Characterization of Differential Cesium Toxicity and Cesium-affected Transcription of K^+ or Na^+ Transporter Genes in Model Plants and Horticultural Crops

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Abstract - Pollutant toxicity influences biomass increment and pollutant uptake in phytoremediation; therefore, tolerance to pollutant toxicity is important in determining applicability of candidate plants. This study investigated relative Cs toxicity in *Arabidopsis*, cabbage, lettuce, red pepper, rice, and tomato seedlings through growth, photosynthesis, and/or transcription assays. When treated with 100, 300, 800, or 1,500 μM CsCl, the six plant species showed substantial differences in changes in seedling weight, chlorophyll content, photosynthetic activity, or transcription of K^+ or Na^+ transporter genes, and exhibited higher susceptibility to Cs toxicity in the order of *Arabidopsis* < rice < red pepper < tomato < cabbage < lettuce. Co-treatment with NaCl or mannitol demonstrated that salt or osmotic stress could increase Cs toxicity in *Arabidopsis* seedlings. Among the five K^+ or Na^+ transporter genes, *NHX5*, *SOS1*, *KT1*, *NHD1*, and *HKT1*, a high-affinity potassium transporter gene *HKT1* and a sodium hydrogen antiporter gene *NHD1* showed Cs concentration-dependent decrease in transcription, associating more with Cs toxicity than Cs uptake. In contrast, a low-dose gamma radiation of 8 Gy increased shoot growth slightly but decreased Cs uptake in seedlings. Taken together, these results suggest that the differential Cs toxicity to these six plant species could be somewhat associated with the distinctive transcription of K^+ or Na^+ transporter genes and that salt or osmotic stress and gamma radiation could indirectly modulate Cs toxicity or Cs uptake.

Key words : Cesium toxicity, DNA damage response, Gamma radiation, Phytoremediation

INTRODUCTION

Cs exists in the form of a stable isotope (^{133}Cs) as a trace element in soils and radioisotopes such as ^{134}Cs and ^{137}Cs as products of nuclear technologies. The latter isotopes emit beta and gamma radiation, causing serious problems to biological systems in the environment (White and Broadley 2000). Therefore, phytoremediation of radioactive Cs, a toxic environmental pollutant, has received much attention as a promising technique to reduce radiation risk to organisms in the environment, especially since the nuclear accidents at Chernobyl in 1986 and Fukushima in 2011 (Zhu and Smolders 2000; Singh *et al*. 2009; Tamaoki *et al*. 2016).

Toxicity of pollutants in phytoremediation is regarded as the relative resistance indicator of candidate plants. Cs is chemically similar to K, an essential macronutrient in plants, but it is toxic to plants by preventing K^+ uptake and interacting with vital K^+-binding sites in protein (Hampton *et al*. 2004). Therefore, the toxicity of Cs, which influences plant growth and biomass increment, is an important consideration in selecting candidate plants applicable for phytoremediation of radio-

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active Cs. The ionizing radiation of radioactive Cs may pose physical toxicity to plants in addition to the chemical toxicity of Cs owing to chemical interactions. For example, *Arabidopsis* plants irradiated with gamma radiation of 3 to 48 Gy displayed dose-dependent DNA damage and transcriptional alterations in DNA damage response genes (Ryu *et al*. 2018).

Soil-to-plant and root-to-shoot transfer factors of pollutants have been critically considered in selecting candidate plants for phytoremediation (Cook *et al*. 2009; Kang *et al*. 2012; Tamaoki *et al*. 2016). As plants with bigger biomass, which are more advantageous in phytoremediation than those with higher transfer factors, produce larger volumes of waste, uptake efficiency of pollutants per dry weight of plants is of great importance when selecting candidate plants for phytoremediation. Transfer of radioactive Cs into plants depends on many factors including root, soil, nutrient, microbe, and ion characteristics as well as concentration and radioactivity of Cs (Zhu and Smolders 2000; Rai and Kawabata 2020). Especially, K^+, a competitive and analogous ion of Cs^+, inhibits the transfer of radioactive Cs into plants (Shaw and Bell 1991; Avery 1995). In addition, salt or osmotic stress influences Cs uptake in plants by modulating plant growth and K^+ transport (White and Broadley 2000; Osakabe *et al*. 2013; Assaha *et al*. 2017; Isobe *et al*. 2019). This factor needs to be further considered in the application of phytoremediation for radioactive Cs owing to the location of many nuclear power plants near coastal areas.

