



REVIEW ARTICLE

Plant uptake of radiocaesium: a review of mechanisms, regulation and application

Y-G. Zhu^{1,3} and E. Smolders²

¹ Department of Soil and Water, and CRC for Molecular Plant Breeding, The University of Adelaide, Glen Osmond, SA 5064, Australia

² Laboratory of Soil Fertility and Soil Biology, Katholieke Univ Leuven, Louvain, Belgium

Received 11 February 2000; Accepted 4 May 2000

Abstract

Soil contamination with radiocaesium (Cs) has a long-term radiological impact because it is readily transferred through food chains to human beings. Plant uptake is the major pathway for the migration of radiocaesium from soil to human diet. The plant-related factors that control the uptake of radiocaesium are reviewed. Of these, K supply exerts the greatest influence on Cs uptake from solution. It appears that the uptake of radiocaesium is operated mainly by two transport pathways on plant root cell membranes, namely the K⁺ transporter and the K⁺ channel pathway. Cationic interactions between K and Cs on isolated K-channels or K transporters are in agreement with studies using intact plants. The K⁺ transporter functioning at low external potassium concentration (often < 0.3 mM) shows little discrimination against Cs⁺, while the K⁺ channel is dominant at high external potassium concentration with high discrimination against Cs⁺. Caesium has a high mobility within plants. Although radiocaesium is most likely taken up by the K transport systems within the plant, the Cs:K ratio is not uniform within the plant. Difference in internal Cs concentration (when expressed on a dry mass basis) may vary by a factor of 20 between different plant species grown under similar conditions. Phytoremediation may be a possible option to decontaminate radiocaesium-contaminated soils, but its major limitation is that it takes an excessively long time (tens of years) and produces large volumes of waste.

Key words: Radiocaesium, potassium, ion competition, plant uptake, phytoremediation.

Introduction

Radiocaesium is one of the most important artificial radionuclides produced by nuclear fission. It has been introduced into the terrestrial environment by nuclear weapons testing, authorized discharge of nuclear waste and accidental release from nuclear facilities, such as the Chernobyl accident in April 1986. Soil contamination with radiocaesium has a long-term radiological impact due to its long physical half-life (30 years for ¹³⁷Cs and 2 years for ¹³⁴Cs) and its high biological availability. Consumption of agricultural produce contaminated with radiocaesium represents the principal route of human exposure to this radionuclide (Shaw and Bell, 1994).

Research on plant uptake of caesium dates back to the early 1940s (Collander, 1941), when studies focused on differences in the uptake of ions from solution and on establishing the suitability of using radioactive isotopes to trace plant uptake of nutrients such as K⁺ (Epstein and Hagen, 1952; Menzel, 1954). Deposition of radiocaesium during nuclear weapons testing in the 1950s and 1960s provided further opportunities for research on mechanisms of radiocaesium transfer to plants by foliar and root uptake pathways (Russell, 1966). This research topic received further attention following the accident at the Chernobyl Nuclear Power Plant in April 1986, which resulted in wide scale deposition of radiocaesium over large areas of soil in Europe and the former Soviet Union. In general, research has focused on the following three areas: (1) mechanisms of plant uptake of radiocaesium; (2) regulations of plant uptake of radiocaesium, for example, by plant traits, soil potassium and mycorrhizas; and (3) formulation of agricultural countermeasures for and remediation of soils contaminated with radiocaesium.

³To whom correspondence should be addressed. Fax: +61 8 8303 6511. E-mail: yongguan.zhu@adelaide.edu.au

Since soil contamination with radiocaesium is still an unsolved problem in many parts of the world, knowledge on plant uptake of radiocaesium will be important for devising effective strategies and developing techniques, such as agricultural countermeasures and phytoremediation, to minimize the transfer of radiocaesium from soil to humans. This paper therefore reviews the current knowledge on plant uptake of radiocaesium in order to piece together information on factors affecting uptake processes (particularly K supply and genetic difference in uptake) and the mechanisms involved. Soil-to-plant transfer factors (TF) for radiocaesium and its distribution within plants are also discussed because these two issues are of direct relevance to human exposure to radiocaesium through the foodchain. TF values for different soil-plant combinations are summarized, which can be used for radiological modelling and assessment. Phytoremediation of radiocaesium, as a potential environmental technology is also discussed in terms of its potentiality and limitations.

Uptake of Cs by plant roots: kinetics and interionic effects

Caesium (Cs) is a weakly hydrated alkaline metal with chemical similarities to potassium (K). Caesium is predominantly present in solution as the free hydrated cation Cs^+ with little or no tendency to form soluble complexes. Caesium can be readily absorbed by plant roots from solution and can be translocated to the above-ground plant parts. Plants grown in nutrient solution typically concentrate Cs in their tissue compared to the outer solution. Wheat plants grown for 70 d in nutrient solutions (with K^+ concentration at 3.5 mM) spiked with carrier-free ^{137}Cs contained 10-fold higher ^{137}Cs concentration in the tissue water than in the outer solution (Smolders and Shaw, 1995). Higher Cs concentration factors are found at lower K concentrations where dry

weight-based shoot to solution ^{137}Cs concentration ratios are found up to 4500 ml g^{-1} (Smolders *et al.*, 1996a).

The mechanisms by which Cs is taken up by plant roots are not completely understood. At least at low K concentrations there is evidence that Cs^+ is absorbed by the K^+ uptake system of the root. This evidence is derived from the observations that K^+ strongly suppresses Cs^+ uptake (Shaw and Bell, 1991; Shaw *et al.*, 1992; Zhu and Shaw, 2000) and that Cs^+ is efficiently transported by an isolated high affinity K^+ uptake transporter of wheat root cells (Schachtman and Schroeder, 1994). Plant roots, however, absorb Cs less efficiently than its nutrient analogue, potassium. This is illustrated in the so-called Cs/K discrimination factor (DF), defined as:

$$DF = \frac{\left(\frac{[Cs]_{\text{plant}}}{[K]_{\text{plant}}}\right)}{\left(\frac{[Cs]_{\text{substrate}}}{[K]_{\text{substrate}}}\right)} \quad (1)$$

