induced by α-particle radiation on plants are not clearly understood. In this study, radiation effects were examined using different total doses (1, 10, 100 Gy, respectively) of ^{241}Am, α-particle on *Arabidopsis* embryos. No significant difference in the germination percentage was observed between the 3 levels of doses and the control. Germination speed and root length were increased by treatment with the 1-Gy dose of α-particles, and decreased by treatment with 10- and 100-Gy doses. Moreover, the bending degree of roots increased with radiation dose, and the roots showed an "S" shape when treated with the 100-Gy dose. Root bending under the 100-Gy dose was inhibited by scavengers of reactive oxygen species (ROS). Root gravitropism and root length may respond to the consistency of ROS induced by irradiation.

Further analysis of the physiological effects revealed that an increase in α-particle radiation intensity enhanced the activity of catalase and the content of malondialdehyde, but superoxide dismutase activity was reduced by treatment with 100-Gy radiation of α-particles, suggesting that the high linear energy transfer of α-particles may cause a relatively high level of membrane lipid preoxidation and high accumulation of ROS. ROS showed both physiological and morphological responses following exposure to α-particle radiation in *Arabidopsis* embryos.

Key words: Alpha-particle radiation; *Arabidopsis* embryos; Enzyme activity; Reactive oxygen species

INTRODUCTION

Alpha (α)-particle radiation is present in the occupational environment (i.e., medical imaging and cancer therapy) and in the residential environment, primarily from radon gas (Chauhan et al., 2011). Radon gas exposure accounts for as much as 55% of the background radiation dose (Garnier-Laplace et al., 2004). The concentration factors of ^{241}Am for seston of the Yenisei River were 2.8-6.9 x 10^5 (Zotina et al., 2010). Nearly 9% of cosmic rays, which enter the earth's atmosphere, are α-particles. As a form of ionizing radiation, its biological effects have been widely studied. α-particle radiation exposure has been shown to result in a variety of genetic lesions, including chromosomal damage (Kennedy et al., 1996), gene mutations (Hei et al., 1988), induction of micronuclei (Bilbao et al., 1989), sister chromatic exchanges (Nagasawa and Little, 1992), bystander mutagenic effects (Li et al., 2010), and DNA double-strand break (Hu et al., 2005a). To date, studies of α-particle radiation have been performed primarily using animal tissues and cells (Belyakov et al., 2003; Wong et al., 2010). Accordingly, plant physiological and morphological responses induced by α-particle radiation are not well understood. External irradiation by α-particles is an unconventional method of stimulating α-particle exposure. As an important radioisotope in the nuclear industry and other fields, contamination by ^{241}Am is a serious concern due to its high toxicity and long half-life. More than 98% of the total ^{241}Am could be adsorbed from ^{241}Am solution of 0.32-1.1 x 10^{-7} M by the soil at pH 4-9 (Liu et al., 2007). We investigated whether α-particles emitted from ^{241}Am radiation decreased the growth rate of plants such as *Arabidopsis thaliana* and whether morphological or physiological changes occurred.

Arabidopsis is a widely used specimen in plant biology research. The shoot apical meristem and root apical meristem cell groups of an *Arabidopsis* seed are nearly entirely responsible for the postembryonic development of the plant architecture (Capron et al., 2009). The shoot apical meristem is responsible for development of the aerial parts of the plant, while the root apical meristem leads to development of the subterranean root system (Kaya et al., 2001; Capron et al., 2009). Previous *Arabidopsis*-based studies have indicated some specific mechanisms of plants induced by other types of irradiation, such as UV radiation (Jiang et al., 1997; Danon and Gallois, 1998), gamma radiation (Jiang et al., 1997), and microbeam radiation (Yang et al., 2007). Ionizing radiation typically induces production of reactive oxygen species (ROS), which includes singlet oxygen, superoxide anion , hydrogen peroxide (H_2O_2), and hydroxyl radical. ROS play a key role in the biological effects of radiation exposure.

Plant cells are distinguishable from mammalian cells by the thick cell wall that provides protection and structure. Because of the short penetration distance of an α-particle, the embryos of *Arabidopsis* were dissected from the seeds and the *Arabidopsis* embryos were irradiated to estimate the biological effects of α-particle radiation on *Arabidopsis* embryos.

