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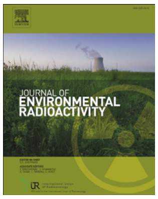

Mechanistic interpretation of the varying selectivity of Cesium-137 and potassium uptake by radish (*Raphanus sativus* L.) under field conditions near Chernobyl

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ABSTRACT

The selectivity of cation uptake by radish (*Raphanus sativus* L.) growing in the field near Chernobyl varies during the growth season. It is hypothesised that this is a consequence of variation in ^{137}Cs (Cs_{ss}) and potassium (K_{ss}) concentrations in the soil solution or the amount of dissolved potassium available to the plants. In the experiments reported here, it was observed that (1) Cs_{ss} and K_{ss} were positively correlated, (2) the selectivity for uptake of ^{137}Cs versus potassium (r) increased exponentially with decreasing Cs_{ss} and K_{ss}, and (3) the ^{137}Cs concentration, but not the potassium concentration, in plant material, increased abruptly upon the simultaneous reduction of K_{ss} and Cs_{ss} below about 10 μg ml^{-1} and 6.7 Bq l^{-1}, respectively. It is thought that potassium enters root cells from the soil solution through constitutively-expressed, inward rectifying K^+ channels (KIRC) and K^+/H^+-symporters, whose abundance increases when plants become potassium-deficient. Cesium is thought to enter root cells through non-specific cation channels (NSCC) and, in plants lacking sufficient potassium, through K^+/H^+-symporters. It is argued that the increase in r, together with the abrupt increase ^{137}Cs concentration in plant tissues, when K_{ss} and Cs_{ss} decrease simultaneously cannot be attributed to competition between Cs^+ and K^+ for transport though KIRC, NSCC or K^+/H^+-symporters and that the most plausible explanation of these phenomena is an increase in the abundance of K^+/H^+-symporters in plants exhibiting incipient potassium deficiency.

1. Introduction

Cesium, which is not required by plants, is taken up from the soil solution by various cation transporters in the plasma membrane of root cells (White and Broadley, 2000; Zhu and Smolders, 2000; White et al., 2010). These include constitutively-expressed, nonselective cation channels (NSCC), such as those encoded by the *AtCNGC* and *AtGLR* gene families in the model, nonmycorrhizal, brassicaceous plant *Arabidopsis thaliana* (L.) Heynh., and K^+/H^+-symporters, such as AtHAK5 in *A. thaliana*, whose abundance increases when plants become potassium deficient (Broadley et al., 2001; Hampton et al., 2004, 2005; Payne et al., 2004; Qi et al., 2008; Kanter et al., 2010; White and Karley, 2010; White et al., 2010; Adams et al., 2013). It has been demonstrated that NSCC mediate most cesium uptake by root cells in potassium-replete plants, but that K^+/H^+-symporters mediate most cesium uptake by root cells in potassium-deficient plants (Broadley et al., 2001; Hampton et al., 2005; Qi et al., 2008; Juri Ayub et al., 2008). The NSCC generally show little selectivity between Cs^+ and K^+, whilst the K^+/H^+-symporters often have slightly greater affinity and maximum transport capacity for K^+ than for Cs^+ (Sacchi et al., 1997; White and Broadley, 2000; Juri Ayub et al., 2008; White et al., 2010).

By contrast, potassium is an essential plant nutrient (White and Karley, 2010). The plasma membrane of root cells contains at least two distinct transport systems for K^+ uptake (White and Karley, 2010; White, 2013). These two systems differ in their molecular mechanisms and can work simultaneously. A low-affinity transport system, exemplified by the inward-rectified K^+-channel (KIRC)

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formed by AtAKT1 and AtKT1 in *A. thaliana*, catalyses most potassium uptake in potassium-replete plants and at millimolar potassium concentrations in the rhizosphere solution (White and Karley, 2010; White, 2013). This transport system is inhibited by extracellular cesium (White and Broadley, 2000; White, 2013). A high-affinity system, exemplified by the K^+/H^+-symporter AtHAK5 in *A. thaliana*, catalyses most potassium uptake in potassium-deficient plants and at submillimolar potassium concentrations in the rhizosphere solution (White and Karley, 2010; White, 2013). The KIRC generally have a high selectivity for K^+ versus Cs^+ and contribute little to cesium uptake by root cells under typical soil conditions (White and Broadley, 2000; Broadley et al., 2001; White et al., 2010).

It is clear that a different complement of transport proteins catalyses the uptake of cesium and potassium by plant root cells. Variation in this complement is thought to account for differences between plant species both in their absolute accumulation of cesium and in their ratios of cesium versus potassium in shoot tissues when grown under the same conditions (White et al., 2003, 2010; White and Karley, 2010; Broadley and White, 2012). It has been speculated that plant species with greater shoot cesium concentrations and shoot cesium/potassium quotients have greater ratios of CNGC:KIRC or HAK5:KIRC in the plasma membranes of their root cells (Hampton et al., 2005; White and Karley, 2010; White et al., 2010).

Several studies have reported that the same plant species, sampled from the same field site but at different times, can differ in its tissue ^{137}Cs concentration by over an order of magnitude (e.g. Prorok et al., 2006, 2011, 2012). Since these plants have similar tissue potassium concentrations, this implies that the selectivity of their accumulation of ^{137}Cs and potassium varies temporally (Prorok et al., 2006). It also implies that neither total soil ^{137}Cs concentration nor total soil K concentration, which do not vary greatly under natural conditions at a particular site, are sole determinants of ^{137}Cs concentration or ^{137}Cs/potassium quotient in plant tissues. In addition, when plants are grown in natural soils, their shoot ^{137}Cs concentration is often observed to vary during the growing season and this has been attributed to variation in soil exchangeable potassium concentration (Salt et al., 2004).