values of DF below unity indicate that K is more efficiently absorbed than Cs. Most reported Cs/K DFs in plants exposed to nutrient solution are below 1 (Menzel and Heald, 1955; Middleton *et al.*, 1960; Cline and Hungate, 1960; Nishita *et al.*, 1962; Baligar *et al.*, 1979; Smolders *et al.*, 1996b). The Cs/K DF typically range between 0.01 and 0.8 and vary with K concentrations, species and type of plant tissue (Table 1). A Cs/K DF above unity has only been reported once for a plant part (bean trifoliolate), but this may reflect a different internal distribution of Cs and K since the Cs/K DF of the entire plant was still below unity (Cline and Hungate, 1960). Solution culture studies show that Cs/K DFs are always lower than corresponding Rb/K DFs (Menzel and Heald, 1954; Baligar *et al.*, 1979). This means that Rb is a more suitable analogue for K in plants than Cs. Rubidium-86 is indeed often used as tracer for K in plants, but it has been reported that there is also Rb/K discrimination that may

Table 1. The Cs to K discrimination factor of plants grown in nutrient solution: the discrimination factor is defined in equation (1)

| Plant | Exposure time | K in solution (mM) | Cs in solution (μM) | Cs-K discrimination factor | Reference |
|----------------------------|-----------------|--------------------|----------------------------------|----------------------------|--------------------------------|
| Millet, entire plant | 40 d | 2.8 | 14 | 0.22 | Menzel and Heald, 1955 |
| Sunflower | up to flowering | 2.8 | 14 | | Menzel and Heald, 1955 |
| Flower | | | | 0.12 | |
| Leaves | | | | 0.17–0.20 | |
| Petioles | | | | 0.10–0.15 | |
| Stems | | | | 0.12 | |
| Roots | | | | 0.29 | |
| Barley roots | 2 h | 0.01–10 | carrier-free ^{137}Cs | 0.15–0.35 | Middleton <i>et al.</i> , 1960 |
| Barley shoots | 2 h | 0.1 and 10 | carrier-free ^{137}Cs | 0.06 and 0.50 | Middleton <i>et al.</i> , 1960 |
| Bean, first trifoliolate | 16 d | 0.07–2.0 | 20 | 0.1–0.8 | Cline and Hungate, 1960 |
| Bean (different parts) | 44 d | 2.5–15 | carrier-free ^{137}Cs | 0.01–0.1 | Nishita <i>et al.</i> , 1962 |
| Spring wheat, entire plant | 11 d | 0.025–1.0 | carrier-free ^{137}Cs | 0.04–0.26 | Smolders <i>et al.</i> , 1996 |

cause errors in estimating K fluxes in plants when based on ^{86}Rb fluxes (Marschner and Schimansky, 1970).

Interionic effects on Cs uptake by plant roots have been intensively studied and these effects are important in predicting the uptake of radiocaesium from soil. Among all alkaline metals and NH_4^+ it appears that K^+ is the most important cation that competes with Cs^+ uptake (Bange and Overstreet, 1960; Handley and Overstreet, 1961; Shaw and Bell, 1991; Shaw *et al.*, 1992; Shaw, 1993). It has long been recognized that lowering K concentrations in solution strongly increase Cs uptake by plants (Cline and Hungate, 1960; Nishita *et al.*, 1962). These previous studies are difficult to analyse as there is little information on the actual K concentrations in solution during the experimental period. Low K concentrations are typically difficult to maintain in solution culture. More recent studies, in which the experimental period was either short or where K concentrations were maintained within reported boundaries, do allow the analysis of the K/Cs interaction in more detail. A summary of 10 different studies is given in Fig. 1 where the plant to solution Cs concentration ratio (the so-called concentration factor, CF) is plotted as a function of solution K concentration. All these studies refer to Cs uptake at carrier-free (i.e. containing a negligible amount of stable caesium) radiocaesium concentration and where K concentrations are controlled to maintain within 40%

of initial value during plant growth. The CF for radiocaesium for each species are reduced by at least one order of magnitude with increasing solution K up to about 1 mM K^+ (Fig. 1). The largest effects are found roughly between 10 μM and 250 μM K; above about 250 μM K there is almost no further K effect on Cs uptake for most species. Uptake of ^{137}Cs by the alga *Selenastrum capricornutum* is reduced 10-fold between 80 μM K and 1500 μM K (Corisco and Carreiro, 1990). The consequence of the large effect of K on Cs uptake in the micromolar K concentration range is that ^{137}Cs uptake from soil can be reduced by K fertilization at low soil K status (Belli *et al.*, 1995; Roca and Vallejo, 1995). Many soils typically have K concentrations in pore water below 250 μM (Wolt, 1994).

Increasing concentrations of NH_4^+ reduce uptake of Cs in short-term studies (Shaw *et al.*, 1992) or have no effect in complete nutrient solutions (Smolders *et al.*, 1997a). Soil solution concentrations of NH_4^+ are typically below 1 mM in aerobic soils (Wolt, 1994), and it seems that varying NH_4^+ concentrations are unlikely to affect the root uptake process to any extent in soils. Increasing NH_4^+ concentrations do, however, affect plant availability of ^{137}Cs in soil, but this effect is due to NH_4^+ effectively mobilizing Cs in soils (Sanchez *et al.*, 1999). Increasing concentrations of Ca^{2+} and Mg^{2+} slightly reduced the uptake of Cs. Uptake of Cs in spinach was reduced 3-fold

