Journal of Plant Biology, December 2004, 47(4) : 314-321

Alterations in the Photosynthetic Pigments and Antioxidant Machineries of Red Pepper (*Capsicum annuum* L.) Seedlings from Gamma-Irradiated Seeds

Jin-Hong Kim*, Myung-Hwa Baek, Byung Yeoup Chung, Seung Gon Wi, and Jae-Sung Kim
Division of Radiation Application Research, Korea Atomic Energy Research Institute, Daejeon 305-353, Korea

To characterize the stimulatory effects of low-dose gamma radiation on early plant growth, we investigated alterations in the photosynthesis and antioxidant capacity of red pepper (*Capsicum annuum* L.) seedlings produced from gamma-irradiated seeds. For two cultivars (Yeomyung and Joheung), three irradiation groups (2, 4, and 8 Gy, but not 16 Gy) showed enhanced development, although Fv/Fm, the maximum photochemical efficiency of Photosystem II (PSII), did not differ significantly among any of the four groups. In contrast, values for 1/Fo - 1/Fm, i.e., a measure of functional PSII content, decreased in the irradiated groups of 'Yeomyung' but increased in those of 'Joheung'. Pigment analyses and enzyme activity assays revealed that irradiation altered the compositions of photosynthetic pigments (chlorophylls and carotenoids) as well as the activities of antioxidant enzymes (superoxide dismutase and glutathione reductase). However, these shifts were not directly related to the increase in early growth, although they were cultivar- and developmental stage-dependent. In addition, the effects of irradiation on the enzymatic activities measured here were at opposition between the two cultivars.

Keywords: antioxidant enzyme, carotenoid, chlorphyll a fluorescence, low-dose radiation, photosynthesis

Hormesis, defined as a dose-response phenomenon, is characterized by a counter-intuitive switchover from low-dose stimulation to high-dose inhibition, an action occasionally encountered in the course of a toxicity assay (Calabrese, 2002). The hormetic effects of low-dose ionizing radiation on plants and photosynthetic microorganisms are manifested as accelerated cell proliferation (Conter et al., 1986; Taguchi et al., 1994; Okamoto and Tatara, 1995; Chakravarty and Sen, 2001), stimulated germination and growth (Koepp and Kramer, 1981; Thiede et al., 1995; Al-Safadi and Simon, 1996; Lee et al., 1998; Charbaji and Nabulsi, 1999; Kim et al., 2000, 2001a, 2002a), improved stress-resistance (Zaka et al., 2002; Lee et al., 2002a, 2003), and/or increased yield (Stan and Croitoru, 1970; Wiendl et al., 1995; Kim et al., 1998; Al-Safadi et al., 2000). In many cases, such effects could be characterized as the modulation of photosynthesis and antioxidant machineries. For instance, increases in the actual quantum yield of photosynthetic electron transport, the net photosynthesis rate, and/or stress-resistance to UV-B and high light are accompanied by the enhanced activities of antioxidant enzymes, e.g., peroxidase, catalase, and superoxide dismutase (SOD) (Wada et al., 1998; Kim et al., 2001a, 2002a; Zaka et al., 2002; Lee et al., 2002a, b, 2003).

However, at least for plant cells, no unifying models have been proposed for the underlying mechanisms of radiation hormesis, although it is well documented that all ionizing radiation can produce free radicals from the water in cells (Luckey, 1980; Miller, 1987) and release biologically important, low-molecular weight compounds through various reactions of radicals with their neighboring cellular components (Luckey, 1991; Eidus, 2000). This may be due to differences in the sensitivity of cells. Our previous reports have also shown that the cellular effects of ionizing radiation vary according to plant species, irradiation dose, and accompanying environmental stress (Lee et al., 1998, 2002a and b, 2003; Kim et al., 1998, 2000, 2001a, 2002a).

In the present study of two red pepper cultivars treated with low-dose gamma radiation, our objective was to examine the cultivar- and developmental stage-dependent alterations in hormetic effects, in terms of the modulation of photosynthesis and antioxidant machineries. To do so, we analyzed chlorophyll fluorescence, determined chlorophyll and carotenoid contents, and assayed for the activities of SOD and glutathione reductase (GR), which work in the first and last steps, respectively, of the ascorbate-

---

*Corresponding author; fax +82-42-868-8061
e-mail jhongkim@pusan.ac.kr

glutathione cycle to scavenge reactive oxygen species (ROS) in plant cells.

MATERIALS AND METHODS

Plant Materials and Gamma-Irradiation

Red pepper (*C. annuum* L. cv. Yeomyung and Joheung) seeds were commercially produced in 1999 by Choongang Seed Company and Dongbu Hannong Seed Company in Korea, respectively. They were irradiated with low doses of gamma radiation (2, 4, 8, or 16 Gy), which were generated by a gamma irradiator (^{60}Co, *ca.* 150 TBq of capacity, AECL) at the Korea Atomic Energy Research Institute (KAERI). Following seeding, the plants were reared in a greenhouse at Chungnam National University in Korea, from late July to early September, 2003. The natural growing conditions included incident light intensity and an uncontrolled photocycle and temperature regime that changed each day.