When plants are studied in the laboratory, the selectivity for the uptake of cesium versus potassium is observed to increase markedly as the rhizosphere potassium concentration is reduced below a threshold of about 0.3 mM (11.7 $\mu g\ K^+\ ml^{-1}$; Zhu and Smolders, 2000). This is thought to be a consequence of an increase in shoot cesium concentration as the potassium concentration in the rhizosphere solution, or soil exchangeable potassium concentration, decreases (e.g. Menzel, 1954; Shaw et al., 1992; Zhu and Smolders, 2000; Frissel et al., 2002; Hampton et al., 2004; Kanter et al., 2010). These observations have been attributed both to direct effects, for example a reduction in K^+ competition with Cs^+ for transport across the plasma membrane of root cells or reduced K^+ relief of Cs^+ blockade of KIRC as rhizosphere potassium decreases (Shaw et al., 1992; White and Broadley, 2000; Zhu and Smolders, 2000; Juri Ayub et al., 2008), and to indirect effects, for example a decline in the potassium nutrition of plants increasing the abundance of K^+/H^+-symporters and, thereby, increasing cesium uptake and the selectivity of uptake of cesium versus potassium (White and Broadley, 2000; Zhu and Smolders, 2000; Hampton et al., 2004, 2005; White et al., 2010). Prorok et al. (2011, 2012) have suggested that the dissolved potassium per unit volume of soil (C_K), which represents the amount of potassium available to a plant, determines the selectivity of accumulation of ^{137}Cs and potassium by plants in the field rather than the potassium concentration in the soil solution. These authors observed that, for all plants and soils, when $C_K < 0.5\ \mu g\ cm^{-3}$ uptake could be more selective for ^{137}Cs than potassium, but when C_K was between 0.5 and 4 $\mu g\ cm^{-3}$ uptake was more selective for potassium than ^{137}Cs (Prorok et al., 2006, 2011, 2012). These authors suggest that this phenomenon might be attributed to soil water content. They reason that, under natural conditions, soil pores are filled, or partly filled, by soil solution. The more soil solution the roots have access to, the greater will be their ability to acquire potassium. The ability to acquire potassium determines, in part, whether a plant is potassium-replete or potassium-deficient, and the abundance of the high-affinity K^+/H^+-symporter (HAK5). If plants become potassium deficient, the abundance of the high-affinity K^+/H^+-symporter increases, the ratio HAK5:KIRC increases, more ^{137}Cs is taken up, and the selectivity for ^{137}Cs versus potassium increases.

This paper investigates whether the temporal variation in shoot ^{137}Cs concentration and shoot ^{137}Cs/potassium quotient of radish (*Raphanus sativus* L.) observed in the field under natural conditions might be explained by changes in either the potassium concentration of the soil solution or potassium phytoavailability and the likely molecular mechanisms that underlie such variations. Radish was chosen for these experiments since it is a rapidly-growing, non-mycorrhizal member of the Brassicaceae family.

2. Materials and methods

2.1. Field sites and their soil properties

Experiments were performed at three field sites within the 10 km Exclusion Zone of the Chernobyl Nuclear Power Plant designated site D (51°22′29.2″N, 29°54′0.1″E), which had a peaty soil, site B (51°22′33.6″N, 29°54′5.1″E), which had a sandy-loam soil, and site B2 (51°22′29.5″N, 29°54′6.3″E), which had a sandy soil (Table 1). Chemical and physical properties of the top 20 cm of the soils at each site were determined on 18 September 2012 using the methods described by Aleksandrova and Naidenova (1986). Soils were first air-dried, then ground in a porcelain mortar and sieved through a mesh with holes of 1 mm diameter. Large particles (>1 mm) were almost absent. Soil density (ρ, $g\ cm^{-3}$) was determined gravimetrically. Soil organic matter was determined by the Turin method (Aleksandrova and Naidenova, 1986), assuming 1.79 for the quotient of humic substances/soil organic carbon (Arinushkina, 1970). The Cation Exchange Capacities of soils were determined by cation displacement using 1 M NH_4Cl. Concentrations of exchangeable Na^+ and K^+ were assayed by atomic absorption using a C-115.M1 spectrophotometer (SEMI Ltd., Sumy, Ukraine) and concentrations of exchangeable Ca^{2+} and Mg^{2+} were assayed using a trilonometric method (Khopkar, 1998). Soil pH was

Table 1
Chemical and physical properties of soils at experimental sites D, B and B2.

	Site D	Site B	Site B2
pH_{KCl}	4.56	4.78	4.92
Organic carbon (%)	6.37	0.58	1.16
Organic matter (%)	11.40	1.04	2.08
Density ($g\ cm^{-3}$)	0.85	1.41	1.42
^{137}Cs content ($Bq\ kg^{-1}$)	15,200	16,900	10,600
External gamma dose rate ($mR\ h^{-1}$)	200	380	350
Cation exchange capacity (CEC)			
Na ($mg\text{-}eq\ g^{-1}$)	0.001913	0.000891	0.000913
K ($mg\text{-}eq\ g^{-1}$)	0.00105	0.000609	0.000494
$\sum Ca + Mg$ ($mg\text{-}eq\ g^{-1}$)	0.178	0.016	0.04
CEC ($mg\text{-}eq\ g^{-1}$)	0.18096	0.0175	0.041
Particle size analysis			
0.25–0.05 mm (%) [sand]	78.46	85.90	93.06
0.05–0.01 mm (%)	18.78	10.65	5.48
0.01–0.005 mm (%)	1.82	2.50	1.08
0.005–0.001 mm (%)	0.94	0.95	0.38