

Some elements are more equal than others: soil-to-plant transfer of radiocaesium and radiostrontium, revisited

Commentary on “Disparity in ^{90}Sr and ^{137}Cs uptake in Alpine plants: Phylogenetic effect and Ca and K availability”, by T. Guillaume et al.

Martin R. Broadley · Philip J. White

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In the current issue, Guillaume et al. (2012) present a study reporting the soil-to-plant transfer of the caesium (Cs) and strontium (Sr) radionuclides, ^{137}Cs and ^{90}Sr , in an Alpine environment. These radionuclides were among those released and deposited in large quantities during above-ground weapons tests post-1945, and, more recently, as a consequence of the accidents including those at Chernobyl in 1986 (Smith et al. 2000), and Fukushima in 2011 (Yasunari et al. 2011). Due to their long half-lives ($t_{1/2}$ ^{90}Sr =29.1 years; $t_{1/2}$ ^{137}Cs =30.1 years) and high energy emissions of beta and gamma radiation, understanding and predicting the

transfer of these radionuclides in the environment is of interest from a radioecological/health protection perspective. There is still considerable uncertainty regarding transfer and downstream effects of chronic exposure to low levels of ionising radiation on both humans and other biota (Beresford et al. 2004; Copplestone et al. 2010).

One positive consequence of the release to the environment of long-lived anthropogenic radionuclides such as ^{137}Cs and ^{90}Sr is that they become de facto tracer elements which can be used to explore a range of environmental processes including nutrient cycling and soil erosion (e.g. Owens et al. 1996). Furthermore, studies of soil-to-plant transfer of ^{137}Cs and ^{90}Sr from the radioecological literature (e.g. Andersen 1967; Frissel et al. 2002) can be used to provide insights into the transport dynamics of the macronutrient elements K and Ca in plants (e.g. White and Broadley 2000, 2003), since these elements are chemical analogues of Cs and Sr, respectively. The study of Guillaume et al. (2012) is a valuable addition to this field.

In Guillaume et al. (2012), soil and plant samples were taken at six sites from an Alpine valley, in Switzerland, at an elevation of 2,000 m. In total, 12 species of plant were sampled representing 12 plant families. Soil was sampled at three horizons. The authors conducted detailed soil-to-plant transfer analysis on these data. From their analyses, it is

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M. R. Broadley (✉)
Plant and Crop Sciences Division, School of Biosciences,
Sutton Bonington Campus, University of Nottingham,
Loughborough LE12 5RD, UK
e-mail: martin.broadley@nottingham.ac.uk

P. J. White
The James Hutton Institute,
Invergowrie,
Dundee DD2 5DA, UK

clear that ^{137}Cs uptake by plants is highly dependent on soil type. For example, shoot activity concentrations of ^{137}Cs were considerably lower when soil exchangeable K concentrations were higher, especially in the upper soil horizons. Similarly, soil exchangeable Ca concentrations affected soil-to-plant transfer of ^{90}Sr , albeit to a lesser degree than the effect of soil exchangeable K concentrations on soil-to-plant transfer of ^{137}Cs . Based on these observations, the authors hypothesise that plant effects are therefore more important for predicting soil-to-plant transfer of ^{90}Sr than for ^{137}Cs , and they discuss the potential for phylogenetic influences on soil-to-plant transfer of Sr and Cs. Whilst it is of course impossible to infer general phylogenetic trends in soil-to-plant transfer from a sample of 12 families, each comprising a single species, there are nevertheless some remarkable consistencies between this study and the literature which are worth highlighting.