Growth Test

Germination rates were recorded at 12 days after sowing (DAS), and the leaf areas, stem lengths, and diameters were measured at 20, 20, and 26 DAS, respectively, using a digital caliper (CD-6"CS; Mitutoyo, Japan) and an area meter (LI-3100; LI-COR, USA). Length was defined as the distance from the top of the stem to the soil level; diameter was measured 1 cm above the soil line. To measure leaf areas, fully expanded first or second leaves were harvested and maintained in moistened vinyl bags. Area was recorded within 1 h at room temperature (RT).

Chlorophyll Fluorescence Analysis

Chlorophyll (Chl) fluorescence of 5-mm-diameter discs cut from the detached leaves was measured with a Chl fluorometer (IMAGING-PAM, Walz, Germany). Readings were taken after the samples were dark-adapted for 10 min at RT. The maximal quantum yield of Photosystem II (PSII), i.e., photosynthetic efficiency, was calculated as the ratio of variable fluorescence (Fv) to the maximum yield of fluorescence (Fm), according to the method of Genty et al. (1989). Variable fluorescence was obtained by subtracting the initial Chl fluorescence (Fo) from the maximum yield. To use 1/Fo - 1/Fm as a measure of functional PSII content, all fluorescence yields (Fo and Fm) were normalized to the mean Fo value for the controls, as described by Kim et al. (2001b).

Pigment Analysis

Photosynthetic pigments were analyzed according to the method of Gilmore and Yamamoto (1991). Harvested seedlings (≥ 30) were immediately frozen in liquid nitrogen and ground with a mortar and pestle. Pigments were extracted from about 0.5 g samples of this seedling powder with 3 cm^3 of ice-cold 100% acetone. Cell debris was removed twice by centrifuging at 19,000g (Micro 17R; Hanil, Korea) for 10 min at 4°C. The pigment extracts were then filtered through a 0.2 μm syringe filter, and separated in an HPLC system (HP 1100 series; Hewlett Packard, Germany) on a Spherisorb ODS-1 column (Alltech, USA), as described by Gilmore and Yamamoto (1991). Pigment concentrations were estimated by using the conversion factors for peak area (in nanomoles) that had been determined for this solvent mixture by Gilmore and Yamamoto (1991). The de-epoxidation index was calculated as a percentage of $A \times 0.5 + Z$ of $V + A + Z$, where A is antheraxanthin, Z is zeaxanthin, and V is violaxanthin. This parameter was then used to indicate the degree of de-epoxidation in the xanthophyll cycle.

Enzyme Assay

Seedlings (≥ 30) were harvested and ground to fine powder with liquid nitrogen. Enzymes were extracted from the powder (about 0.5 g) with an optimized medium including 50 mM potassium phosphate buffer (pH 7.8), 0.1 mM EDTA, 0.5% (v/v) Triton X-100, and 1% (w/v) PVP. Their activities were expressed on the basis of protein concentration, as determined with a Bio-Rad Protein Assay kit (Bio-Rad Laboratories, USA). We followed the method of Bradford (1976), using bovine serum albumin (BSA) as a standard.

Superoxide dismutase (SOD; EC 1.15.1.1) activity was estimated by using SOD-dependent inhibition of the reduction of nitroblue tetrazolium (NBT) to form purple formazan by superoxide, as described by Beyer and Fridovich (1987). The reaction mixture contained 50 mM potassium phosphate buffer (pH 7.8), 0.1 mM EDTA, 9.9 mM L-methionine, 57 μM NBT, 0.025% (w/v) Triton X-100, 0.8 μM riboflavin, and enzyme extract. After 7 min of illumination at RT, the photoreduction of NBT in the mixture was measured at 560 nm, and an inhibition curve was made against different volumes of the enzyme extract. One unit of SOD activity was defined as the amount of SOD causing half the maximum inhibition of NBT photoreduction.

Glutathione reductase (GR; EC 1.6.4.2) activity was assayed by a method modified from those of Schaedle and Bassham (1977) and Fryer et al. (1998), based on the decrease in absorbance at 340 nm that was due to the oxidation of NADPH to $NADP^+$ over 5 min. The reaction mixture was composed of 50 mM potassium phosphate buffer (pH 7.8), 0.1 mM NADPH, 0.5 mM oxidized glutathione (GSSG), and enzyme extract. This reaction was initiated by the addition of NADPH at RT. Correction was also made for the non-GR-dependent oxidation of NADPH by excluding GSSG from the original reaction mixture. One unit of GR activity was defined as the amount of GR necessary to oxidize 1 nmole NADPH for 1 min, using an absorbance coefficient for NADPH at 340 nm of 6.2 mM^{-1} cm^{-1}.