Aspects of uptake mechanisms, regulation, and application have been intensively studied in phytoremediation of radioactive Cs (White and Broadley 2000; Zhu and Smolders 2000; Rai and Kawabata 2020). Many plant species including grass, flower, and crop plants have proved to be potential or poor candidates to phytoextract stable or radioactive Cs from soils and solutions (Cook *et al*. 2009; Moogouei *et al*. 2011; Tamaoki *et al*. 2016). In contrast, the effects of ionizing radiation or salt (or osmotic) stress on toxicity and uptake efficiency of Cs in plants remain unexplored or poorly explored till date. In this study, we analyzed the effects of environmental factors on phytoremediation of Cs in terms of ionizing radiation, salt (or osmotic) stress, and different plant species.

MATERIALS AND METHODS

1. Plant materials, chemical treatment, and gamma irradiation

Arabidopsis thaliana (ecotype Columbia-0), rice (*Oryza sativa* L. ssp. *japonica* 'Dongjin-byeo'), cabbage (*Brassica rapa* L. subsp. *pekinensis*), lettuce (*Lactuca sativa* L.), red pepper (*Capsicum annuum* L.), and tomato (*Solanum lycopersicum* L.) seeds were surface sterilized with 2.5% sodium hypochlorite or 20% bleach solution, and cultivated on a 1/2 Murashige and Skoog (MS) medium with 1.5% sucrose and 0.65% Phytoagar under a 16 h light/8 h dark cycle at 23°C. For chemical treatment, the MS media included CsCl (100, 300, 800, or 1,500 μM), NaCl (100, 150, or 200 mM), and/or mannitol (100, 200, or 300 mM). Fourteen-day-old seedlings were harvested and used for growth, photosynthesis, and transcription assays. Alternatively, the seedlings were further irradiated with 8 Gy for 120 h at a dose rate of 66.67 $mGy \cdot h^{-1}$ and 1,600 $mGy \cdot day^{-1}$ for 5 days in a gamma-phytotron with a 400 Ci ^{60}Co source at the Advanced Radiation Technology Institute (Jeollabuk-do, Korea), and then used for Cs uptake assay.

2. Cs uptake assay

Harvested samples of whole seedlings, shoots, and roots were thoroughly washed with distilled water and dried in an oven at 60°C for 72 h, and then ground with a mortar and pestle. Approximately 0.2 g of the sample was digested in 10 mL HNO_3 using a microwave digestion system (Multiwave 3000, Anton Paar GmbH, Graz, Austria) as previously described (Kang *et al*. 2012). After cooling for 2 h, the samples were centrifuged at 10,000 × g for 15 min, and the supernatant was passed through a 0.45 μm nitrocellulose filter following dilution with distilled water (1 : 20, v/v). The concentration of Cs was determined using an inductively coupled plasma-mass spectrophotometer (ICP-MS; model 7500ce; Agilent Technologies, Santa Clara, CA, USA).

3. Growth assay

To evaluate seedling growth, dry weight, fresh weight, and/or chlorophyll content of seedlings were measured. Chlorophyll content was determined as previously described (Kim *et al*. 2009). Seedlings were ground with liquid nitrogen and vigorously agitated in ice-cold 100% acetone at 4°C for 1 h in darkness. Cell debris was twice removed by centrifugation at 4°C and 15,000 × g for 15 min. Concentration was calculated using the following equation: total chlorophyll = $18.09 \times A_{644.8} + 7.05 \times A_{661.6}$.