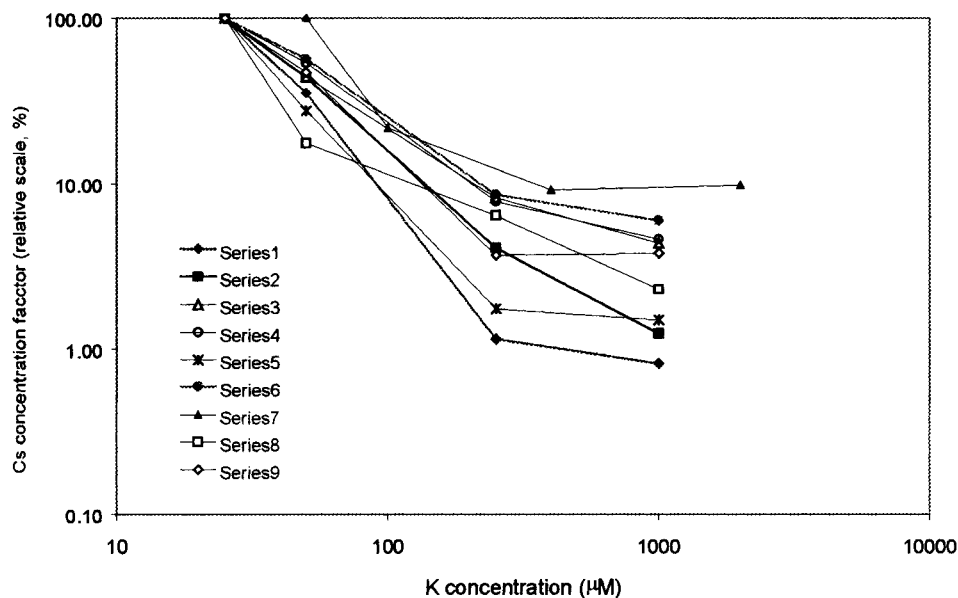


Fig. 1. The relationship between external K^+ concentration and concentration factor of radiocaesium by various plant species. Series 1: (Smolders *et al.* 1996a); spring wheat shoot (dry weight-based); exposure time 11 d; age at harvest = 18 d. Series 2: (Waegeneers *et al.*, unpublished results); winter barley shoot (dry weight-based); exposure time = 10 d; age at harvest = 17 d. Series 3: (Waegeneers *et al.*, unpublished results); ryegrass shoot (dry weight-based); exposure time = 10 d; age at harvest = 17 d. Series 4: (Waegeneers *et al.*, unpublished results); *Agrostis* shoot (dry weight-based); exposure time = 10 d; age at harvest = 17 d. Series 5: (Waegeneers *et al.*, unpublished results); lettuce shoot (dry weight-based); exposure time = 13 d; age at harvest = 20 d. Series 6: (Waegeneers *et al.*, unpublished results); bean leaves (dry weight-based); exposure time = 10 d; age at harvest = 17 d. Series 7: (Gommers *et al.*, unpublished results); willow shoot clone (dry weight-based); exposure period = 26 d; age at harvest = 26 d. Series 8: (Zhu, 1998); spring wheat root (dry weight-based) exposure time = 63 d; age at harvest = 63 d. Series 9: (Zhu, 1998); broad bean root, exposure time = 60 d; age at harvest = 60 d.

with increasing Ca+Mg concentrations (at constant Ca/Mg ratio) from 0.27 to 7.0 mM (Smolders *et al.*, 1997a). The interpretation of these results is that divalent cations compete with Cs uptake through competition in the apoplast (Smolders *et al.*, 1997a). Increasing concentrations of stable Cs reduce uptake of radiocaesium (Handley and Overstreet, 1961; Shaw *et al.*, 1992), but there is little effect below 10 μM Cs (Shaw *et al.*, 1992). Concentrations of stable Cs in soil pore waters are estimated to be below 1 nM (Wauters, 1994). In consequence, stable Cs may not be an important factor affecting the root uptake process in soil. In addition, uptake of ^{137}Cs by plant roots is proportional to solution activities since ^{137}Cs is released as a carrier-free isotope. Solution culture studies with wheat confirmed that shoot and root ^{137}Cs activities increase proportionally to ^{137}Cs activities in nutrient solution, up to 100 kBq l^{-1} , the highest concentration tested (Zhu *et al.*, 2000; J Buysse, unpublished data).

Uptake of Cs by plant roots: possible mechanisms

The strong relationship between K concentration and Cs uptake (Fig. 1) calls for a detailed analysis. This strong effect may be expected if it is assumed that Cs is absorbed by the K uptake system with a constant DF between the two cations. Equation (1) shows that the CF for Cs is inversely proportional to solution K if the DF is constant and if plant K is not a function of solution K. The last condition is roughly met above 10 μM K since the Michaelis constant for K uptake is below this value in long-term studies (Glass, 1989). A more detailed analysis of the Cs–K concentration relationship shows that the CF can decrease even more than proportionally to the reciprocal of the K concentration. As an example, the 5-fold increase in the concentration of K between 50 and 250 μM decreases the CF for spring wheat 30-fold. It is yet unclear why K may have a *more* than proportional effect on Cs at a given K concentration range. One speculation is that diffusive limitations in the unstirred layer around plant roots increase the Cs/K concentration ratio above that in the bulk nutrient solution at low K concentrations (see Smolders *et al.*, 1996a, for more details on this hypothesis). Above about 250 μM K, there is little further K competition for Cs uptake by most plant species (Fig. 1, but also Cline and Hungate, 1960). It can be shown that the Cs–K DF therefore increases with increasing solution K in the high K concentration range.

Carrier and channel modes have been proposed as possible mechanisms with a molecular basis for the transport of K^+ across cell membranes of plant roots (Nissen, 1991). Carrier-mediated transport is facilitated by a high-affinity system (transporter) within cell

membranes operating predominantly at low external K concentration (often < 0.3 mM). Potassium is transported across the plasma membrane against the electrochemical gradient via this system (Maathuis and Sanders, 1994). The structure and transport mechanisms of a high affinity K uptake transporter were elucidated in 1994 (Schachtman and Schroeder, 1994). This transporter (HKT1) is probably a K^+ - H^+ cotransporter and has a selectivity sequence of $\text{K}^+ > \text{Cs}^+ > \text{Rb}^+ > \text{Na}^+ > \text{NH}_4^+$ (Schachtman and Schroeder, 1994). Expressing and voltage clamping HKT1 in *Xenopus* oocytes showed that Cs was transported efficiently at 86% of the rate of K at equal concentrations of 1 mM. However, more recent results indicated that HKT1 is a Na^+/K^+ cotransporter, and is highly selective for K^+ and Na^+ (Gassmann *et al.*, 1996). Nevertheless, it has been suggested that multiple high-affinity K^+ transport systems may be involved in K^+ uptake (Wang *et al.*, 1998) and the selectivity of an individual transporter for K^+ and Cs^+ has yet to be determined. Channel-mediated transport is a low-affinity system operating at high external potassium concentration, typically above 0.5–1 mM K (Maathuis and Sanders, 1997). The first identification of K^+ channel cDNAs from plants were made in 1992 (Sentenac *et al.*, 1992). The channel KAT1 was cloned from *Arabidopsis thaliana*, which is a voltage-dependent inward rectifying K^+ channel (IRC) that operates at high K concentrations and has a selectivity $\text{K} > \text{Rb} > \text{Na} > \text{Cs}$ (Schachtman *et al.*, 1992). Maathuis and Sanders also reported a similar selectivity of K^+ channel for monovalent cations (Maathuis and Sanders, 1995). The channel can even be blocked by Cs at carrier Cs concentrations (e.g. 1 mM Cs^+ , Becker *et al.*, 1996).