Data Analysis

Statistical analysis of the data was performed by Tukey's honestly significant difference (HSD) test ($P < 0.05$), using SPSS for Windows Release 11.0.1 (SPSS, USA).

RESULTS AND DISCUSSION

Seed Germination and Early Seedling Growth from Gamma-Irradiated Seeds

The effects of low-dose gamma radiation on germination and early seedling growth were investigated in two red pepper cultivars ('Yeomyung' and 'Joheung')

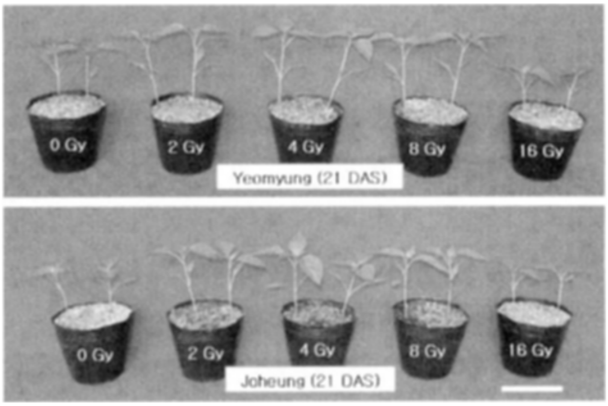

Figure 1. Effect of low-dose gamma radiation on early growth of two red pepper cultivars. Pictures present 'Yeomyung' and 'Joheung' seedlings from gamma-irradiated seeds at 21 DAS. Radiation doses include 0, 2, 4, 8, or 16 Gy. Scale bar shown as white line corresponds to 10 cm.

Table 1. Seed germination and early growth of two red pepper cultivars treated with gamma radiation. Germination rate, stem length, leaf area, and stem diameter were measured at 12, 20, 20, and 26 d after sowing (DAS), respectively. Stem length was the distance from the top of each stem to the soil level; diameter was recorded 1 cm above the soil. For leaf-area measurements, only fully expanded first or second leaves were used. All values are means ± SD (n = 30) except for germination rate (n = 15). Means followed by different letters(a, b, and c) within each cultivar are significantly different at $P = 0.05$ by Tukey's HSD test.

Cultivar	Dose (Gy)	Germinationrate (%)	Stem length (cm)	Stem diameter (mm)	Leaf area (cm^2)
Yeomyung	0	97.3 ± 4.5 a	6.7 ± 0.6 a	2.1 ± 0.2 ab	6.5 ± 1.1 a
	2	96.0 ± 6.3 a	8.2 ± 1.2 b	2.2 ± 0.2 abc	8.2 ± 1.4 b
	4	96.7 ± 4.9 a	8.0 ± 1.1 b	2.3 ± 0.3 c	8.4 ± 1.9 b
	8	98.0 ± 4.1 a	7.9 ± 0.9 b	2.3 ± 0.2 bc	8.8 ± 1.8 b
	16	96.7 ± 4.9 a	6.5 ± 0.8 a	2.1 ± 0.2 a	6.9 ± 1.1 a
Joheung	0	82.7 ± 10.3 a	6.1 ± 0.7 a	2.0 ± 0.3 a	6.8 ± 1.4 a
	2	85.3 ± 9.9 a	7.6 ± 0.7 c	2.4 ± 0.2 b	9.5 ± 1.5 b
	4	80.7 ± 10.3 a	6.9 ± 0.8 b	2.2 ± 0.3 b	8.8 ± 1.4 b
	8	83.3 ± 16.3 a	7.2 ± 0.7 bc	2.3 ± 0.2 b	9.8 ± 1.9 b
	16	82.0 ± 10.8 a	6.2 ± 0.6 a	2.0 ± 0.2 a	6.8 ± 1.2 a

(Fig. 1). Seeds for irradiation at 2, 4, 8, or 16 Gy were commercially produced in 1999 as described above. In both cultivars, all irradiation groups except the 16-Gy dose showed 13 to 25, 5 to 20, or 26 to 44% increases over their non-irradiated counterparts in stem length, diameter, and leaf area, respectively (Table 1). However, we observed no significant differences in germination rates between the two groups, or any compatible dose dependency when all the stem lengths, diameters, and leaf areas were considered within the range of effective doses. Nonetheless, for seeds produced in 1998 and 1997 from two other cultivars, 'Daemyung' and 'Wang', low-dose gamma irradiation (2~16 Gy) had increased germination rates by 16 to 26% (1998 seed) and 31 to 41% (1997) (data not shown). These overall results are quite similar to those from our earlier reports (Lee et al., 1998; Kim et al., 1998, 2000, 2001a, 2002a), in which low-dose gamma-irradiation stimulated germination and early seedling growth in Chinese cabbage, red pepper, onion, spinach, bottle gourd, pumpkin, and soybean. Therefore, based on all these findings, we expected that gamma radiation should have greater stimulating effects on old seed with low germinative activities (Kim et al., 2001a), even though this response would still be a function of species/cultivar, physiological status of the seed, and the particular dose of radiation.