4. Photosynthesis assay

To evaluate photosynthetic activity, chlorophyll fluores-

Table 1. Primer sequences of *Arabidopsis* genes used for qPCR

Gene name	Primer sequence (forward/reverse)	Description
AtACT2 (*At3g18780*)	5′-GCCCAGAAGTCTTGTTCCA-3′/5′-ATCACAGCACTTGCACCAAG-3′	Actin2
AtHKT1 (*At4g10310*)	5′-TCGGACAGTTCCATCGAGGA-3′/5′-GGAGAAAGTGAGAGGTGAGAT-3′	High-affinity potassium transporter1
AtKT1 (*At2g26650*)	5′-CATTTACCACCTCGTCTGCAA-3′/5′AGCAGGTCATTGGATACTCCT-3′	Potassium transporter1
AtNHD1 (*At3g19490*)	5′-TGGGTCTTGGAGTTCTTTGGAT-3′/5′-TACAACACCGATAGCACTTGCA-3′	Sodium hydrogen antiporter1
AtNHX5 (*At1g54370*)	5′-TCATGATCTACCAGAGGGTCA-3′/5′-GTATCCTCGTCAGATGAAGCT-3′	Sodium hydrogen exchanger5
AtSOS1 (*At2g01980*)	5′-TCCTCCTGCATTTTGTGAACCT-3′/5′-CTTCCCAGTGAGGACTTCGT-3′	Sodium overly sensitive1

Parentheses represent Arabidopsis Genome Initiative (AGI) numbers. All primers for genes were designed from mRNA sequences of the respective gene on the NCBI site. *AtACT2* was used as an endogenous control

Table 2. Primer sequences of rice, cabbage, lettuce, red pepper, and tomato genes used for qPCR

Plant species	Gene name	Primer sequence (forward/ reverse)
Rice	*ACT*	5′-CCTCTTCCAGCCTTCCTTCAT-3′/5′-ACGGCGATAACAGCTCCTCTT-3′
	HKT	5′-CCAGTAAATGAGAATATGAT-3′/5′-TATCCAATGGCCTTTGGATATT-3′
	NHD	5′-TCAGCAATTATAGACAATGTT-3′/5′-TCCATTCCCATGAAAGCCACACC-3′
Cabbage	*ACT*	5′-AGCTCTTCAGTGGAGAAGA-3′/5′-TTCATGATGGAGTTGTAAGT-3′
	HKT	5′-CCCACGAATGAGAACATGAT-3′/5′-TATCCCATCTTCTTGCGATTCT-3′
	NHD	5′-ACAAGAGCGTCTTGATGATGCT-3′/5′-TTGAATGTTGCTGGACGTCA-3′
Lettuce	*ACT*	5′-AGCTCTTCAGTGGAGAAGA-3′/5′-TTCATGATGGAGTTGTAAGT-3′
	HKT	5′-CCTCCAGTTCTGAGACTTACGAT-3′/5′-GAACTCCATTCCATTGATGAA-3′
	NHD	5′-TCAGCAATTATAGACAATGTT-3′/5′-TCCATTCCCATGAAAGCCACACC-3′
Red pepper	*ACT*	5′-TAACATTGTACTTAGTGGTGGTT-3′/5′-TTGGAAGGTACTTAGAGAAGCCA-3′
	HKT	5′-CCAGTAAATGAGAATATGAT-3′/5′-TATCCAATGGCCTTTGGATATT-3′
	NHD	5′-TCAGCAATTATAGACAATGTT-3′/5′-TCCATTCCCATGAAAGCCACACC-3′
Tomato	*ACT*	5′-GGTATTGCTGATAGAATGAGCA-3′/5′-AATAGAGGGACCAGATTCGTCA-3′
	HKT	5′-CAAGGCATGCTGGTCTATCT-3′/5′-GGTTGTGATAATGATATGTACTCCA-3′
	NHD	5′-TCAGCAATTATAGACAATGTT-3′/5′-TCCATTCCCATGAAAGCCACACC-3′

All primers for genes were designed from mRNA sequences of the respective gene on the NCBI site. *ACT* was used as an endogenous control.

cence was measured from the adaxial surface of leaves after 5 min dark incubation using a chlorophyll fluorometer (HandyPEA, Hansatech Instruments Ltd., Norfolk, UK) as described previously (Kim *et al*. 2010). The maximum photohemical efficiency (Fv/Fm) and the performance index of photosynthesis (PI) were calculated from the following equations: $Fv/Fm = 1 - Fo/Fm$ and $PI = [\gamma_{RC}/(1-\gamma_{RC})][\phi_{Po}/(1-\phi_{Po})] \times [\psi o/(1-\psi o)]$ (Thach *et al*. 2007).