The competition studies on isolated K transporters are in agreement with the overall pattern of Cs uptake at various K concentrations (Fig. 1). The K^+ transport system operating at low K concentrations can transport Cs^+ efficiently whereas Cs^+ permeates only slowly in K^+ channels operating at K concentrations above 0.5–1 mM. This model is supported by results reported by Sacchi *et al.*, who demonstrated that at low external potassium concentration (≤ 0.25 mM K), Cs^+ , Rb^+ and K^+ have similar kinetic constants in subapical maize root segments ($K_m = 26, 26$ and $22 \mu\text{M}$ and $V_{\text{max}} = 3.62, 3.94$ and $4.09 \mu\text{mol h}^{-1} \text{g}^{-1} \text{FW}$) (Sacchi *et al.*, 1997). At higher K concentrations, the selectivity for K strongly increases. Other evidence for this model is derived from Cs uptake kinetics in the aquatic plant *Riccia fluitans* growing at different external K^+ concentrations (Fernandez *et al.*, 1997). The high affinity transport system follows the Michaelis-Menten equation (i.e. saturation kinetics), and is believed to be carrier-mediated (H^+ -cotransporter), whereas the low affinity one exhibits linear kinetics, and is expected to be channel-mediated.

Table 2. Total radiocaesium efflux over the elution period and the rates of efflux from cytoplasm and vacuole at the beginning of elution (values in brackets represent s.e., $n=4$; data from Zhu *et al.*, 1999)

| External K level | Total efflux (Bq g ⁻¹) | Percentage of the total uptake (%) | ϕ_{co}^a (Bq g ⁻¹ min ⁻¹) | ϕ_{vo}^b (Bq g ⁻¹ min ⁻¹) |
|------------------|------------------------------------|------------------------------------|---|---|
| 50 μ M | 292.2 (42.03) | 4.0 (1.25) | 7.2 (1.88) | 0.4 (0.08) |
| 100 μ M | 183.6 (41.33) | 12.1 (1.46) | 19.2 (3.68) | 1.7 (0.30) |

^a ϕ_{co} , efflux rate from cytoplasm at $t=0$.

^b ϕ_{vo} , efflux rate from vacuole at $t=0$.

It is yet unclear why the low Cs uptake rate at high K concentrations is almost unaffected by increasing K concentrations. It may be possible that Cs enters the plant with uptake systems other than the K channels because its permeability in these channels is small. Another hypothesis is that Cs influx occurs through the K channels but that the ratio of Cs to K in the efflux part varies with K supply. The effect of external potassium concentration on efflux of ¹³⁷Cs has been demonstrated for wheat roots (Zhu *et al.*, 1999). Efflux of ¹³⁷Cs was found to be greater with high external potassium concentration (0.1 mM) than that with low potassium concentration (0.05 mM) (Table 2), which implied that the inhibitory effects of external potassium on radiocaesium uptake is partly due to efflux, this result provides a further explanation on how potassium regulates plant uptake of radiocaesium.

Field-grown crop plants are subjected to potassium starvation due to temporal and spatial variation in bioavailable potassium in the soil, resulting in the fluctuation of internal potassium concentration, which may also play an important part in regulating plant uptake of radiocaesium (Jones *et al.*, 1991). It is therefore important to quantify the effects of internal potassium status on plant uptake of radiocaesium. Potassium starvation could induce the expression of K⁺ transporters, such as HKT1 (Wang *et al.*, 1998), these high affinity K⁺ transporters have low discrimination between K⁺ and Cs⁺ (Sacchi *et al.*, 1997), therefore may also increase Cs⁺ uptake. Recently Zhu *et al.* demonstrated that 3 d after withdrawal of potassium from the growth medium of wheat seedlings, the subsequent uptake of radiocaesium increased dramatically (Fig. 2) (Zhu *et al.*, 2000). Study on uptake kinetics showed that potassium starvation caused substantial reduction in the K_m value and increase in the V_{max} value (of Cs⁺). It was also observed that the effect of starvation was to some extent compensated by resupply of potassium in the growth medium, especially at K⁺ concentration over 250 μ M. This finding is in accordance with the mechanism discussed above that, when external potassium concentration increased to a certain level (>200 μ M), the K⁺ uptake system transits from carrier-mediated (K⁺ transporters) to channel-mediated which discriminates

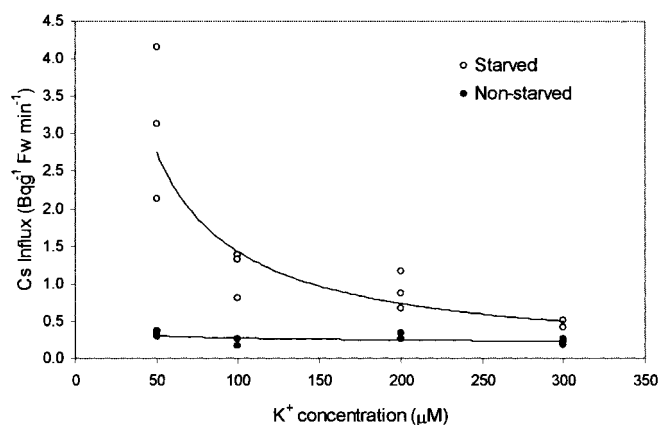


Fig. 2. Effect of K starvation on ¹³⁷Cs uptake by spring wheat at different external K concentrations (absorption time 90 min, Zhu *et al.*, 2000).

against Cs⁺. Therefore, both Cs⁺ uptake and the effect of potassium starvation were greatly reduced with resupply of potassium.