PSII Photochemical Efficiency and Functional PSII Content

We used Chl fluorescence analysis to test whether the modulation in PSII photochemistry was an underlying mechanism for increased early growth in irradiated groups. Initial Chl fluorescence, Fo, was improved mainly in the irradiation groups of 'Yeomyung' but decreased in those of 'Joheung', while maximal yield of fluorescence, Fm, increased in all irradiation groups of both cultivars, except for the 2-Gy dose (Fig. 2A and B). However, values for Fv/Fm, a measure of PSII photochemical efficiency, did not differ significantly between the irradiated and non-irradiated groups in either cultivar (Fig. 2C). Similar results have been reported with potato plants (Kim et al., 2002b). In contrast, functional PSII content, 1/Fo - 1/Fm, was noticeably different between the two groups, although it was not correlated with greater

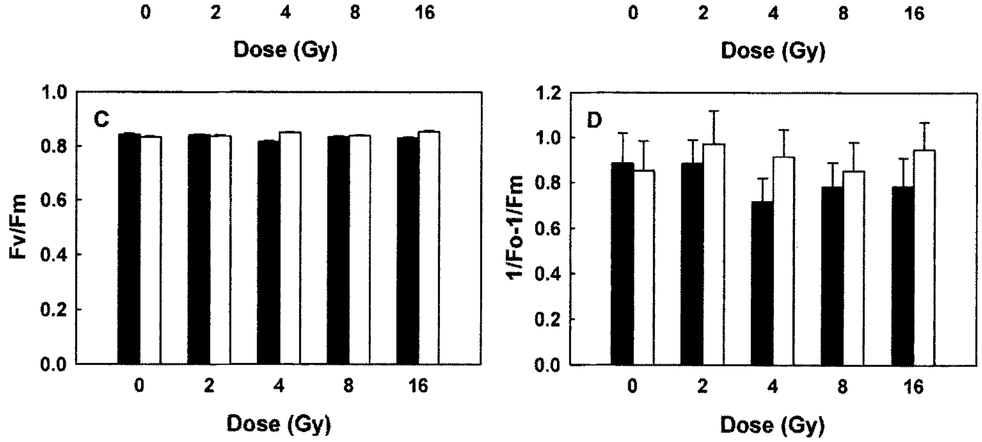

Figure 2. Photosynthetic efficiency and functional PSII content in irradiated and non-irradiated groups of two red pepper cultivars. **A**, initial Chl fluorescence (Fo); **B**, maximum yield of fluorescence (Fm); **C**, photosynthetic efficiency (Fv/Fm); **D**, functional PSII content (1/Fo-1/Fm). Chl fluorescence values were measured at 20 DAS. Black and white bars represent 'Yeomyung' and 'Joheung', respectively. All values are means ± SD (n = 6).

early growth (Fig. 2D). This parameter of 1/Fo - 1/Fm has often served to represent functional PSII content (Lee et al., 2002; Kim and Lee, 2002, 2003) because the former is linearly correlated with the latter (Lee et al., 1999; Kim et al., 2001b). Its values decreased primarily in our irradiation groups of 'Yeomyung', but rose in the 'Joheung' groups (Fig. 2D). This discrepancy is thought to be due to cultivar specificity, e.g., more delayed development in 'Joheung', as suggested in Table 1. Accordingly, the degree to which PSII photochemistry was affected in the irradiation groups depended on cultivar and developmental stage. Nevertheless, any changes in that photochemistry did not account for the increased early growth at doses of 8 Gy or below.

Photosynthetic Pigments

Alterations in PSII photochemistry may indicate changes in photosynthetic pigments, including Chl and carotenoids. Although the Chl content generally decreased in the irradiation groups of 'Yeomyung' and 'Joheung', the ratio of Chl *a*/*b* remained at about 0.26 for both the irradiated and the non-irradiated tissues of the two cultivars (detailed data not shown). Therefore, we ruled out the possibility that these changes contributed to fluctuations in photochemistry after low-dose gamma-irradiation as suggested in Fig. 2.

The carotenoids comprise carotenes and their oxygenated derivatives (xanthophylls), which participate in various antioxidant responses as well as photosynthesis (Larson, 1988; Frank and Cogdell, 1993; Demmig-Adams et al., 1996; Edge et al., 1997). Xanthophylls are synthesized from α- and β-carotenes (Fig. 3), the latter quenching the singlet oxygen produced by PSII reaction centers and, thereby, protecting P680 from photodamage (Rivas et al., 1993;

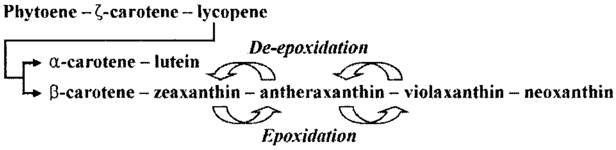

Figure 3. Xanthophyll cycle biosynthetic pathway in higher plants.

