Abstract Here, we review cesium uptake and accumulation in rice. Cesium is an alkaline metal, and its uptake is affected by potassium nutrition. Several transporters for cesium have been described. The distribution of cesium in the rice plant body differs from that of potassium, suggesting differential transport/storage mechanisms for cesium and potassium in rice. Cesium concentration in rice differs among cultivars, and it would be possible to determine the gene(s) responsible for cesium uptake/accumulation in future. This knowledge will form the foundation for the development of low radiocesium-accumulating cultivars.

Keywords Accumulation • Cesium • Cultivars • Potassium • Transporter • Uptake

4.1 Introduction

After the Fukushima Daiichi nuclear power plant accident in March 2011, radioactive nuclides were emitted and widely diffused in the environment, including across agricultural areas in Japan. Radiocesium, one of the emitted nuclides, has relatively long half lives (2.06 years for $^{134}\text{Cs}$, 30.2 years for $^{137}\text{Cs}$), and contamination of the environment and foods with radiocesium has been and will be of concern for a long time. Radiocesium deposited in soil sticks to soil particles; however, a small portion is redistributed into a soil solution that is readily absorbed by plants. Uptake and transport of cesium (Cs) by plants is an important determinant of the degree of radiocesium contamination of foods. Elucidating the uptake and transport processes involved and their mechanisms is important for minimizing the contamination of agricultural products. In this short article, aspects of Cs transport are reviewed with a major focus on rice, and future perspectives are also discussed.
4.2 Possible Transporters Involved in Cs Uptake

Several factors are likely to affect radiocesium uptake from the soil. A very good review of such factors was published recently (Yamaguchi et al. 2012). The radiocesium from the Fukushima accident was mostly present on the soil surface. Given the uneven distribution of radiocesium, the root architecture is likely to affect its uptake. Plants with roots near the soil surface may absorb more radiocesium than those with deeper root systems. Recently, a gene involved in the determination of root architecture in rice, namely “deep roots and shallow roots,” has been identified (Uga et al. 2009). However, to my knowledge, the relationship between root architecture and radiocesium uptake has not yet been established, despite this being an important aspect of radiocesium uptake from the soil by rice. Lateral distribution of radiocesium will change over time because of natural and human activities, and depending on the distribution, desirable root architectures may also change over time.

Cs is an alkaline metal that is taken up by plants in the form of Cs\(^+\). Potassium (K) is an essential plant nutrient that is a major component of fertilizers. Cs transport has been discussed in conjunction with K transporters. It is well established that the mechanism of Cs absorption by a root is similar to the mechanism of K absorption, following Michaelis–Menten kinetics (White and Broadley 2000). Inhibition of Cs absorption by the addition of K has also been shown in hydroponics and soil cultures (Smolders and Tsukada 2011), suggesting that Cs is taken into plants through K transporters. It is also known that the antagonism of K in Cs absorption is restricted, and under excessive Cs/K ratios, the effect is very much limited.

A number of K transporters have been identified in plants, and Cs transport has been demonstrated for several of these K transporters. The KUP/HAK/KT family, the family of high-affinity K\(^+\) transporters, has been shown to participate in Cs absorption (White and Broadley 2000). Yeast expressing Arabidopsis thaliana KUP1 absorbs K\(^+\), and its activity is affected by the presence of Cs\(^+\) (Fu and Luan 1998). Under high K conditions, voltage-insensitive cation channels (VICCS), independent cation channels, participate in Cs absorption (White and Broadley 2000). In the case of A. thaliana, VICCs are coded by the AtCNGC and AtGLR gene families. Although to my knowledge, no experimental evidence is currently available, rice homologs of the abovementioned transporters are likely to play a role in Cs uptake and distribution. Notably, these transporters represent only a subset of all the transporters involved in Cs uptake and transport in plants. As discussed below, Cs and K distribution within rice plants differs. This could possibly be attributed to differences in the relative transport of K and Cs among transporters or to the presence of Cs-specific transporters.

After absorption by roots, Cs is loaded to the xylem to reach the aerial portions of plants; this is followed by phloem transport to reach the grains. Different types of transporters are involved in these processes. In the case of K, the loading of K is mediated by SKOR; however, its involvement in Cs transport has not been demonstrated.
4.3 Cs-Specific Transporters?