MATERIAL AND METHODS

Embryo dissection from seeds and α-particle radiation

Natural origin *A. thaliana* (ecotype Columbia) seeds were obtained from the Nottingham *Arabidopsis* Stock Center, UK. All seeds were placed in 1.5-mL centrifuge tubes, which were pretreated at 4°C with sterile water for 3 days to synchronize germination and thoroughly washed prior to dissection (Fu and Harberd, 2003). Embryos were then obtained by divesting of the testae of seeds using forceps. Whole embryos were placed on a 3.5-μm thick Mylar membrane, which formed the base of a dish. To maintain air humidity approaching 100%, drops of water were added to the Mylar membrane.

Prepared embryos were irradiated with α-particles emitted from a ^{241}Am-radiation source. The average α-particle energy of the embryo layer was 3.5 MeV. The dose rate was 1.28 cGy/min for the irradiated group. Embryo groups were irradiated at doses of 1, 10, and 100 Gy. Radiation times were 47 min, 7 h 49 min, and 78 h 8 min, respectively. Embryos were then incubated with controls on Murashige and Skoog (MS) medium (mixed 8 g agar with 1 L water). The temperature in the growth chamber was 23°C, with an illumination of approximately 6.02 x 10^{19} photons·m^{-2}·s^{-1}. A 16-h light/8-h dark cycle was used. Seedlings were transplanted into nutrient soil in pots (Φ = 90 mm) in the same growth room until 4 leaves appeared.

The penetration depth of irradiation in *Arabidopsis* embryos is simulated and predicted by the program SRIM (2003), and results show that the depth is approximately 22 μm.

Assessment of embryo germination

Germination ability can be tested by germination speed and germination rate. Germination speed indicates the speed and uniformity of germination, while germination rate is the percentage of seeds that germinate normally under given conditions over a sufficient period of time. The method used to test germination ability was modified from the method described by Munir et al. (2001). The number of germinant was recorded after 4 days. The germination speed for the total number of 4-day germinant was divided by the total number of viable seeds. The number of germinant after 7 days was also recorded, and the germination rate was calculated: total number of 7-day germinant divided by total number of viable seeds.

Determination of alteration on root gravitropism induced by α-particle

Root images were acquired using a digital camera (DSC-F505V, SONY). Curvature degree was determined using a protractor and the Image J software (NIH, Bethesda, MD, USA). "N" was marked if the degree was below 30°, while "S" indicated a curvature degree above 30°.

ROS localization

Five-day-old seedlings were used to localize the generation of ROS in the root. A total of 50 μM CM-H_2DCFDA (Sigma, St. Louis, MO, USA) was used as a molecular probe, and the roots were stained for 30 min. Next, the roots were washed with sterilized water. The roots were observed using fluorescence microscopy.

Enzyme activity measurement

Leaf tissues (0.2-1.0 g) were homogenized in 50 mM ice-cold phosphate-buffered saline, pH 7, containing 1% polyvinylpyrrolidone, then centrifuged at 10,000 *g*, 4°C for 10 min. The supernatant was used as an enzyme source and was used to determine the activities of superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6), and contents of malondialdehyde (MDA). CAT, SOD, and MDA Activity Assay Kits, obtained from the Nanjing Jiancheng Bioengineering Institute (Jiangsu, China), were used to measure CAT, SOD, and MDA activities, respectively. One unit of SOD activity is defined as the amount of enzyme required to inhibit the reduction of NBT by 50% per mg protein, and 1 U CAT activity was defined as the amount of enzyme required for 0.50-0.55 H_2O_2 absorbance of substrate of 1 g protein per second. The model of the spectrophotometer was the TU-1901(Beijing Puxi, Beijing, China).

Data analysis

Data are reported as means ± standard errors of the mean (SE) and statistical significance was analyzed using Origin 6.0 (Microcal Software, Northampton, MA, USA). If the probability was less than 0.05, the values of treatments were considered to be significantly different when compared to controls. For a statistical evaluation of difference, the PASW Statistics 18.0 software (SPSS, Inc., Chicago, IL, USA) was used. The means of at least 3 repetitions of each parameter were assessed. The significance of the differences between every 2 treatments was evaluated by the analysis of the variance based on the method of Tukey contrasts (one-way analysis of variance test) with a P value of 0.05.

