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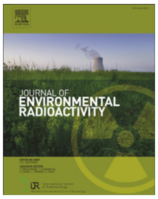

Theoretical model of the effect of potassium on the uptake of radiocesium by rice

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ABSTRACT

After the accident at the Fukushima Dai-ichi Nuclear Power Plant owned by Tokyo Electric Power Company on 11 March 2011, potassium was applied to fields in the Tohoku and Kanto areas of Japan to reduce radiocesium uptake by crops. Despite the intense studies relating to the effect of potassium application on availability of radiocesium in the soil, physiological changes of radiocesium uptake by crops in response to K^+ concentration around roots remains elusive. In the present study, we developed physiological models describing the effect of K^+ on the uptake of radiocesium by rice. Two Cs^+:K^+ competition models were evaluated using a wide range of data obtained from pot and field experiments: the model assuming a uniformity in the gene expression of K^+ transporter (Model I) and the model assuming the increase in the gene expression of K^+ transporter in response to K^+ concentration below threshold (Model II). The root-mean-square deviation between the measured and estimated values was larger in Model I than in Model II. Residuals were positively correlated with K^+ in Model I but showed no deflection in Model II. These results indicate that Model II explains the effect of K^+ on the uptake of radiocesium better than Model I. Model II may provide the appropriate countermeasures in inhibiting the transfer of radiocesium from soil to crop. The effect of changes in the variables in Model II on the relationship between available K^+ in soil and ^{137}Cs uptake by plant was simulated. An increase in available $^{137}Cs^+$ in soil enhanced the response of ^{137}Cs uptake to K^+. The effects of Michaelis–Menten constant for Cs^+ were the inverse of the $^{137}Cs^+$ effect. The effect of Michaelis–Menten constant for K^+ showed the same tendency as that of $^{137}Cs^+$, but the effect was much less than that of $^{137}Cs^+$. An increase in the threshold of K^+ below which the gene expression of K^+ transporter increases enhanced the response of ^{137}Cs uptake to K^+ in the high-K^+ range.

1. Introduction

A large amount of radionuclides was released into the environment after the accident at the Fukushima Dai-ichi Nuclear Power Plant owned by Tokyo Electric Power Company on 11 March 2011. Radiocesium (^{134}Cs and ^{137}Cs) in agricultural products has been intensively monitored because radiocesium has a relatively long half-life and a high biological availability, and consumption of food contaminated with radiocesium is the principal route of internal exposure to radiocesium (Zhu and Smolders, 2000). The Japanese Ministry of Health, Labor and Welfare has established provisional regulation values for radioactive substances in food (500 Bq kg^{-1} for grains) in March 2011 and a new limit (100 Bq kg^{-1} for grains) in April 2012. Elevated radiocesium concentrations exceeding the Japanese provisional regulation value were found in brown rice (unpolished rice) from some paddy fields in the northern part of Fukushima Prefecture in 2011 (Saito et al., 2012). On the basis of previous research (Ehlken and Kirchner, 2002; Fujimura et al., 2013; Saito et al., 2012; Tsumura et al., 1984), large amounts of potassium (K) were applied to paddy fields in the Tohoku and Kanto areas of Japan, including Fukushima Prefecture, in 2012 and 2013 to reduce radiocesium levels in future harvests of brown rice. Theoretical models describing the effect of K^+ on radiocesium uptake by crops may suggest the appropriate amount of K to apply to radiocesium-contaminated areas to efficiently reduce radiocesium levels in crops in such areas.

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Availability of radiocesium for plants is strongly influenced by soil properties such as clay content, and K and ammonium statuses (Absalom et al., 2001; Sawhney, 1972). Cesium (Cs) is strongly adsorbed by clay minerals, notably illite (Sawhney, 1966; Tsumura et al., 1984). Since K^+ and ammonium ion are significant competitors for adsorption of Cs^+ in the clay minerals, increasing in K^+ and ammonium ion in soil results to increase in dissociate radiocesium (Absalom et al., 2001; Sawhney, 1972), which is available for plants. Models to describe the availability of radiocesium in soil were developed by Absalom et al. (1999, 2001) and Smolders et al. (1997). These models dynamically estimated the availability of radiocesium in soil, but transfer of radiocesium from soil solution to plant was only empirically estimated.

Because Cs is a group I alkali metal with chemical properties similar to those of K, plant roots take up Cs^+ through K^+ transport pathways (Qi et al., 2008). A high-affinity and a low-affinity system have been proposed for the transport of K^+ from soil to root (Zhu and Smolders, 2000). The high-affinity system operating at low external K^+ concentration (often below 0.3 mM) can transport Cs^+ efficiently whereas Cs^+ permeates only slowly in the low-affinity system operating at high external K^+ concentration (above 0.5–1 mM) (Zhu and Smolders, 2000). This indicated that the competitive effect of K^+ on the uptake of Cs^+ was important at low external K^+ concentration.

Shaw and Bell (1991) developed a physiological model for the solution-to-root uptake of radiocesium in wheat, focusing on the Cs^+:K^+ competition in wheat seedlings. Their model accurately described Cs^+ uptake by wheat roots during the 15 minute-experiment. In the present work, we developed models describing the effect of K^+ concentration in soil on radiocesium uptake by rice plants through the cultivation period (from transplanting to harvest) and on the radiocesium concentration in brown rice on the basis of the Cs^+:K^+ competition model developed by Shaw and Bell (1991). We developed two models hypothesizing that the K^+ transport system involves transport of Cs^+ from soil to plant. The velocity of Cs^+ uptake is dependent on the gene expression of K^+ transporters in the roots. Because the gene expression is greatly enhanced (several-fold) by low K^+ concentration in the root medium (Ma et al., 2012), one of two models integrated the change in the gene expression of K^+ transporter into the Cs^+:K^+ competition model. The gene expression of K^+ transporter was not considered in the other model. Both models were evaluated by using data obtained from pot and field experiments.