5. Transcription assay

Total RNA was extracted using a RNeasy Plant Mini Kit (QIAGEN, Hilden, Germany) and cDNA was synthesized from the RNA samples using oligo (dT) primers and a LaboPass™ cDNA Synthesis Kit (Cosmogenetech, Seoul, Korea). The quantitative PCR amplifications were performed at 95°C for 30 s, followed by 40 cycles of 95°C for 10 s, 58°C for 10 s, and 72°C for 1 min with the gene-specific primers (Tables 1 and 2) in a CFX Connect™ Real-Time PCR Detection System (Bio-Rad Laboratories, Hercules, CA, USA) using an iTaq Universal SYBR® Green Supermix (Bio-Rad Laboratories). *AtACT2* or *ACT* was used as an endogenous control. The relative mRNA expression data of three biological replicates in the quantitative PCR were normalized against the reference genes *AtACT2* or *ACT*.

RESULTS AND DISCUSSION

1. Effect of gamma radiation on Cs uptake

Radioactive Cs emits beta and gamma radiation. Uptake

and distribution of radioactive ^{137}Cs is similar to that of stable ^{133}Cs in rice plants (Tsukada *et al*. 2002). To investigate the effect of gamma radiation on Cs uptake in plants, *Arabidopsis* seedlings grown in CsCl-containing medium were further irradiated with gamma radiation of 8 Gy for 5 days. This irradiation was chosen not to inhibit seedling growth by a preliminary experiment. Treatments of 100∼800 μM CsCl did not affect seedling growth, whereas the seedlings treated with 1,500 μM displayed substantial growth inhibition (Fig. 1a and b). Although the shoot weight was slightly increased in the irradiated groups, the seedling weight was not substantially affected by gamma irradiation of 8 Gy. When the content of Cs was analyzed separately in the whole seedlings, shoots, and roots, an increase of approximately 2-fold more in the shoots than in the roots was observed depending on the concentration (Fig. 1c). In addition, the uptake of Cs was slightly but commonly inhibited in the irradiated groups of whole seedlings. Radiation-induced growth inhibition and metabolic disturbance as well as DNA damage response depends on the radiation dose and plant development stage (Kim *et al*. 2005; Kim *et al*. 2008; Kim *et al*. 2009; Kim *et al*. 2011; Ryu *et al*. 2018). These results suggest that gamma radiation from radioactive Cs may alter Cs uptake as well as plant growth and biomass. The inhibitory effects of gamma radiation on biomass and Cs uptake need to be explored during the whole lifetime of candidate plants.