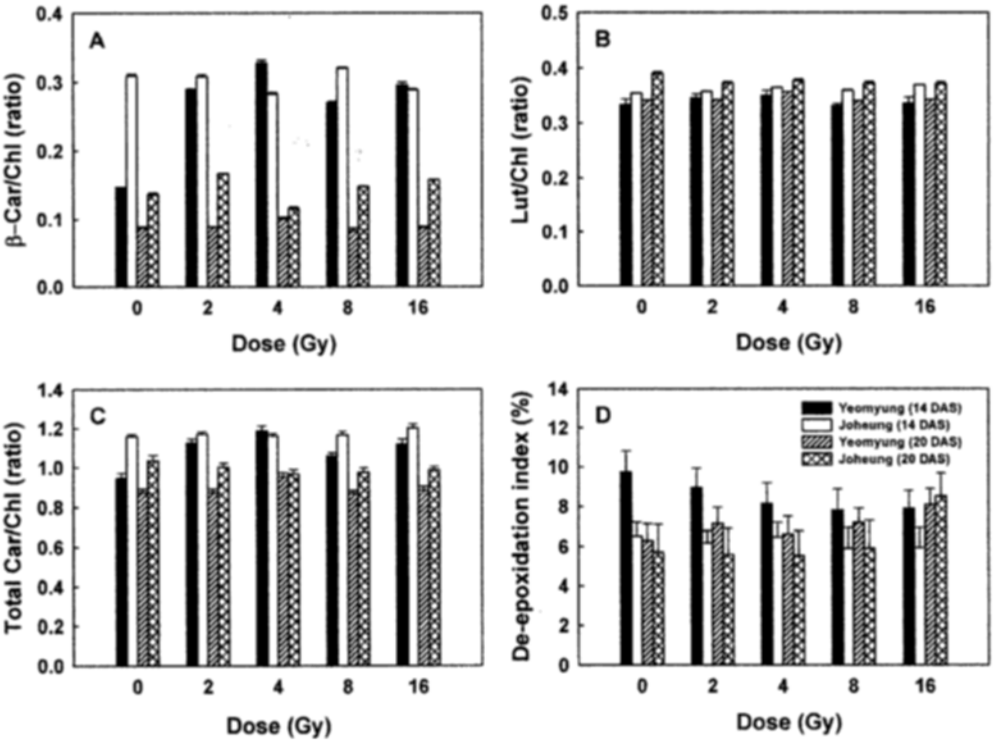

Figure 4. Differences in photosynthetic pigment contents between irradiated and non-irradiated groups of two red pepper cultivars. **A**, **B**, and **C**, respectively, indicate amounts of β-carotene, lutein, and total carotenoids relative to Chl. Total carotenoids include neoxanthin, violaxanthin (V), antheraxanthin (A), lutein, zeaxanthin (Z), and β-carotene. De-epoxidation index in **D** is defined as percentage of A × 0.5 + Z of V + A + Z (see Materials and Methods). All values are means ± SD (n = 3).

Telfer et al., 1994). Lutein, one of the β-carotene-derived xanthophylls, is a structural component of the subunits of the light-harvesting complexes (Bishop, 1996). It also contributes to the dissipation of excess absorbed light energy so that plants are guarded against photo-oxidative damage (Niyogi et al., 1997). Among the xanthophylls, violaxanthin, antheraxanthin, and zeaxanthin are involved in down-regulating PSII function under excess light energy, action that constitutes the xanthophyll cycle (Thiele and Krause, 1994; Demmig-Adams and Adams III, 1996; Gilmore, 1997). Here, the ratios of β-carotene, lutein, and total carotenoids to Chl were generally higher in the irradiated tissues of 'Yeomyung' at 14 DAS than in the non-irradiated counterparts, but, at 20 DAS, they were similar between the irradiated and non-irradiated groups except at the 4-Gy dose level (Fig. 4A-C). In contrast, differences in the ratios were not noticeable between the groups of 'Joheung' at 14 DAS. However, in 'Joheung' at 20 DAS, the ratio of β-carotene to Chl was higher in the irradiated tissues than in the non-irradiated ones, while those of lutein and total carotenoids to Chl were lower in the former. These results suggest that the differences in carotenoids-to-Chl ratios that arose between the irradiated and non-irradiated groups varied by cultivar and developmental stage. This idea is partly supported by the fact that the de-epoxidation index for the xanthophyll cycle decreased in a dose-dependent manner in the groups of both cultivars at 14 DAS, while it increased in the same manner at 20 DAS (Fig. 4D).