RESULTS

α-particle induced effects on germination ability and root length of *Arabidopsis* embryos

Germination rate was not significantly different between irradiated groups and the non-irradiated group (96%, $P > 0.05$), while α-particle-induced effects on germination speed were significant. The group treated with 1-Gy doses of α-particle had a higher germination speed (82.4%) than the non-irradiated group (70.8%), but the 10-Gy group showed a lower germination speed than the non-irradiated group (42.3%), and a significantly inhibitory effect on germination speed was observed at a dose of 100 Gy (29.1%; Table 1). Morphologically, germination speed was stimulated when treated with low-dose α-particles, but stunted at higher doses of α-particle.

Table 1. Germination percentage, germination speed, root length, and root curvature angle of *Arabidopsis* embryos irradiated with graded doses of α-particles.

Radiation doses (Gy)	Germination percentage	Germination speed (%)	Root length (cm)	Root curvature angle (°)
Control (0)	96.0 ± 1.8^{A}	70.8 ± 13.5^{B}	2.6 ± 0.3^{B}	12.5 ± 2.4^{C}
1	96.1 ± 1.7^{A}	82.4 ± 8.9^{A}	3.3 ± 0.4^{A}	13.3 ± 2.3^{C}
10	96.3 ± 1.2^{A}	42.3 ± 14.7^{C}	2.2 ± 0.3^{C}	28.7 ± 3.5^{B}
100	96.2 ± 0.9^{A}	29.1 ± 13.1^{D}	1.6 ± 0.4^{D}	69.1 ± 4.8^{A}

Data are reported as means ± SE and pooled from 3 individual experiments. Data with different letters in the same column are significantly different ($P < 0.05$) from each other.

Similar effects were observed on the root length of *Arabidopsis* embryos cultivated on the MS medium. After 10 days, the root length of plants in the 1-Gy group significantly increased to 3.3 cm, while those of the non-irradiated group were 2.6 cm. The root length of the 10- and 100-Gy groups decreased to 2.2 and 1.6 cm, respectively, which differed significantly from the control ($P < 0.05$; Table 1).

α-particle induced effects on root gravitropism

Root gravitropism has been examined physiologically and genetically, with many studies proposing that columella cells are the primary contributors to root gravitropism. α-particle radiation can cause cell activation by efficiently producing DNA double-strand breaks and through irreparable DNA damage. However, the effects of such DNA changes on root gravitropism have not been clearly defined. In this study, α-particle induced effects on root gravitropism showed a positive correlation with irradiation dose ($r = 0.98$). The curvatures of roots treated with 1, 10, and 100 Gy were 13.3°, 28.7°, and 69.1°, respectively, which were higher than values in the non-irradiated group (Table 1). Additionally, the root shape after 100-Gy treatment showed an "S" shape (data not shown).

α-particle radiation induces ROS accumulation in *Arabidopsis* root tips

Several lines of evidence suggest that ROS serves as a signaling molecule in plants. In this study, ROS generation in the primary root tip of *Arabidopsis* was monitored using CM-H_2DCFDA (Molecular Probes, Eugene, OR, USA). Fluorescent expression in the 100-Gy group was much more significant than that in the non-irradiated group (data not shown), indicating that α-particle radiation may have stimulated ROS accumulation in the *Arabidopsis* root tip, further mediating root gravitropism.

Scavenging of ROS inhibits *Arabidopsis* root gravitropism and root growth

To confirm that α-particle radiation accelerates production of ROS, the effects of root treatment with vitamin C (Vc; Sigma), an antioxidant, were investigated. Treatment with 0.2 mM Vc inhibited root gravitropism in the 100-Gy group, but treatment with 0.02 mM Vc had no similar effect (Table 2). This indicated that a high concentration of ROS in *Arabidopsis* embryo roots was induced by 100-Gy α-particle radiation, and that irradiation further induced ROS mediated root gravitropism.

Table 2. Root length of the 6th day seedlings on vitamin C (Vc) containing MS medium.