There is a large literature reporting variation in the ability of plants to take up and accumulate Cs and Sr,

and their chemical analogues K and Ca in their shoots (e.g. Andersen 1967; Broadley and Willey 1997; Thompson et al. 1997; Broadley et al. 1999a,b, 2003, 2004; Frissel et al. 2002; White and Broadley 2003; White et al. 2003; White 2005; Willey et al. 2005; Lettner et al. 2006; Willey and Tang 2006; Anjos et al. 2007; Watanabe et al. 2007; Willey 2010). In plant phylogenetic terms, it has previously been noted that among the angiosperms, monocot species (e.g. including species from the grass family, Poaceae) tended to have lower shoot Cs concentrations than species from the Eudicots, in particular, species of the Asteraceae, Brassicaceae and Amaranthaceae families (Broadley et al. 1999a; White et al. 2003; Willey et al. 2005; Willey 2010). However, this phenomenon is probably only a general trend at best (e.g. see Fig. 1a, c and e). Indeed, when one looks at stable Cs concentrations in the leaves from a much wider sample group of plants ($n > 2,000$ observations; Watanabe et al. 2007), monocot families do not have low Cs concentrations in their leaves compared to other

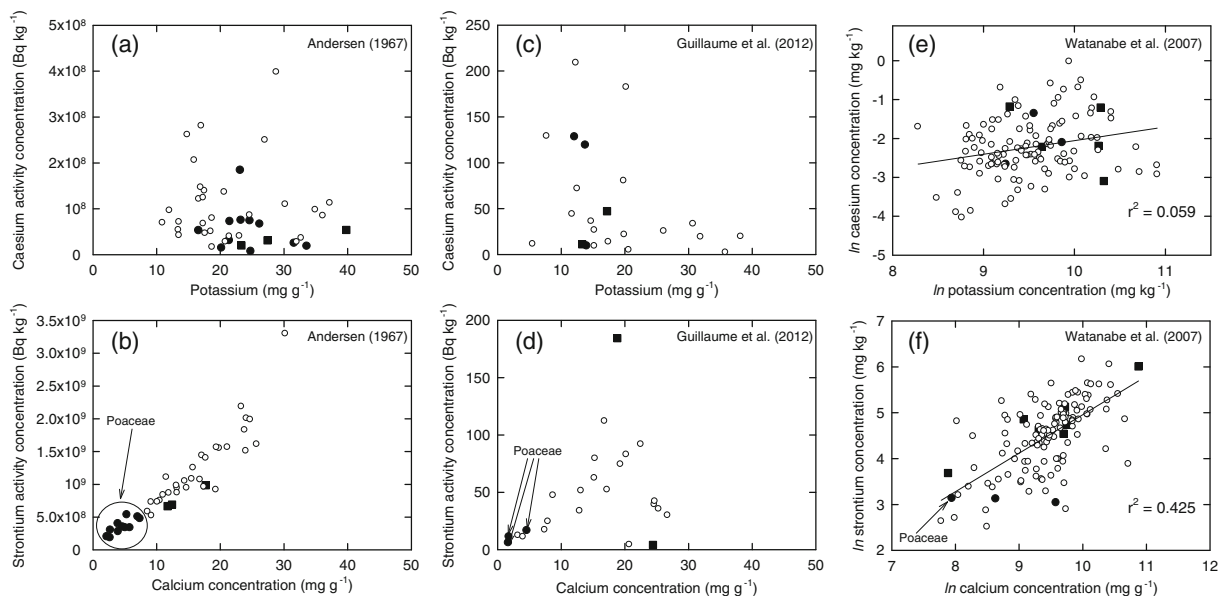


Fig. 1 Relationships between shoot (radio)caesium and potassium (a,c,e) or (radio)strontium and calcium (b,d,f) concentrations observed in three independent studies. *Black circles* are commelinoid monocots (with Poaceae highlighted specifically in Panels b,d,f); *black squares* are non-commelinoid monocots; *open circles* are other taxa. Notes: (a,b) Redrawn from Andersen (1967) based on shoot data for 44 different plant species grown in pots, containing 1.2 kg of loamy sand soil containing either (a)

307.1 kBq ^{137}Cs or (b) 92.5 kBq ^{89}Sr per kg of dry soil. (c,d) Redrawn from Table 1 in Guillaume et al. (2012) based on shoot data for 12 species of Alpine plants sampled from six different sites; raw data with no normalisation. (e,f) Redrawn from Watanabe et al. (2007) based on family-level estimated means for up to 140 families of vascular plant (and $>2,000$ individual data)

plant families (Fig. 1e). Similarly, whilst there are clear phylogenetic associations between plants and their capacity to accumulate K, based on wider datasets, monocot families do not appear to have characteristically low shoot K concentrations (Thompson et al. 1997; Broadley et al. 2004). Consistent with these observations, monocot species had variable shoot K concentrations and Cs activity concentrations (Fig. 1c) in the study of Guillaume et al. (2012).