Antioxidant Enzymes - SOD and GR

Because protein contents (data not shown) were relatively lower in the irradiated groups, similar to the observations made concerning Chl trends, it is unlikely that the irradiation-induced stimulation of seedling growth (Table 1) was necessarily and positively correlated with changes in protein and chlorophyll contents. Likewise, the alterations in SOD and GR activities were not directly related to the stimulatory effects of low-dose gamma radiation on growth (Fig. 5). Those two enzymes are the first and last components, respectively, in the ascorbate-glutathione cycle, mainly operating in the chloroplasts (Mullineaux and Creissen, 1997; Asada, 1999). Therefore, one might predict that they are involved in the growth process by maintaining photosynthetic activity under high light intensities at midday. However, SOD content generally increased in the irradiation groups of 'Yeomyung', but decreased in those of 'Joheung' (Fig. 5A), while the reverse was true for GR with regard to the two cultivars (Fig. 5B). As a result, concerted increases in the activities of antioxidant enzymes could not be assumed in these irradiated plants, a response that has frequently been reported in transgenic plants that show enhanced tolerance under environmental stress (Gupta et al., 1993; McKersie et al., 1993; Slooten et al., 1995). Together with the results of our pigment analysis (Fig. 4), this also implies that the existence of an irradiation-induced differential regulatory system is related to the antioxidant machineries in the chloroplasts.

In conclusion, gamma-irradiation induced alterations in the photosynthetic pigments and antioxidant mechanism, but these actions were not directly related to the acceleration of early growth in our irradiated plants. However, changes in the pigments and antioxidant activities were correlated with cultivar and developmental stage. Moreover, we demonstrated here that SOD and GR, the major antioxidant

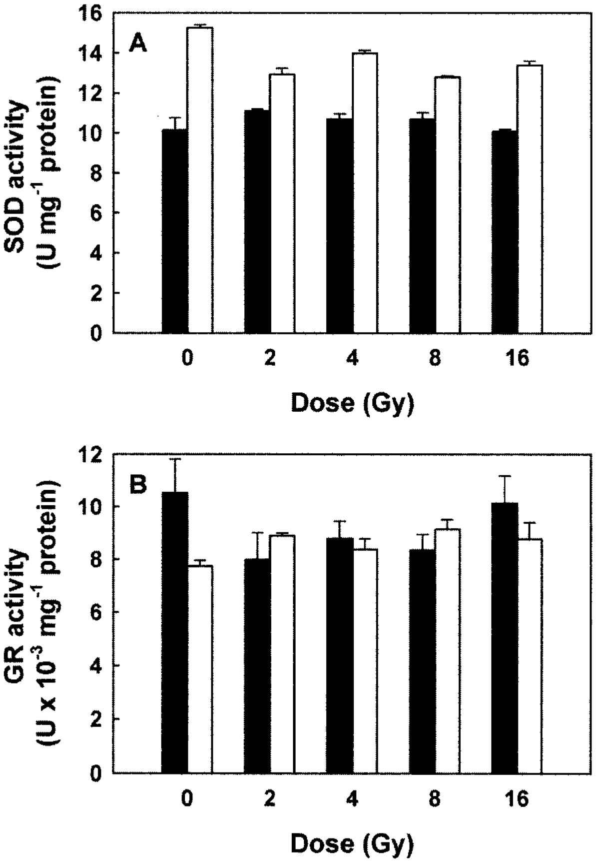

Figure 5. SOD and GR activities in red pepper seedlings from gamma-irradiated seeds. Plants were harvested at 14 DAS. Black and white bars represent 'Yeomyung' and 'Joheung', respectively. All values are means ± SD (n = 3).

enzymes in chloroplasts, were oppositely affected by irradiation when the two red pepper cultivars were compared.

ACKNOWLEDGMENT

This project has been carried out under the Nuclear R&D Program by the Ministry of Science and Technology, Korea

Received July 6, 2004; accepted August 20, 2004.

LITERATURE CITED

Al-Safadi B, Simon PW (1996) Gamma irradiation-induced variation in carrots (*Daucus carota* L.). J Amer Soc Hort Sci 121: 599-603

Al-Safadi B, Ayyoubi Z, Jawdat D (2000) The effect of gamma irradiation on potato microtuber production *in vitro*. Plant Cell Tiss Org Cult 61: 183-187

Asada K (1999) The water-water cycle in chloroplasts: Scavenging of active oxygens and dissipation of excess photons. Annu Rev Plant Physiol Plant Mol Biol 50: 601-639

Beyer WF, Fridovich Y (1987) Assaying for superoxide dismutase activity: Some large consequences of minor changes in conditions. Anal Biochem 161: 559-566