Genetic difference in plant uptake of radiocaesium

Genetic differences in plant mineral nutrition have been widely recognized by both agronomists and molecular biologists. Genetic variation in radiocaesium uptake is evident from the wide range of transfer factors observed for different species. Kopp *et al.* found that different types of crops grown on radiocaesium-contaminated sewage sludge displayed a 10-fold range in the radiocaesium transfer factor (Kopp *et al.*, 1990). Prister *et al.* observed a 20-fold range in the radiocaesium transfer factor for different natural species from a peaty meadow soil (Prister *et al.*, 1993). Genetic variation in radiocaesium uptake has also been found in tree plants. For example, Ertel and Ziegler observed that ¹³⁷Cs activities caused by root uptake from global fallout in trees of a Bavarian forest varied in the order of spruce > larch > sycamore maple (Ertel and Ziegler, 1991). A wide range of plant species have been screened for accumulation of radiocaesium (or stable caesium) (Broadly and Willey, 1997; NJ Willey, personal communication).

Among 30 plant taxa examined by Broadly and Willey, it was found that there were maximum differences between *Chenopodium quinoa* and *Koeleria macrantha* of 20-fold in tissue Cs concentrations (Broadly and Willey, 1997). More recent work by Willey and his co-workers (personal communication) has led to the general conclusion that the highest caesium accumulation occurs in families such as Amaranthaceae, Chenopodiaceae and Brassicaceae. However, Nisbet and Woodman pointed out that, for agricultural crops, genetic differences in TFs are quite small, especially when TF is expressed on a fresh weight basis for the plant (Nisbet and Woodman, 2000).

Genetic difference in plant uptake of radiocaesium could be altered by growth conditions, such as external potassium concentration. In a solution culture experiment under five nutritional scenarios with a range of K and Ca concentrations, Buisse *et al.* observed significant differences in total plant radiocaesium concentrations between clover, radish, maize, and sunflower (Buisse *et al.*, 1996). Nevertheless, the largest difference in ^{137}Cs concentration among the four plant species was found at the lowest K concentration (*c.* 0.25 mM), which implies that crop selection as a measure to reduce ^{137}Cs transfer from soil to food chain may not have significant effects without taking into consideration the external potassium concentration. The smaller difference in radiocaesium uptake among the four plant species at external potassium concentration above 0.25 mM may be due to the fact that root uptake of K^+ and Cs^+ is mainly operated by a channel-mediated system. The interaction between nutrient regimes and accumulation of Cs was also observed in six different species in the family Gramineae (Broadly and Willey, 1997).

Genetic differences in the uptake of radiocaesium by crops can result from a number of plant physiological parameters, such as plant growth strategies, growth rate, plant demand on potassium, rooting pattern, degree of mycorrhizal infection, ion transport systems on plasma membranes of root cells, and root growth rate. Plant demand on potassium seems to be important for caesium uptake. This was demonstrated in the plant families of Chenopodiaceae and Gramineae (Broadly and Willey, 1997). Discrimination of plant roots between K and Na may also play a role in Cs uptake. Most of the halophytes have long been known to show little discrimination between K and Na, while the high proportion of halophytes is in the family of Chenopodiaceae (Flowers *et al.*, 1986), to which many plant species with high capacity of taking up radiocaesium from soil belong (NJ Willey, personal communication).

Understanding the genetic variation in plant accumulation of radiocaesium will be very useful in three aspects: (1) selection of suitable crops grown in soils with a low level of radiocaesium contamination so as to minimize its transfer to food chains, but there is little difference on

a fresh mass basis, which is the form that people eat; (2) data on genetic variation could be integrated into models predicting the fate of radiocaesium in various soil-plant systems and for radiological assessment; (3) selection of plant species for the purpose of phytoremediation of soil contaminated with a high level of radiocaesium such as in vicinity of nuclear facilities (see section below).

Soil-to-plant transfer factors of Cs

The soil-to-plant transfer factor (TF, normally expressed as Bq kg^{-1} dry weight plant tissue/ Bq kg^{-1} dry mass soil) is often used to describe the uptake of radiocaesium from soil. Typical soil-to-plant transfer factors for agricultural plants have recently been compiled (Nisbet and Woodman, 2000) and these values are listed in Table 3. Soil properties, especially soil texture and potassium status have a major effect on the soil-to-plant transfer of radiocaesium (Bilo *et al.*, 1993; Guivarch *et al.*, 1999). It can be seen from Table 3 that TF values for agricultural plants are normally within the range of 0.001–1 for mineral soils with textures of loam or clay. For organic or sandy soils, TF values could be more than 1 or even as high as 28.5 for some agricultural crops (Sanchez *et al.*, 1999; Nisbet and Woodman, 2000). The relationship between TFs for radiocaesium and soil exchangeable K could, in some cases, be described by a negative power function (Nisbet *et al.*, 1999). These power function relationships accounted for $\sim 37\%$ of the variability in TF, and suggested that the TF for radiocaesium increases exponentially below a critical level of exchangeable K of around 0.2 meq per 100 g soil (Bilo *et al.*, 1993; Nisbet, 1995). By analysing a large database, Nisbet and Woodman found that TFs for radiocaesium appear to be independent of radiocaesium concentrations in the soil for concentrations that vary over five orders of magnitude (Nisbet and Woodman, 2000). This validates the use of the TF approach to predict plant uptake of radiocaesium in agricultural systems.