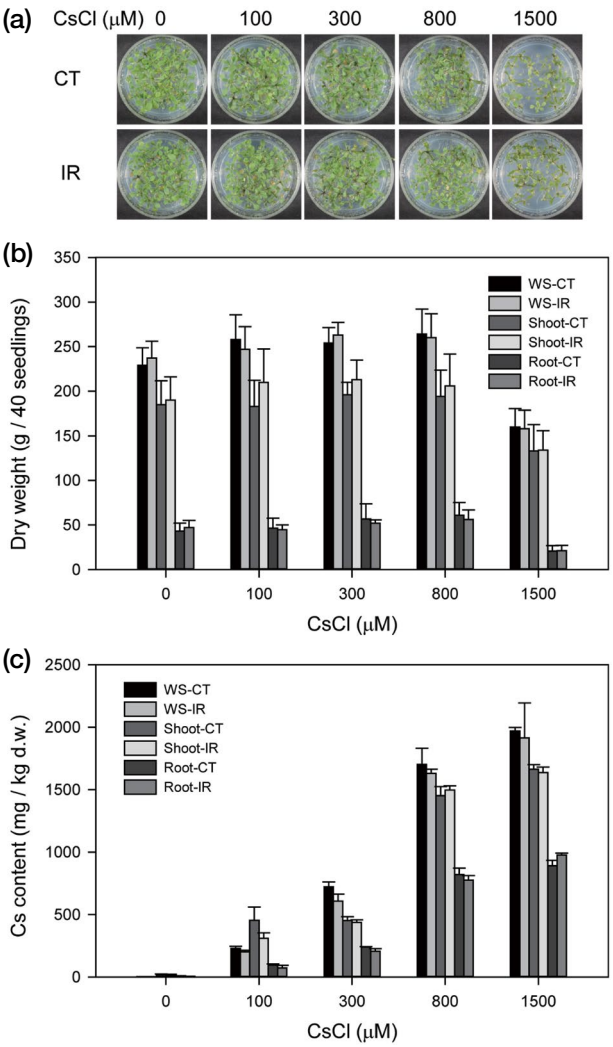

Fig. 1. Change in Cs uptake and toxicity in *Arabidopsis* seedlings exposed to gamma radiation. (a) and (b) images and dry weights of seedings treated with CsCl (100, 300, 800, or 1,500 μM) and gamma radiation (8 Gy), respectively. (c) Cs content in seedling, shoot, and root. CT, control; IR, ionizing radiation (gamma radiation); WS, whole seedling; shoot, aerial part of seedling; and root, the remaining part of seedling except shoot. All samples of WS, shoot, and root were separately harvested and analyzed for determination of dry weight and Cs content. Data are the mean ± SE from three independent experiments.

2. Effect of salt or osmotic stress on Cs toxicity and transcription of K^+ or Na^+ transport genes

Salt or osmotic stress is a global environmental factor that influences plant growth and development by interfering with water and solute uptake or K^+ homeostasis in plants (White and Broadley 2000; Osakabe *et al*. 2013; Assaha *et al*. 2017; Isayenkov and Maathuis 2019). However, it was recently reported that application of NaCl promoted growth in quinoa and Cs uptake by quinoa (Isobe *et al*. 2019). To investigate the effect of salt or osmotic stress on Cs toxicity in plants, various concentrations of NaCl (100, 150, or 200 mM) or mannitol (100, 200, or 300 mM) were co-treated to *Arabidopsis* seedlings with 300 or 800 μM CsCl, (concentrations that were shown to cause no significant growth inhibition in *Arabidopsis*, Fig. 1a and b). These salt or osmotic stress treatments caused growth inhibition in seedlings in a concentration-dependent manner and revealed the substantial toxicity of 300 or 800 μM CsCl (Fig. 2a). This result implies that salt or osmotic stress may increase Cs toxicity in *Arabidopsis*. To elucidate the mechanism of increased Cs toxicity, we investigated transcription activity of K^+ (*AtHKT1* and *AtKT1*) or Na^+ transporter genes (*AtNHX5*, *AtNHD1*, and *AtSOS1*) (Table 1), which are directly or indirectly associated with Cs uptake (White and Broadley 2000; Zhu and Smolders 2000; Rai and Kawabata 2020). Single treatment of CsCl decreased transcription of *AtSOS1*, *AtNHD1*, and *AtHKT1*, whereas that of NaCl or mannitol induced *AtNHX5* and *AtSOS1* but inhibited *AtHKT1* (Fig. 2b). Co-treatment with CsCl and NaCl or mannitol fur-