Bishop NI (1996) The β,ε-carotenoid, lutein, is specifically required for the formation of the oligomeric forms of the light harvesting complex in the green alga, *Scenedesmus obliquus*. J Photochem Photobiol B: Biol 36: 279-283

Bradford MM (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of dye binding. Anal Biochem 72: 248-254

Calabrese EJ (2002) Hormesis: Changing view of the dose-response, a personal account of the history and current status. Mutat Res 511: 181-189

Chakravarty B, Sen S (2001) Enhancement of regeneration potential and variability by γ-irradiation in cultured cells of *Scilla indica*. Biol Plant 44: 189-193

Charbaji T, Nabulsi I (1999) Effect of low doses of gamma irradiation on in vitro growth of grapevine. Plant Cell Tiss Org Cult 57: 129-132

Conter A, Dupouy D, Delteil C, Planel H (1986) Influence of very low doses of ionizing radiation on *Synechococcus* lividus metabolism during the initial growth phase. Arch Microbiol 144: 286-290

Demmig-Adams B, Adams III WW (1996) The role of xanthophyll cycle carotenoids in the protection of photosynthesis. Trends Plant Sci 1: 21-26

Demmig-Adams B, Gilmore AM, Adams III WW (1996) *In vivo* functions of carotenoids in higher plants. FASEB J 10: 403-412

Edge R, McCarvey DJ, Truscott TG (1997) The carotenoids as anti-oxidants: A review. J Photochem Photobiol B: Biol 41: 189-200

Eidus LK (2000) Hypothesis regarding a membrane-associated mechanism of biological action due to low-dose ionizing radiation. Rad Environ Biophys 39: 189-195

Frank HA, Cogdell RJ (1993) The photochemistry and function of carotenoids in photosynthesis, *In* A Young, G Britton, eds, Carotenoids in Photosynthesis. Chapman & Hall, London, pp 252-326

Fryer MJ, Andrews JR, Oxborough K, Blowers DA, Baker NR (1998) Relationship between CO_2 assimilation, photosynthetic electron transport, and active O_2 metabolism in leaves of maize in the field during periods of low temperature. Plant Physiol 116: 571-580

Genty B, Briantais JM, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim Biophys Acta 90: 87-92

Gilmore AM (1997) Mechanistic aspects of xanthophyll cycle-dependent photoprotection in higher plant chloroplasts and leaves. Physiol Plant 99: 197-209

Gilmore AM, Yamamoto HY (1991) Resolution of lutein and zeaxanthin using a nonencapped, lightly carbon-loaded C-18 high-performance liquid chromatographic column. J Chromatogr 543: 137-145

Gupta AS, Heinen JL, Holaday AS, Burke JJ, Allen RD (1993) Increased resistance to oxidative stress in transgenic plants that overexpress chloroplastic Cu/Zn superoxide dismutase. Proc Natl Acad Sci USA 90: 1629-1633

Kim J-H, Lee C-H (2002) Decrease of photochemical efficiency induced by methyl viologen in rice (*Oryza sativa* L.) leaves is partly due to the down-regulation of PSII. J Photosci 9: 65-70

Kim J-H, Lee C-H (2003) Mechanism for photoinactivation of PSII by methyl viologen at two temperatures in the leaves of rice (*Oryza sativa* L.). J Plant Biol 46: 10-16

Kim J-S, Baek M-H, Lee H-Y, Lee Y-K (2001a) Effects of low dose gamma irradiation on the germination and physiological activity of old red pepper (*Capsicum annuum* L.) seed. J Kor Assoc Rad Prot 26: 409-415

Kim J-S, Baek M-H, Lee Y-K, Lee H-Y, Yoo J-C (2002a) Effect of low-dose gamma radiation to enhance germination rate in bottle gourd and pumpkin seeds. Kor J Environ Agr 21: 202-207

Kim J-S, Kim J-K, Lee Y-K, Baek M-W, Kim J-G (1998) Effects of low dose gamma radiation on the germination and yield components of Chinese cabbage. Kor J Environ Agr 17: 274-278

Kim J-S, Lee E-K, Baek M-H, Kim D-H, Lee YB (2000) Influence of low dose γ radiation on the physiology of germinative seed of vegetable crops. Kor J Environ Agr 19: 58-61

Kim J-S, Lee H-Y, Baek M-H, Kim J-H, Kim SY (2002b) Effects of low dose γ radiation on the dormancy, growth and physiological activity of seed potato (*Solanum tuberosum* L.). J Kor Soc Hort Sci 43: 596-602

Kim S-J , Lee C-H, Hope AB, Chow WS (2001b) Inhibition of photosystem I and II and enhanced back flow of photosystem I electrons in cucumber leaf discs chilled in the light. Plant Cell Physiol 42: 842-848

Koepp R, Kramer M (1981) Photosynthetic activity and distribution of photoassimilated ^{14}C in seedlings of *Zea mays* grown from gamma-irradiated seeds. Photosynthetica 15: 484-489