Plants grown in soil contain a number of nonessential elements such as Cs. Nonradioactive Cs is present in the environment and foods. Cs is not an essential element for plants or animals. Cs is not very toxic to plants and animals compared with other heavy metals such as cadmium (Cd) and arsenic (As). It has long been believed that plants do not have specific transporters for nonessential toxic elements and that their uptake is mediated by transporters for essential nutrients that are chemically similar. For example, As in the form of arsenate is taken up by phosphate transporters (Zhao et al. 2009), and arsenite is taken up by aquapolin-like proteins (Ma et al. 2008; Kamiya et al. 2009). Cd transport is mediated by IRT1, an iron transporter (Nakanishi et al. 2006), and more recently, Os Nramp5 has been reported to function as a manganese (Mn) and Cd transporter (Ishimaru et al. 2012; Sasaki et al. 2012). A few years ago, a sensational report (Ueno et al. 2010) was published in PNAS in which the authors claimed that rice HMA3 is a transporter that is highly specific to Cd. This claim was based on their analysis of transgenic plants, which reportedly showed altered Cd accumulation without changes in other major metal contents. HMA3 is present on the vacuolar membrane and regulates Cd transport from roots to shoots. This claim of a Cd-specific transporter led to increased interest in the field, and the authors also discussed possible reasons why Cd-specific transporters had evolved. However, according to one of the authors, their manuscript did not include several transgenic plants overexpressing Os HMA3 at a much higher level than the two transgenic lines reported in the manuscript. These strong overexpressors had reduced Zn concentration in the grains but were not included in the manuscript. The authors claimed that Os HMA3 is highly specific to Cd. One of the authors presented further analysis of the transgenic plants reported in the PNAS paper at an annual meeting of the Japanese Society of Soil Science and Plant Nutrition in Tottori, Japan in September 2012. The concentrations of Zn in the roots of transgenic plants were shown to be reduced, further suggesting that OsHMA3 is not actually Cd-specific at all. The general concept of toxic metals being taken up by plants through transporters for essential elements still stands, and it is probably also the case for Cs transport in rice. Notably, however, the relative specificity for Cs differs among K transporters, and this may be a basis for the differential distribution of Cs and K in rice plants, as described below.

4.4 Cs Distribution in Rice

After being taken up by rice, Cs is transported and distributed to the aerial portions of plants. Radiocesium distribution was studied Tsukada et al. (2002a, b). In their studies, the patterns of radiocesium derived from fallout were examined in field-grown rice. They found that 65% of the radioactivity was recovered in straws, 10% in polished rice, 10% in bran, and 10% in husks. The overall distribution patterns
were somewhat similar to those for K; however, the relative concentration differed among tissues. Cs tends to accumulate in old leaves rather than young leaves. Such differential distribution can be attributed to differing specificity of the transporters. Alternatively, Cs and K may differ in their ability to bind to materials in living cells.

### 4.5 Variation in Rice Cs Concentrations Among Different Cultivars

Needless to say, it is crucial to reduce radiocesium contamination of foods. One practical way to reduce contamination is to use cultivars that accumulate less Cs in their grains. For this purpose, it is important to understand that there is variation in Cs uptake among plant species and cultivars. In the case of Cd, a large variation in Cd concentration in the leaves and grains among different cultivars of rice was used to identify genes important for Cd transport and to generate rice cultivars with reduced Cd accumulation or high Cd accumulation for phytoremediation.

In *A. thaliana*, quantitative trait locus (QTL) analysis of ecotypes with different Cs concentrations was used to identify the genetic locus that regulates Cs uptake in plants. Cs accumulation was found to be mainly regulated by QTLs in chromosomes 1 and 5 (Kanter et al. 2009). AtCNGC1 is very close to QTL on the 5th chromosome, and the amino acid sequence of CNGC1 reportedly differs between cultivars, suggesting that CNGC1 participates in Cs absorption (White and Broadley 2000).