In contrast to Cs and K, there is abundant evidence in the literature that phylogeny is very strongly associated with variation in shoot Sr and Ca concentrations; this is again borne out in the study of Guillaume

et al. (2012) (Fig. 1d). Thus, from samples collected in the field (Thompson et al. 1997; Watanabe et al. 2007), meta-analyses of literature-based leaf/shoot concentration data and experiments performed under controlled conditions (Broadley et al. 2003; White and Broadley 2003; Willey and Fawcett 2005) have consistently shown major phylogenetic differences in shoot Sr and Ca concentrations among plants. The most striking example is seen in commelinoid monocot groups, notably grasses (Poaceae), rushes (Juncaceae) and sedges (Cyperaceae), which appear to have strong limits on the Ca (and Sr) concentrations in their leaves. This phenomenon correlates with cell wall

Table 1 Transport proteins in *Arabidopsis thaliana* with the potential to catalyse Cs^+ fluxes across the plasma membranes of root cells, and their K^+/Cs^+ selectivity based on electrophysiological evidence

(White et al. 2010). Data for the expression of these transporters in root cells and their regulation by K starvation is reviewed by White and Karley (2010)

Transporter	Selectivity	Gene family	Expression pattern in root	Effect of K starvation on expression		
KIRC	KIRC: $P_{\text{Cs}}/P_{\text{K}}=0.07-0.43$	Shaker (7 members)	AtAKT1: Epidermis, cortex, endodermis.	Unaffected		
			AtKAT1: Vasculature.	–		
			AtKC1: Root hairs, epidermis, cortex, endodermis.	Unaffected		
KORC	KORC: $P_{\text{Cs}}/P_{\text{K}}=0.12-0.31$ AtSKOR: $P_{\text{Cs}}/P_{\text{K}}=0.15$	Shaker (2 members)	AtSKOR: Pericycle, xylem parenchyma.	Downregulated		
			AtGORK: Root hairs.	Unaffected		
NORC	$P_{\text{Cs}}=P_{\text{K}}$	Unknown	–	–		
VICC	ScVICC: $P_{\text{Cs}}/P_{\text{K}}=0.85$ AtVICC: $P_{\text{Cs}}/P_{\text{K}}\approx 1.00$ ThVICC: $P_{\text{Cs}}/P_{\text{K}}=0.43$ AtCNGC2: $G_{\text{Cs}}/G_{\text{K}}=0.64$	AtCNGC (20 members)	AtCNGC1, AtCNGC2, AtCNGC3, AtCNGC5, AtCNGC6, AtCNGC8, AtCNGC9, AtCNGC10, AtCNGC12, AtCNGC13, AtCNGC14, AtCNGC15, AtCNGC17, AtCNGC18, AtCNGC19: Root.	Unaffected		
			AtGLR (20 members)	All expressed in roots.	Unaffected	
				AtGLR1.1: Collet, lateral roots.	Upregulated	
				AtGLR1.2, AtGLR1.3: Root.	Unaffected	
				AtGLR2.1: Throughout root, except tip.	Unaffected	
		AtGLR2.3, AtGLR2.4, AtGLR2.8: Root.		–		
		DACC HACC	ScDACC: $P_{\text{Cs}}/P_{\text{K}}=0.85$ unknown	Unknown Annexins (7 members)	AtGLR3.1: Vasculature.	–
					AtGLR3.2: Stele.	Unaffected
					AtGLR3.3, AtGLR3.5, AtGLR3.6: Root.	–
					All expressed in roots.	–
AnnAt1: Throughout root.	–					
H^+/K^+ symport	AtHAK5 [Cs]	AtKUP (13 members)	AnnAt2: Collet endodermis, initiating laterals, tip epidermis.	–		
			AtKUP1, AtKUP4, AtKUP5, AtKUP6, AtKUP7, AtKUP8, AtKUP10: Root.	Unaffected		
			AtKUP2: Growth zones.	Unaffected		
			AtKUP3: Root.	Upregulated		
			AtHAK5: Root.	Upregulated		