The relationship between soil K supply and TF is different from that between solution K and CF shown in Fig. 1. Increasing K supply can mobilize Cs in soil through ion exchange reactions, thereby obscuring the effect of increasing K on the CF of Cs. Smolders compared the TF values for Cs (ryegrass) between 30 different soils and found that the radiocaesium concentration ratio of grass-soil solution followed the same trend as that shown here in Fig. 1 (Smolders, 1997b). This analysis showed that plant uptake of radiocaesium can be predicted from soil solution concentrations of both Cs and K. Based on this concept, models have been developed to predict soil-to-plant transfer of radiocaesium from readily available soil parameters

Table 3. Recommended values and 95% confidence intervals for TF ($Bg\ kg^{-1}$ dry matter per $Bq\ kg^{-1}$ dry mass soil) for radiocaesium for mature edible parts (Nisbet and Woodman, 2000)

| Crop | Soil type | N^a | N^b | Recommended value | 95% confidence intervals ^d | |
|------------------|-----------|-------|-------|-----------------------|---------------------------------------|----------------------|
| | | | | | Lower | Higher |
| Cereal | Sand | 2.8 | 25 | 2.1×10^{-3} | 1.7×10^{-3} | 2.5×10^{-1} |
| | Loam | 358 | 23 | 1.4×10^{-2} | 4.5×10^{-4} | 4.2×10^{-1} |
| | Clay | 49 | 11 | 1.1×10^{-2} | 5.7×10^{-4} | 2.1×10^{-1} |
| | Organic | 54 | 7 | 4.3×10^{-2} | 3.8×10^{-3} | 4.9×10^{-1} |
| Tubers | Sand | 89 | 13 | 1.1×10^{-1} | 1.4×10^{-2} | 8.9×10^{-1} |
| | Loam | 173 | 14 | 2.9×10^{-2} | 2.9×10^{-3} | 2.8×10^{-1} |
| | Clay | 20 | 5 | 2.9×10^{-2} | 3.4×10^{-3} | 2.5×10^{-1} |
| | Organic | 15 | 5 | 5.5×10^{-3} | 6.0×10^{-3} | 5.1×10^{-1} |
| Green vegetables | Sand | 72 | 7 | 2.1×10^{-1} | 2.6×10^{-2} | 1.7 |
| | Loam | 100 | 12 | 1.2×10^{-1} | 1.2×10^{-2} | 1.2 |
| | Clay | 34 | 5 | 6.6×10^{-2} | 7.6×10^{-3} | 5.8×10^{-1} |
| | Organic | 7 | 2 | 2.9×10^{-1} | 1.6×10^{-2} | 5.5 |
| Brassicas | Sand | 36 | 7 | 1.2×10^{-1} | 1.3×10^{-2} | 1.2×10^{-1} |
| | Loam | 40 | 9 | 2.8×10^{-2} | 5.9×10^{-3} | 1.3×10^{-1} |
| | Clay | 13 | 2 | 4.4×10^{-2} | 9.6×10^{-3} | 2.0×10^{-1} |
| | Organic | 11 | 4 | 2.1×10^{-1} | 5.7×10^{-3} | 7.5×10^{-1} |
| Root vegetables | Sand | 38 | 9 | 5.4×10^{-2} | 8.7×10^{-3} | 3.3×10^{-1} |
| | Loam | 52 | 11 | 3.7×10^{-2} | 1.5×10^{-3} | 9.0×10^{-1} |
| | Clay | 13 | 3 | 2.2×10^{-2} | 3.5×10^{-3} | 1.4×10^{-1} |
| | Organic | 12 | 4 | 7.9×10^{-2} | 3.3×10^{-3} | 1.9 |
| Legumes | Sand | 47 | 8 | 7.4×10^{-2} | 6.1×10^{-3} | 9.0×10^{-1} |
| | Loam | 74 | 11 | 1.1×10^{-2} | 6.4×10^{-4} | 1.8×10^{-1} |
| | Clay | 13 | 2 | 3.8×10^{-3} | 1.8×10^{-3} | 8.0×10^{-3} |
| | Organic | 0 | — | 3.5×10^{-2c} | — | — |
| Onions | Sand | 20 | 3 | 1.3×10^{-2} | 3.6×10^{-3} | 4.6×10^{-2} |
| | Loam | 11 | 2 | 8.5×10^{-3} | 1.3×10^{-3} | 5.7×10^{-2} |
| | Clay | 7 | 1 | 5.6×10^{-3} | 9.5×10^{-4} | 3.3×10^{-3} |
| | Organic | 5 | 1 | 6.7×10^{-3} | 2.8×10^{-4} | 1.6×10^{-1} |

^aNumber of observations.^bNumber of studies.^cValue extrapolated using scaling factor for loamy soil.^dPopulation confidence intervals.

(Roca *et al.*, 1997; Smolders *et al.*, 1997b; Absalom *et al.*, 1999). Absalom *et al.* recently developed a model using three key soil properties underlying the plant availability of radiocaesium: the labile radiocaesium distribution coefficient (K_{dl}), the solution K^+ concentration ($[m_K]$), and radiocaesium concentration factor (CF, $Bg\ kg^{-1}$ plant/ $Bq\ dm^{-3}$ soil solution) (Absalom *et al.*, 1999). The model was first parameterized using radiocaesium uptake data in a pot trial, then was tested for a wide range of soil and crop combinations showing that model predictions of activity concentrations in crops were in generally good agreement with observed values.

Distribution of Cs within plants

Caesium has a high mobility within a plant. Similarly to K, Cs can be distributed to leaves, flowers and fruits. Short-term uptake studies show that significant fractions of Cs are transported from the root to the shoot within the first 2 h (Middleton *et al.*, 1960; Buysse *et al.*, 1995). Dry weight-based caesium concentrations are often higher in roots than in leaves and stems (Cline and Hungate, 1960; Smolders and Shaw, 1995; Zhu, 1998).

The differences in Cs concentrations between plant tissues are small during vegetative growth and different distribution patterns are found for different species (Menzel and Heald, 1955). The root : shoot Cs concentration ratio increases with decreasing K supply (Buysse *et al.*, 1996; Smolders *et al.*, 1996a; A Gommers *et al.*, unpublished results). Tissues that have low K concentrations (on a dry weight basis), such as ears, fruits or wood, are also low in Cs. Concentrations of ^{137}Cs in the grain of winter wheat and winter barley were on average 3–5-fold lower than corresponding concentrations in straw (Bilo *et al.*, 1993). The Cs distribution within the plant does not, however, exactly reflect that of K. Gommers *et al.* showed that when expressed on a dry weight basis ^{134}Cs concentrations in willow plants varied 10–20-fold between different tissues and ^{134}Cs concentration decreased from roots > leaves > stems > wood (Gommers *et al.*, 2000). The K concentrations in these tissues followed the same trend but there were only less than 5-fold differences in concentration. Menzel and Heald showed that the Cs:K ratio's varied up to 5-fold between the different tissues (leaves, root, stems, flowers) of buckwheat, sunflower, sweet clover, millet, and oats (Menzel and Heald, 1955).