A large variation in Cs concentration has been reported among different plant species, including crops and vegetables. Rice is a low accumulator of Cs. The transfer factor for radiocesium from the soil to rice grains is mostly in the range of 0.001–0.0002. This means that when rice is grown in soils of 5,000 Bq/kg it will accumulate 5–25 Bq/kg radiocesium in its polished grains, and I believe that this is below the provisional regulation level (500 Bq/kg) as well as the new standard (100 Bq/kg) for radiocesium contamination in food set by the Japanese government.

To determine the degree of variation among rice cultivars, Ishikawa et al. measured the concentrations of nonradioactive Cs among different specimens from the World Rice Core Collection obtained from Tsukuba (Yamaguchi et al. 2012). There was a 30-fold difference in Cs concentrations in the grains of these different rice cultivars. Our group also conducted a field study in Fukushima Prefecture in 2011 (Fig. 4.1), and we found large variation among cultivars (more than 20-fold). Notably, the difference observed under field conditions will also be caused by the uneven distribution of Cs in the field; however, the observed difference was far greater than the uneven distribution of Cs that is normally observed, suggesting a wide variation in Cs concentration among rice cultivars. It is expected that this variation will facilitate the identification of the gene responsible for Cs transport in rice and that this can be used to reduce Cs concentrations in the grains in future.
Future Perspectives

Many studies have established the physiological characteristics of Cs uptake, transport, and accumulation in plants, including rice; however, the molecular mechanisms of Cs transport and accumulation in rice remain largely unknown. Several transporters have been identified in *A. thaliana* that affect Cs transport; however, studies on rice are necessary to reduce radiocesium uptake and transport into grains. As seen in previous studies on toxic elements, it is most likely that the transporters will be identified through molecular and genetic approaches. The relatively large variation in Cs accumulation in rice grains may allow us to identify the transporter and/or other genes involved in Cs transport and accumulation.

As mentioned above, Cs transporters responsible for Cs uptake and distribution are most likely to be transporters of (an) essential element(s). Cs transporters identified in *A. thaliana* are K transporters, and if such a gene is mutated, it is likely that K transport would be affected. However, in the case of Cd accumulation in rice, Ishikawa et al. successfully reduced the Cd concentration in grains by screening mutant Koshihikari for reduced Cd concentration, and this did not require molecular understanding of the transport process. It turned out that the gene disrupted in their mutant that caused the reduced Cd accumulation in the grains was Os Nramp5, an Mn transporter. According to their press release and their presentation at the annual meeting of the Japanese Society of Soil Science and Plant Nutrition, the growth of this particular mutant line in the field was identical to that of the wild-type Koshihikari. I expect that this mutant line will be cultivated in farms in Japan in the near future and that this will reduce the risk of Cd uptake by humans. Notably, the Tos17 disruption line of Os Nramp5 grows poorly in the field (Sasaki et al. 2012), suggesting the importance of selecting an appropriate allele for practical purposes.

![Fig. 4.1](image-url) Distribution of cold Cs (Cs-133) concentration in different rice cultivars grown in a rice field in Fukushima. More than 100 cultivars representing Japanese and overseas were grown in a rice field in Fukushima Prefecture in 2011. Cold Cs (Cs-133) concentration in brown rice was determined. Concentration was arranged in an ascending order. Concentration of each cultivar is shown by a bar. A wide range of difference in Cs concentration was observed.
It should be possible to screen mutant elite Japanese cultivars for reduced Cs accumulation in grains using a similar approach. This may allow us to identify the responsible gene(s) using a forward genetic approach, and with such basic understanding, we will be able to reduce Cs contamination not only in rice but also in other plant/vegetable species.