Vc content for dipping (mM)	Radiation doses (Gy)	MS + 0.2 mM Vc		MS + 0.02 mM Vc		MS	
		RL (mm)	RG	RL (mm)	RG	RL (mm)	RG
2	100	3.6 ± 0.7^{A}	N	11.6 ± 2.7^{A}	S	5.3 ± 1.8^{C}	S
0.5	100	2.2 ± 0.6^{B}	N	12.0 ± 2.1^{A}	S	7.2 ± 0.7^{B}	S
0	100	2.3 ± 0.3^{B}	N	8.2 ± 2.2^{B}	S	5.2 ± 1.6^{C}	S
0	0	3.3 ± 0.4^{A}	N	6.6 ± 2.0^{C}	N	9.2 ± 2.0^{A}	N

Data are reported as means ± SE for N = 3. Embryos pre-dipped with 0, 0.5, or 2 mM Vc, and irradiated with 100-Gy α-particles. The embryos were planted on Murashige and Skoog (MS) medium plates containing 0.2, 0.02, or 0 mM Vc. The control group received no irradiation. RL = root length; RG = root gravitropism. "N" = root gravitropism is "normal". "S" = root gravitropism is inhibited and root shape shows an "S" curve. Data with different letters in the same column are significantly different ($P < 0.05$) from each other.

Effects of Vc on root length of *Arabidopsis* embryos were also examined here. The root length of the 100-Gy group, which had been pretreated with 0.5 or 2 mM Vc, recovered on 0.02 mM Vc-containing MS medium, but was inhibited on 0.2 mM Vc-containing MS medium (Table 2).

We also investigated the effect of other antioxidants on gravitropism and root growth. Antioxidants such as *N*-acetyl-Cys and trolox, among others, showed an inhibitory effect on root gravitropism, similar to that of Vc (data not shown). All of these results suggest that α-particle radiation stimulates the production of ROS, which mediates root gravitropism and root growth of *Arabidopsis* embryos.

Changes of anti-oxidative enzymes and membrane peroxidation in *Arabidopsis* embryos treated with α-particle radiation

Plants possess antioxidant enzymatic systems that can scavenge ROS above a certain threshold. SOD and CAT, antioxidant enzymes, protect plants against oxidative damage caused by an adverse environment, such as UV-B or ion irradiation. CAT in *Arabidopsis* was activated after α-particle radiation, and its activity increased with increasing radiation doses. CAT activity in the 1-, 10-, and 100-Gy groups was 72.9, 85.9, and 102.6 U/g, respectively, while that of the control group was 61.8 U/g. These values were significant higher at 18, 39, 66% than control values at 1-, 10-, and 100-Gy radiation treatment, respectively. SOD activity was not significantly altered following treatment with 1- and 10-Gy doses of α-particles, but was decreased by 100-Gy doses (Table 3). Several researchers have also reported that a similar inhibition effect on SOD activity can be induced by ^{60}Co γ-rays (Kumar et al., 2011) and UV-B (Ren et al., 2007).

Table 3. Effects of the α-particle radiation on activity of catalase (CAT) and superoxide dismutase (SOD) and on content of malondialdehyde (MDA).

Radiation doses (Gy)	CAT activity (U/g)	SOD activity (U/g)	MDA content (nmol/g)
Control (0)	61.8 ± 7.1^{D}	407.6 ± 13.5^{A}	1.3 ± 0.2^{D}
1	72.9 ± 8.4^{C}	422.1 ± 18.9^{A}	1.7 ± 0.3^{C}
10	85.9 ± 7.9^{B}	412.5 ± 21.4^{A}	2.4 ± 0.5^{B}
100	102.6 ± 8.1^{A}	365.2 ± 15.7^{B}	3.7 ± 0.4^{A}

Data are reported as means ± SE and pooled from 3 individual experiments. Data with different letters in the same column are significantly different ($P < 0.05$) from each other.

MDA, a product of lipid peroxidation, can be used to measure the level of membrane damage. α-particle radiation promoted MDA production in *Arabidopsis* embryos, and MDA content was increased with the radiation doses. MDA content at 100 Gy was 3.7 nmol/g fresh weight (Table 3), which was 2.8 times higher than the control value. This suggests that irreparable membrane peroxidation can be induced by high linear energy transfer α-particle radiation.