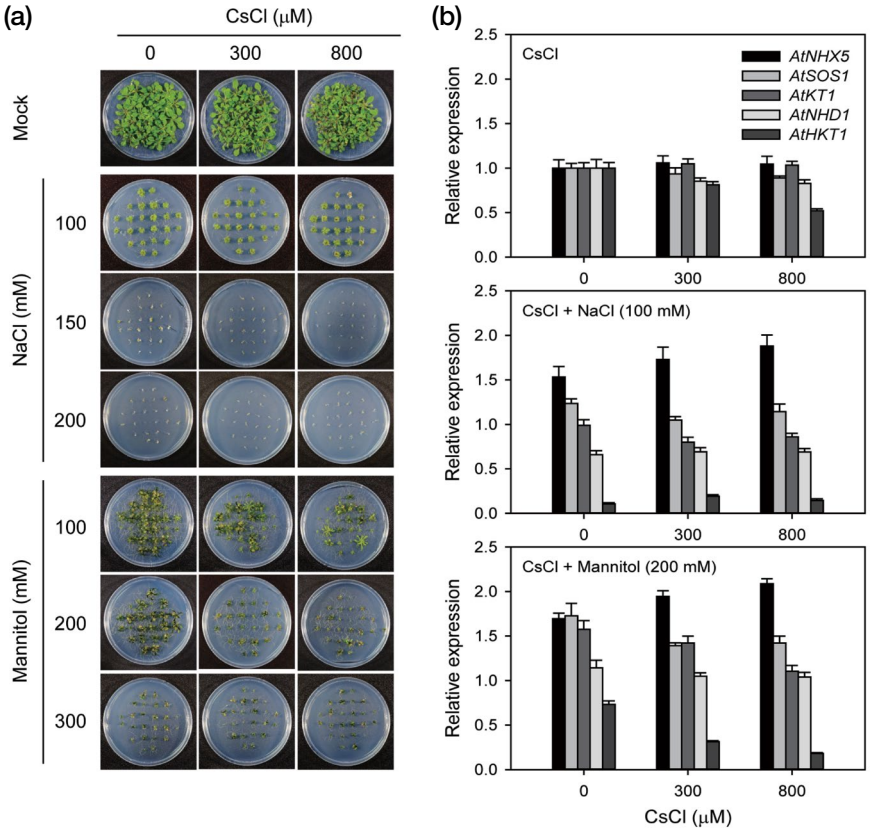

Fig. 2. Change in Cs toxicity and gene expression in *Arabidopsis* seedlings under salt or osmotic stress. (a) images of seedings treated with CsCl (300 or 800 μM) and NaCl (100, 150, or 200 mM) or mannitol (100, 200, or 300 mM). (b) change in transcription levels of *AtHKT1*, *AtKT1*, *AtNHX5*, *AtNHD1*, and *AtSOS1* genes after treatment with CsCl (300 or 800 μM) and NaCl (100 mM) or mannitol (200 mM). Data are the mean ± SE with n = 9 from three independent experiments.

ther increased transcription of *AtNHX5*. The former (CsCl + NaCl) also decreased transcription of *AtSOS1* and *AtKT1*, whereas the latter (CsCl + mannitol) substantially inhibited that of *AtSOS1*, *AtNHD1*, *AtKT1*, and *AtHKT1*. These results suggest that treatment of NaCl and mannitol may inhibit the uptake of K^+ and Cs^+ by decreasing the transcription of K^+ transporter genes such as *AtHKT1* and *AtKT1*. Therefore, the increased Cs toxicity under salt or osmotic stress could be attributed to the altered homeostasis of K^+ but not to the uptake of Cs^+.

3. Differential Cs toxicity and transcription of K^+ or Na^+ transport genes in various plant species

Many plant species including grass, flower, and crop plants have been considered as candidates for phytoremediation of stable or radioactive Cs from soils and solutions (Cook *et al*. 2009; Moogouei *et al*. 2011; Tamaoki *et al*. 2016). Herein, we attempted to evaluate a monocot model plant rice (*Oryza sativa* L.) and four horticultural crops - cabbage (*Brassica rapa* L.), lettuce (*Lactuca sativa* L.), red pepper (*Capsicum annuum* L.), and tomato (*Solanum lycopersicum* L.) as candidate plants for phytoremediation or phytoextraction of Cs. The toxicity of Cs and its associated transcription of five K^+ and Na^+ transporter genes are shown in a dicot model plant *Arabidopsis* (Fig. 2). The relative Cs toxicity and transcription of two K^+ or Na^+ transporter genes (*HKT* and *NHD*), which decreased substantially with CsCl treatment, were investigated in five plant species - rice, cabbage, lettuce, red pepper, and tomato. Treatments of 100~1,500 μM CsCl decreased seedling growth, fresh weight, and chlorophyll content in a concentration-dependent manner, suggesting the increasing Cs toxicity in the order of rice < red pepper < tomato < cabbage < lettuce seedlings (Fig. 3). In addition, chlorophyll fluorescence analysis was performed to determine the Fv/Fm and the PI, which have been used to represent photosynthetic activity in plants (Thach *et al*. 2007; Kim *et al*. 2010). Fv/Fm and PI demonstrated the highest tolerance in rice and the highest sensitivity