Acknowledgments The data of Cs concentration in field-grown rice were obtained with the help of the following people: Inui Yayoi, Masataka Kajikawa, Atsumi Nakata, Koji Jasai, Shimpei Uraguchi, Takuya Sakamoto, Yuko Kawara, Kayoko Aizawa, Haruka Fujita, Tomoko Hirano, Li Ke, Naoya Sawaki, Koshiro Oda, Ryuichiro Futagoishi, Nobuhiro Tsusaka, Satomi Takahashi, Naoyuki Sotta, Junpei Takano, Shinji Wakuta, Akira Yoshinari, Tatada Uehara, Shigeki Takata, Hayato Nagano, Kyoko Miwa, Izumi Aihara, Takuya Oshima, Kaoru Ebana, Satoru Ishikawa, Kuni Sueyoshi, Hiroshi Hasegawa, Mitsuo Chino, Tetsumo Miruma, Mari Miruma, Jun Furukawa, and Daisuke Kobayashi. This study was supported in part by the Mitsui Foundation for Environmental Sciences and the Ministry of Agriculture, Forestry and Fisheries of Japan.

Open Access This article is distributed under the terms of the Creative Commons Attribution Noncommercial License which permits any noncommercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

References

Fu HH, Luan S (1998) AtLUP1: a dual-affinity K+ transporter from Arabidopsis. Plant Cell 10:63–73
Ishimaru Y, Takahashi, R, Khurram B, Shimo H, Senoura T, Sugimoto K, Ono K, Yano M, Ishikawa S, Arao T, Nakanishi H, Nishizawa NK (2012) Characterizing the role of rice NRAMP5 in manganese, iron and cadmium transport. Sci Rep 2. doi:10.1038/srep00286 (article number 286)
Kamiya T, Tanaka M, Mitani N, Ma JF, Maeshima M, Fujiwara T (2009) NIP1;1, an aquaporin homolog, determines the arsenite sensitivity of Arabidopsis thaliana. J Biol Chem 284:2114–2120
Kanter U, Hauser A, Michalke B, Draxl S, Schaffner AR (2009) Caesium and strontium accumulation in shoots of Arabidopsis thaliana: genetic and physiological aspects. J Exp Bot 61:3995–4009
Ma JF, Yamaji N, Mitani N, Xu XY, Su YH, McGrath SP, Zhao FJ (2008) Transporters of arsenite in rice and their role in arsenic accumulation in rice grain. Proc Natl Acad Sci USA 105:9931–9935
Nakanishi H, Ogawa I, Ishimaru Y, Mori S, Nishizawa NK (2006) Iron deficiency enhances cadmium uptake and translocation mediated by the Fe²⁺ transporters OsIRT1 and OsIRT2 in rice. Soil Sci Plant Nutr 52:464–469
Sasaki A, Yamaji N, Yokosho K, Ma JF (2012) Nramp5 is a major transporter responsible for manganese and cadmium uptake in rice. Plant Cell 24:2155–2167
Smolders E, Tsukada H (2011) The transfer of radio cesium from soil to plants: mechanisms, data, and perspectives for potential countermeasures in Japan. Integr Environ Assess Manage 7:379–381
Tsukada H, Hasegawa H, Hisamatsu S, Yamasaki S (2002a) Rice uptake and distributions of radioactive ¹³⁷Cs, stable ¹³³Cs and K from soil. Environ Pollut 117:403–409
Tsukada H, Hasegawa H, Hisamatsu S, Yamasaki S (2002b) Transfer of Cs-137 and stable Cs from paddy soil to polished rice in Aomori, Japan. J Environ Radioact 59:351–363
Ueno D, Yamaji N, Kono B, Huang CH, Ando T, Yano M, Ma JF (2010) Gene limiting cadmium accumulation in rice. Proc Natl Acad Sci USA 107:16500–16505
Uga Y, Okuno K, Yano M (2009) Dro1 a major QTL involved in deep rooting of rice under upland field conditions. J Exp Bot 62:2485–2949
White PJ, Broadley MR (2000) Mechanisms of caesium uptake by plants. New Phytol 147:241–256
Yamaguchi N, Takata Y, Hayashi K, Ishikawa S, Kuramata M, Eguchi S, Yoshikawa S, Sakaguchi A, Asada K, Wagai R, Makino T, Akahane I, Hiradate S (2012) Behavior of radio cesium in soil-plant systems and its controlling factor: a review. Rep Natl Inst Agro Environ Sci Jpn 31:75–129 (in Japanese)
Zhao FJ, Ma JF, Meharg AA, McGrath SP (2009) Arsenic uptake and metabolism in plants. New Phytol 181:777–794