DISCUSSION

A plant's stiff cell wall can function as a shield, and thus particular biological effects on plants can be induced by exposure to α-particle radiation. The radiation-induced bystander effects *in vivo* has been shown to exist in *A. thaliana* (Wang et al., 2012). Plants exposed to ionizing radiation must overcome direct and indirect deleterious effects (oxidative stress), in which intensity depends on the dose applied. On the basis of our results, we propose that both stimulatory and inhibitory effects can be induced by α-particle radiation of plants. We found that 1-Gy doses of α-particles can stimulate an increase in germination speed, root length, and SOD activity, but the value of these biological indexes decline continually with increasing doses (10 and 100 Gy) of α-particles in *Arabidopsis* embryos. Treatments at doses over 200 Gy were reported to repress shoot growth, and the plants perished following exposure to 800-Gy radiations (Kim et al., 2011). An exact number of proton radiation led to significant inhibition of root hair differentiation, primary root elongation, and lateral root initiation in *Arabidopsis* postembryonic development (Yang et al., 2007).

Recent findings suggested that ROS are important signaling molecules for regulating plant responses to high linear energy transfer α-particle radiation. Free radicals produced by α-particle radiation were found to be involved in genomic instability (Li et al., 2010). Localized α-particle radiation of roots induced short-term up-regulated expression of the homologous recombination-related AtRAD54 gene in non-irradiated aerial plants (Li et al., 2010). CAT can scavenge ROS beyond a threshold, and has been proposed to reflect H_2O_2 content in plants. In the mechanism studied here, the level of CAT significantly increased in irradiated *Arabidopsis* embryos with higher doses of α-particles, suggesting that high concentrations of H_2O_2 were induced in *Arabidopsis* embryos during the study period. Additionally, the 100-Gy dose treatment inhibited activity of SOD, indicating that overproduction of ROS exceeded the ability of the plant to scavenge the ROS. Excess ROS aggravated membrane peroxidation, resulting in high accumulation of MDA in the plant, finally inducing disorder in ROS and related biological responses. It is reported that 10-Gy treatments enhanced antioxidative compound biosynthetic pathways, while a 40-Gy dose up-regulated ROS-scavenging enzyme genes (Gicquel et al., 2012).

Our study showed that the correlation between root growth and irradiation dose was positive ($r = 0.98$) when exposed to irradiation of 0-100 Gy. ROS production in different plant subcellular compartments is the hallmark of the response to many stress stimuli and developmental cues. ROS has been shown to mediate systemic signal networks for plant defense, and takes part in mediating root gravitropism (Joo et al., 2001; Hu et al., 2005b). The shape of the root treated with a 100-Gy dose became "S" shaped, and similar phenomena have been reported previously. Tanaka et al. (2002) reported that heavy-ion microbeams of 120 μm in diameter promoted strong inhibition of root length and induced root curve. Joo et al. (2001) found that uneven accumulation of ROS in maize roots induced root curving, and provided

further evidence by placing H_2O_2-containing agar on one side of the root tips, resulting in root curvature towards the H_2O_2 source. Our investigation of ROS localization in the roots of *Arabidopsis* embryos revealed that more ROS accumulated in root tips treated with 100-Gy doses of α-particle than that of the control group, and that an appropriate concentration of ROS quencher could recover the biological effect induced by α-particle radiation. Thus, both morphological and physiological alterations, induced by α-particle radiation of *Arabidopsis* embryos, may be a response to ROS accumulation in the roots. It is reported that another ROS scavenger, dimethyl sulfoxide, reduced the effects of localized root irradiation on the induction of homologous recombination and expression of the AtRAD54 gene in bystander tissues, suggesting that ROS play a critical role in mediating bystander mutagenic effects in plants (Li et al., 2010).

Radiation-induced bio-effect has been demonstrated in whole organisms as well as in multicellular tissues *in vitro* and single-cell culture systems *in vitro* (Wang et al., 2011; Guo et al., 2013). Recent studies have shown that in response to UV radiation, mitochondria and chloroplasts produce ROS (Nawkar et al., 2013). Additionally, high linear energy transfer α-particle radiation may lead to excess ROS generation, inducing further morphological and physiological effects. Most ROS forms, such as singlet oxygen, superoxide anion, H_2O_2, and hydroxyl radical, inside of cells can react with a variety of molecules, and thus are characteristically highly reactive and unstable.

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