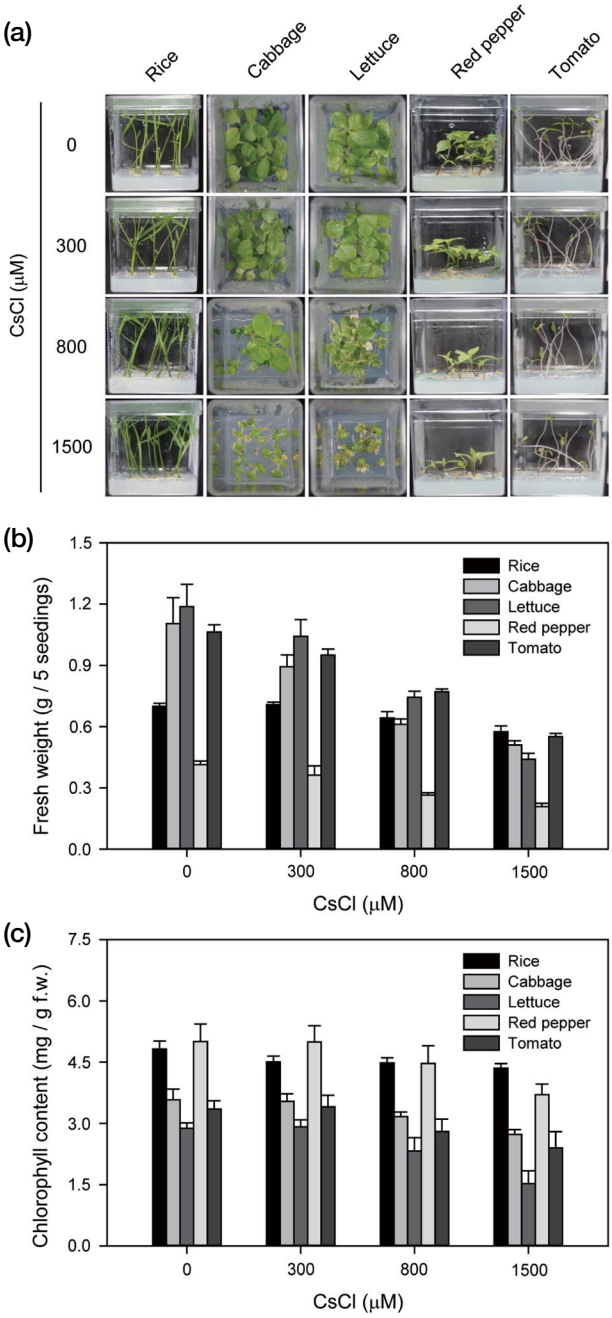

Fig. 3. Difference in growth inhibition in rice, cabbage, lettuce, red pepper, and tomato seedlings after treatment with different concentrations of CsCl. (a), (b), and (c) images, fresh weights, and chlorophyll content of seedings treated with CsCl (300, 800, or 1,500 μM), respectively. Data are the mean ± SE from three independent experiments.

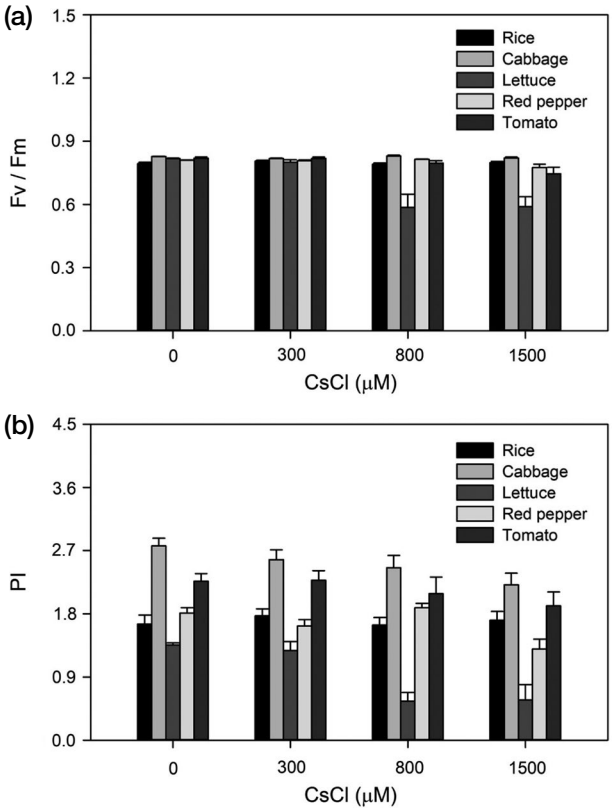

Fig. 4. Difference in photosynthetic activities in rice, cabbage, lettuce, red pepper, and tomato seedlings after treatment with different concentrations of CsCl. (a) and (b) the maximum photochemical efficiency (Fv/Fm) and the performance index of photosynthesis (PI), respectively, obtained from chlorophyll fluorescence analysis. Data are the mean ± SE with n = 15 from three independent experiments.