Table 4. Phytoextraction of radiocaesium from contaminated soils, data derived from Lasat et al. (1998)

| Plant species | Indian mustard | Red root pigweed | Tepary bean |
|--|----------------|------------------|-------------|
| Total ^{137}Cs in soil (kBq m^{-2}) ^a | 2640 ± 480 | 2400 ± 960 | 1680 ± 720 |
| ^{137}Cs removed in shoots (kBq m^{-2}) | 1.2 ± 0.12 | 52 ± 26.4 | 0.8 ± 0.4 |

The different distribution of Cs and K may be related to Cs:K discrimination in each membrane transport. Buysse *et al.* measured the circulation of ^{137}Cs in spinach plants (Buysse *et al.*, 1995). The amount of ^{137}Cs that is recirculated to the root as a fraction of xylem transported ^{137}Cs was calculated from the accumulation of both ^{137}Cs and Ca in the shoot, and their concentration ratio in the xylem. The amount of recirculated Cs varied between 75% and 95% and was always higher than the fraction K that is recirculated (2–77%). This shows that Cs can be transported efficiently in the phloem. The higher fraction of Cs that is recirculated can be attributed to K to Cs selectivity for uptake in leaf cells. Potassium channels mediate K uptake by leaf cells from the xylem. Various K channels have been identified in plant leaf cells and all of these do not transport Cs efficiently and are blocked by micromolar Cs concentrations (Hedrich and Dietrich, 1996). The high affinity K transporter that transports Cs efficiently has only been identified in root cells and not in above-ground plant parts.

Phytoremediation of soils contaminated with radiocaesium

Remediation of soils contaminated with radiocaesium using present physical and chemical technologies may entail high costs. As discussed above, different plant species have different abilities to take up radiocaesium from soil. While this variation has particular relevance in terms of being able to reduce the transfer of radiocaesium from soil to food chains by selecting appropriate crop cultivars/species for soils with low level of contamination with radiocaesium, it can on the other hand be exploited for the purpose of phytoremediation of contaminated soils. Willey and his colleagues (Broadley and Willey, 1997; Willey and Martin, 1997; NJ Willey, personal communication) have obtained relative radiocaesium uptake values in about 200 species and found that the highest values are all in the Chenopodiaceae or closely related families such as Amaranthaceae. Selection of such taxa could be used to increase the phytoextraction of radiocaesium from contaminated soils.

Lasat *et al.* have conducted hydroponic and field experiments to select potential plant candidates for phytoremediation (Lasat *et al.*, 1997, 1998). They identified that red root pigweed (*Amaranthus retroflexus*, which is closely related to the Chenopodiaceae) is an

effective accumulator of radiocaesium which is capable of combining a high degree of uptake of ^{137}Cs with high shoot biomass production (Table 4). Similar results have been obtained in a field trial in radiocaesium-contaminated soil in vicinity of Chernobyl, Ukraine (Dushenkov *et al.*, 1999). However, both of these studies showed that phytoremediation will take an excessively long time to clean up contaminated sites. For example, according to the data from Lasat *et al.* and assuming that TF (soil-to-plant transfer factor) does not change over the remediation period, it may take 40 or more croppings of red pigweed (*Amaranthus retroflexus*) to decontaminate moderately radiocaesium-contaminated soil (Lasat *et al.*, 1998). Further improvements are therefore essential to make phytoremediation a feasible option to clean up Cs-contaminated sites.

The speed of phytoextraction of radiocaesium may be accelerated by applying various amendments and combining other biological approaches. Combination of different chemical amendments may be useful in accelerating phytoextraction. For example, Lasat *et al.* showed that application of NH_4NO_3 (4–80 mmol kg^{-1} soil) might increase plant accumulation of radiocaesium (Lasat *et al.*, 1997, 1998). In field trials, Dushenkov *et al.* showed that application of $(\text{NH}_4)_2\text{SO}_4$ could increase phytoextraction of radiocaesium by *Amaranthus retroflexus* (Dushenkov *et al.*, 1999). While potassium fertilizer should be minimized since plant uptake of radiocaesium is inhibited by potassium.

To speed up the process of selection of suitable plant taxa, a special plant breeding programme assisted by molecular biotechnology may be useful. Recent developments in molecular aspects of plant mineral nutrition, such as identifying and cloning the genes responsible for plant acquisition of K^+ , have provided some promising evidence for the potential acceleration of phytoremediation technology. Molecular aspects of plant acquisition of K^+ is being widely studied for utilization of salt-affected and/or low potassium soils, outcomes from this type of research may well be useful for improving phytoextraction of radiocaesium-contaminated soils.

Another problem arising from current phytoremediation strategies is the accumulation of radioactive biomass. The amount of biomass could be as much as 300 t ha^{-1} after 20 years phytoremediation, which can be reduced dramatically by composting or other methods. However, to remove the top 5 cm (or deeper) of contaminated soil physically (around 800 t ha^{-1}) appears even more

formidable. Additionally, a long period of monocropping will cause serious soil nutrient mining, therefore nutrient management is also an important issue to be considered when designing a phytoremediation practice.

Concluding remarks

In the past few decades, particularly after the Chernobyl accident, significant progress has been made in understanding the biological processes of plant uptake of radiocaesium and its regulation. It is generally accepted that Cs enters plants principally via K transport systems, namely K transporters and channels operating at different external potassium concentrations. Apparently K transporters have a low degree of discrimination against Cs; whereas K channels highly discriminate against Cs. K therefore appears to be one of the major factors influencing plant uptake of radiocaesium. The relationship between external potassium concentrations and uptake of radiocaesium could be described by a negative power function, which has been used as a key function to model the soil-to-plant transfer factors for different soil and plant combinations. However, integration of soil-based models to predict potassium concentrations around roots of field-grown plants will surely increase the accuracy of the prediction of soil-to-plant transfer factors. Phytoremediation to clean up soils contaminated with radiocaesium is potentially useful, but it is not a practical environmental technology at the moment. Further research on agronomic measures and molecular basis for the uptake of radiocaesium by plant species, which have recently been identified as having high capacity to accumulate radiocaesium, is needed.