properties, especially low cation-exchange capacity (White and Broadley 2003; White 2005) and also with a propensity to accumulate high tissue silicon (Si) concentrations (Hodson et al. 2005). Intriguingly, low Ca (and high Si) concentrations are NOT a feature of all monocots; non-commelinoid monocot groups (e. g. Alliaceae) have shoot Sr and Ca concentrations similar to most Eudicot groups (Hodson et al. 2005; Watanabe et al. 2007; Fig. 1f). However, more highly resolved phylogenetic insights into Sr and Ca (and Si) accumulation within the monocots are not yet possible due to a lack of suitable data. Consistent with these observations, the one representative of the Poaceae in the study of Guillaume et al. (2012), *Phleum rhaeticum*, had low capacity for Sr and Ca accumulation, whereas the two non-commelinoid monocot species, *Allium schoenoprasum* (Alliaceae) and *Veratrum album* (Melanthiaceae) both had relatively high Ca concentrations (Fig. 1d). *Allium schoenoprasum* had low shoot Sr activity concentration and *V. album* had high shoot Sr activity concentration. However, the species were not sampled from the same site and the data are, therefore, not strictly comparable in such terms.

In addition to phylogenetic associations, there are intriguing similarities between the Cs/K and Sr/Ca accumulation patterns observed by Guillaume et al. (2012) in an Alpine flora, sampled under field conditions, and an early comparative analysis of Cs/K and Sr/Ca accumulation patterns in agricultural species, conducted under controlled conditions (Andersen 1967). Thus, there is no correlation between shoot Cs and K concentration among species in either study, in contrast to a much stronger correlation between shoot Sr and Ca concentration among species in both studies. It is noteworthy that outlier data in the raw data in Guillaume et al. (2012) is to be expected due to the variation in soils between sites and in the absence of any normalisation of data used here to draw Fig. 1d. The observations of Andersen (1967) have previously been used to develop hypotheses regarding Cs/K and Sr/Ca uptake by plants (White et al. 2010; White and Karley 2010). It has been proposed that the lack of correlation between shoot Cs and K concentration is consistent with the constitutive expression of a selective K^+ transporter such as AKT1, which does not contribute significantly to Cs^+ uptake under typical soil conditions (Broadley et al. 2001), and the expression of other proteins catalysing the non-specific uptake of Cs^+ and K^+ , such as CNGCs or KUPs, which

are regulated by factors including the K^+ status of the plant (Hampton et al. 2004, 2005; Qi et al. 2008; Table 1). One can then speculate that species with higher shoot Cs concentrations and shoot Cs/K quotients have higher *CNGC:AKT1* and/or *KUP:AKT1* expression ratios than plants with lower shoot Cs concentrations and shoot Cs/K quotients (White et al. 2010; White and Karley 2010). Nevertheless, whilst many putative Cs^+ -permeable transporters have been identified in plants (Table 1), such hypotheses remain speculative and await direct analysis through molecular genetic approaches. In contrast to Cs and K, there is a strong correlation between the ability of a plant to accumulate Sr and Ca, and even other divalent cations such as barium. This phenomenon has been cited as evidence for a dominant role for the apoplastic movement of these cations across the root to the xylem (White 2001), whereas transport of Cs and K to the xylem is likely to be primarily symplastic (White and Broadley 2000). Again, these hypotheses remain to be tested directly.

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