in lettuce, substantiating the increasing Cs toxicity in the order of rice, red pepper, tomato, cabbage, and lettuce seedlings (Fig. 4). In contrast, transcription of *HKT*, a high-affinity potassium transporter gene, increased noticeably in red pepper and tomato but decreased in lettuce and rice, except cabbage, whereas that of *NHD*, a sodium hydrogen antiporter gene, was strongly induced in red pepper but inhibited in the order of lettuce, cabbage, rice, and tomato (Fig. 5). Although transcription of *HKT* and *NHD* cannot be directly associated with Cs uptake, this may be a good parameter to reveal Cs toxicity. Therefore, all the data from growth, photosynthesis, and transcription assays suggest that rice and lettuce would be the best and the worst candidate plants, respectively, among the five plant species tested for phytoremediation of Cs. Moreover, maintaining transcriptional activities of K^+ or Na^+ transporter genes under Cs toxicity could be a prerequisite for the potential candidate plants to phytoextract Cs.

CONCLUSION

In this study, Cs toxicity was revealed in the order of rice, red pepper, tomato, cabbage, and lettuce seedlings through growth, photosynthesis, and transcription assays. Salt or osmotic stress could inhibit seedling growth and possibly Cs uptake

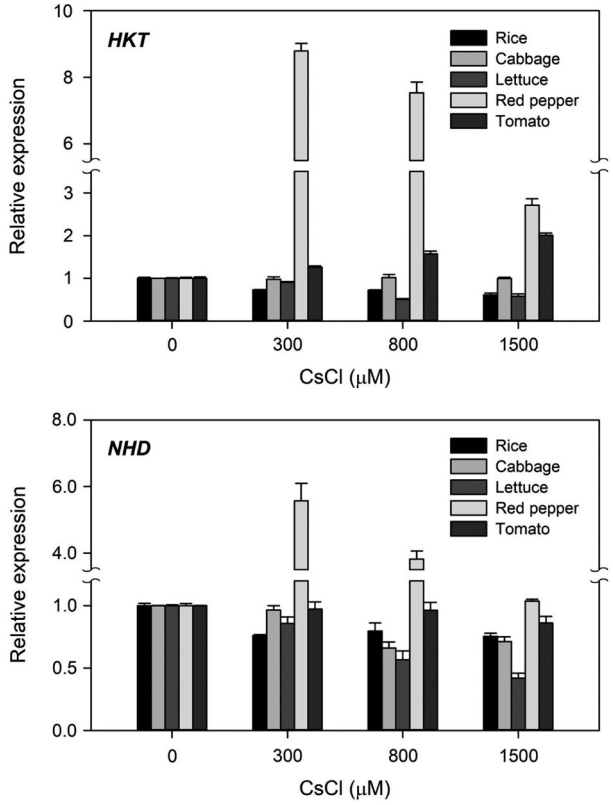

Fig. 5. Difference in transcription levels of *HKT* and *NHD* genes in rice, cabbage, lettuce, red pepper, and tomato seedlings after treatment with different concentrations of CsCl. Data are the mean ± SE with n = 9 from three independent experiments.

by increasing Cs toxicity. In contrast, a low-dose gamma radiation of 8 Gy slightly increased shoot growth but decreased Cs uptake in seedlings. Although soil-to-plant and root-to-shoot transfer factors of pollutants are considered important in phytodosimetry, pollutant toxicity affecting plant growth and pollutant uptake would be the first factor to be evaluated in candidate plants for phytodosimetry. Therefore, the effects of a growth-inhibition-causing high-dose gamma radiation on toxicity and uptake of Cs in phytoremediation of radioactive Cs need to be further explored.

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