Larson RA (1988) The antioxidants of higher plants. Phytochem 27: 969-978

Lee EK, Kim J-S, Lee Y-K, Lee YB (1998) Effect of low dose γ-ray irradiation on the germination and growth in red pepper (*Capsicum annuum* L.). J Kor Soc Hort Sci 39: 670-675

Lee H-Y, Chow WS, Hong YN (1999) Photoinactivation of photosystem II in leaves of *Capsicum annuum*. Physiol Plant 105: 377-384

Lee H-Y, Kim J-S, Baek M-H, Park S-C, Park Y-I (2002a) Effects of low dose γ-radiation on photosynthesis of red pepper (*Capsicum annuum* L.) and the reduction of photoinhibition. Kor J Environ Agr 21: 83-89

Lee H-Y, Kim J-S, Baek M-H, Lee Y-K, Im D-S (2002b) Effects of low dose γ-radiation on the growth, activities of enzymes and photosynthetic activities of gourd (*Lagenaria siceraria*). Kor J Environ Biol 20: 197-204

Lee H-Y, Kim J-S, Baek M-H, Yoo J-C, Kwon S-T (2003) Effects of low dose γ irradiation on physiological activities of radish (*Raphanus sativus*) during early growth and reduction of ultraviolet-B stress. J Kor Soc Hort Sci 44: 314-320

Luckey TD (1980) Hormesis with Ionizing Radiation. CRC Press, Boca Raton, pp 32-38

Luckey TD (1991) Radiation Hormesis. CRC Press, Boca Raton, pp 9

McKersie BD, Chen Y, Beus MD, Bowley SR, Bowler C, Inzé D, D' Halluin K, Botterman J (1993) Superoxide dismutase enhances tolerance of freezing stress in transgenic alfalfa (*Medicago sativa* L.). Plant Physiol 103: 1155-1163

Miller MW (1987) Radiation hormesis in plants. Health Physiol 52: 607-616

Mullineaux PM, Creissen GP (1997) Glutathione reductase: Regulation and role in oxidative stress. *In* JG Scandalios, ed, Oxidative Stress and the Molecular Biology of Antioxidant Defenses. Cold Spring Harbor Laboratory Press, New York, pp 667-713

Niyogi KK (1997) The roles of specific xanthophylls in photoprotection. Proc Natl Acad Sci USA 94: 14162-14167

Okamoto H, Tatara A (1995) Effects of low-dose γ-irradiation on the cell cycle duration of barley roots. Environ Exp Bot 35: 379-388

Rivas ADL, Telfer A, Barber J (1993) Two coupled β-carotene molecules protect P680 from photodamage in isolated photosystem II reaction centres. Biochim Biophys Acta 1142: 155-164

Schaedle M, Bassham JA (1977) Chloroplast glutathione reductase. Plant Physiol 59: 1011-1012

Slooten L, Capiau K, Camp WV, van Montagu M, Sybesma C, Inzé D (1995) Factors affecting the enhancement of oxidative stress tolerance in transgenic tobacco overexpressing manganese superoxide dismutase in the chloroplasts. Plant Physiol 107: 737-750

Stan S, Croitoru A (1970) Effect of low, moderate and high levels of gamma radiations (^{60}Co) on soybean plants. I. Analysis of growth and yield. Stim Newsl 1: 23-25

Taguchi Y, Tsutsumi N, Tatara A, Eguchi H, Tano S (1994) Effects of low-dose γ-irradiation on the root apical meristem of barley. Environ Mut Res Commun 16: 205-209

Telfer A, Dhami S, Bishop SM, Phillips D, Barber J (1994) β-carotene quenches singlet oxygen formed by isolated photosystem II reaction centers. Biochem 33: 14469-14474

Thiede ME, Link SO, Fellows RJ, Beedlow PA (1995) Effects of gamma radiation on stem diameter growth, carbon gain and biomass partitioning in *Helianthus annuus*. Environ Exp Bot 35: 33-41

Thiele A, Krause GH (1994) Xanthophyll cycle and thermal energy dissipation in photosystem II: Relationship between zeaxanthin formation, energy-dependent fluorescence quenching and photoinhibition. J Plant Physiol 144: 324-332

Wada H, Koshiba T, Matsui T, Satô M (1998) Involvement of peroxidase in differential sensitivity to γ-radiation in seedlings of two *Nicotiana* species. Plant Sci 132: 109-119

Wiendl FM, Wiendl FW, Wiendl JA, Vedovatto A, Arthur V (1995) Increase of onion yield through low dose of gamma irradiation of its seeds. Rad Phys Chem 46: 793-795

Zaka R, Vandecasteele CM, Misset MT (2002) Effects of low chronic doses of ionizing radiation on antioxidant enzymes and G_6PDH activities in *Stipa capillata* (Poaceae). J Exp Bot 53: 1979-1987