2. Materials and methods

2.1. Model development

The mechanism for Cs^+ uptake by plants is based on Michaelis–Menten kinetics without inhibitors:

$$V_{\mathrm{Cs}} = \frac{V_{\max(\mathrm{Cs})}[\mathrm{Cs}]}{[\mathrm{Cs}] + K_{\mathrm{m(Cs)}}} \tag{1}$$

where V_{Cs} is the velocity of Cs^+ uptake by plant, $V_{\max(\mathrm{Cs})}$ is the maximum velocity of Cs^+ uptake, [Cs] is the concentration of Cs^+ available for plants, and $K_{\mathrm{m(Cs)}}$ is the Michaelis–Menten constant for Cs^+.

The transport of Cs^+ through the system is affected by inhibitor (K^+). The $K'_{\mathrm{m(Cs)}}$ ($K_{\mathrm{m(Cs)}}$ under competitive inhibition by K^+) is defined as.

$$K'_{\mathrm{m(Cs)}} = K_{\mathrm{m(Cs)}}\left(1 + \frac{[\mathrm{K}]}{K_{\mathrm{m(K)}}}\right) \tag{2}$$

where [K] is the concentration of K^+ available for plants, and $K_{\mathrm{m(K)}}$ is the Michaelis–Menten constant for K^+. As described by Shaw and Bell (1991), the velocity of Cs^+ uptake inhibited by K^+ is

$$\begin{aligned} V_{\mathrm{Cs}} &= \frac{V_{\max(\mathrm{Cs})}\ [\mathrm{Cs}]}{[\mathrm{Cs}] + K_{\mathrm{m(Cs)}}\left(1 + [\mathrm{K}]\big/K_{\mathrm{m(K)}}\right)} \\ &= \frac{V_{\max(\mathrm{Cs})}[\mathrm{Cs}]K_{\mathrm{m(K)}}}{K_{\mathrm{m(Cs)}}}\Bigg/\left([\mathrm{K}] + K_{\mathrm{m(K)}}\left(1 + \frac{[\mathrm{Cs}]}{K_{\mathrm{m(Cs)}}}\right)\right) \end{aligned} \tag{3}$$

Variables such as [Cs], [K], $K_{\mathrm{m(Cs)}}$, and $K_{\mathrm{m(K)}}$ are independent, whereas $V_{\max(\mathrm{Cs})}$ is dependent on the gene expression of K^+ transporter. Expression of K^+ transporter is up-regulated by K^+ deficiency (Ma et al., 2012). This means that $V_{\max(\mathrm{Cs})}$ increases under K^+ deficiency, although Ma et al. (2012) did not fully elucidate the quantitative relationship between [K] and the gene expression of the K^+ transporter. In the case of NO_3^- in *Arabidopsis*, gene expression of high-affinity nitrate transporter is induced linearly with decreasing NO_3^- concentration of culture solution below the threshold (Zhuo et al., 1999). On the basis of the result for the nitrate transporter, the gene expression of K^+ transporter is assumed to be linearly induced by the decrease in [K] below the threshold. The gene expression of K^+ transporter is.

$$E = \beta \quad ([\mathrm{K}] \geq K_{\mathrm{limit}}) \tag{4}$$

$$E = -\alpha([\mathrm{K}] - K_{\mathrm{limit}}) + \beta \quad ([\mathrm{K}] < K_{\mathrm{limit}}) \tag{5}$$

where E is the gene expression of K^+ transporter, K_{limit} is the threshold of [K] below which the gene expression of K^+ transporter increases, α is a proportionality constant, and β is the gene expression of K^+ transporter above K_{limit}. Because $V_{\max(\mathrm{Cs})}$ is positively related to E, $V_{\max(\mathrm{Cs})}$ is

$$V_{\max(\mathrm{Cs})} = \gamma E = \beta\gamma \quad ([\mathrm{K}] \geq K_{\mathrm{limit}}) \tag{6}$$

Table 1
Effect of applied K on exchangeable K^+ content in soil, dry matter production, and uptake of ^{137}Cs in the pot experiments for brown rice.

Applied K (g per pot)	Exchangeable K^+ content ($\mathrm{cmol_c\ kg^{-1}}$)	Dry weight (g per pot)			^{137}Cs activity (Bq per pot)			$[^{137}Cs]_{\text{brown rice}}$ ($\mathrm{Bq\ kg^{-1}}$)
		$DW_{\text{brown rice}}$	DW_{total}	$DW_{\text{brown rice}}/DW_{\text{total}}$	$A_{\text{brown rice}}$	$A_{\text{Cs-137}}$	$[P_{^{137}Cs}]$ ($A_{\text{brown rice}}/A_{^{137}Cs}$)	
0.00	0.038^a	13.3^b	26.7^b	0.50	3.1^a	7.3^a	0.43	220^a
0.08	0.041^b	15.1^{ab}	29.8^{ab}	0.51	2.2^b	6.1^b	0.36	130^b
0.17	0.046^{bc}	14.6^{ab}	28.7^{ab}	0.51	1.3^c	4.6^c	0.28	83^c
0.33	0.059^{bc}	15.6^a	30.2^{ab}	0.52	0.6^d	2.1^d	0.27	34^d
0.50	0.090^c	15.8^a	30.3^a	0.52	0.2^d	0.8^e	0.21	10^d
P value	<0.001	0.01	0.04		<0.001	<0.001		<0.001

Values followed by the same letters (a–e) are not different at the 5% level by the Tukey HSD test.