Acknowledgements

Authors would like to thank Dr Anne Nisbet, National Radiological Protection Board, UK for her special effort in improving the manuscript. We also want to thank Dr G Shaw, Imperial College, UK for his valuable discussion during the period when this review was written. Constructive comments from the anonymous referee are highly appreciated.

References

- Absalom JP, Young SD, Crout NMJ, Nisbet AF, Woodman RFM, Smolders E, Gillett AG. 1999. Predicting soil to plant transfer of radiocaesium using soil characteristics. *Environmental Science and Technology* **33**, 1218–1223.
- Baligar VC, Nielsen NE, Barber SA. 1979. Kinetics of absorption of K, Rb and Cs from solution culture by intact plant roots. *Journal of Plant Nutrition* **1**, 25–37.
- Bange GG, Overstreet R. 1960. Some observations on absorption of cesium by exised barley roots. *Plant Physiology* **35**, 605–608.
- Becker D, Dreyer I, Hoth S, Reid JD, Busch H, Lehnen M, Palme K, Hedrich R. 1996. Changes in voltage activation, Cs⁺ sensitivity, and ion permeability in H5 mutants of the plant K⁺ channel KAT1. *Proceedings of the National Academy of Sciences, USA* **93**, 8123–8128.
- Belli M, Sansone U, Ardiani R, Feoli E, Scimone M. 1995. The effect of fertiliser applications on ¹³⁷Cs uptake by different plant species and vegetation types. *Journal of Environmental Radioactivity* **27**, 75–89.
- Bilo M, Steffens W, Führ F, Pfeffer KH. 1993. Uptake of ^{134/137}Cs in soil by cereals as a function of several soil parameters of three soil types in upper Swabia and North Rhine-Westphalia (FRG). *Journal of Environmental Radioactivity* **19**, 25–29.
- Broadley MR, Willey NJ. 1997. Differences in root uptake of radiocaesium by 30 plant taxa. *Environmental Pollution* **95**, 311–317.
- Buyse J, Van de Brande K, Merckx R. 1995. The distribution of radiocaesium and potassium in spinach plants grown at different shoot temperatures. *Journal of Plant Physiology* **146**, 263–267.
- Buyse J, Van de Brande K, Merckx R. 1996. Genotypic differences in the uptake and distribution of radiocaesium in plants. *Plant and Soil* **178**, 265–271.
- Cline JF, Hungate FP. 1960. Accumulation of potassium, caesium and rubidium in bean plants grown in nutrient solutions. *Plant Physiology* **35**, 826–829.
- Collander R. 1941. Selective absorption of cations by higher plants. *Plant Physiology* **16**, 691–720.
- Corisco JAG, Carreiro MCV. 1990. Etude expérimentale sur l'accumulation et la rétention du ¹³⁴Cs par une microalgue planctonique, *Selenastrum capricornutum* Printz. *Revue des Science de l'eau* **3**, 457–468.
- Dushenkov S, Mikheev A, Prokhnevsky A, Ruchko M, Sorochisky B. 1999. Phytoremediation of radiocaesium-contaminated soil in the vicinity of Chernobyl, Ukraine. *Environmental Science and Technology* **33**, 469–475.
- Epstein E, Hagen CE. 1952. A kinetic study of absorption of alkali cations by barley roots. *Plant Physiology* **27**, 457–474.
- Ertel J, Ziegler H. 1991. Cs-134/137 contamination and root uptake of different forest trees before and after Chernobyl accident. *Radiation and Environmental Biophysics* **30**, 147–157.
- Fernandez JA, Heredia MA, Garcia-Sanchez MJ, Corisco, JAG, Carreiro, MCV, de los Rios AD. 1997. Mechanisms of radiocaesium uptake and accumulation in *Riccia fluitans*. In: Desmet G *et al.*, ed. *Freshwater and estuarine radioecology*. Elsevier.
- Flowers TJ, Hajibagheri MA, Clipson NJW. 1986. Halophytes. *Quarterly Review of Biology* **61**, 313–337.
- Gassmann W, Rubio F, Schroeder JI. 1996. Alkali cation selectivity of the wheat root high-affinity potassium transporter HKT1. *The Plant Journal* **10**, 869–882.
- Glass ADM. 1989. *Plant nutrition: an introduction to current concepts*. Boston/Portola Valley: Jones and Bartlett Publishers, 234.
- Gommers A, Thiry Y, van den Hove H, Vandecasteele CM, Smolders E, Merckx R. 2000. Radiocaesium uptake by 1-year-old willows planted as short rotation crop. *Journal of Environmental Quality* (in press).
- Guivarch A, Hinsinger P, Staunton S. 1999. Root uptake and distribution of radiocaesium from contaminated soils and the enhancement of Cs adsorption in the rhizosphere. *Plant and Soil* **211**, 131–138.
- Handley R, Overstreet R. 1961. Effects of various cations upon absorption of carrier free cesium. *Plant Physiology* **36**, 66–69.
- Hedrich R, Dietrich P. 1996. Plant K⁺ channels: similarity and diversity. *Botanica Acta* **109**, 94–101.

- Jones HE, Harrison A, Positt AF, Clint G. 1991. The effect of potassium nutrition on Cs-137 uptake in two upland species. *Journal of Environmental Radioactivity* **14**, 279–294.
- Kopp P, Gorlich W, Burkart W. 1990. The transfer of caesium-134 and -137 from sewage sludge to plants. In: Desmet G, Nassimbeni P, Belli M, eds. *Transfer of radionuclides in natural and semi-natural environment*. London: Elsevier, 583–590.
- Lasat MM, Ebbs SD, Kochian LV. 1997. Potential for phytoextraction of ^{137}Cs from contaminated soils. *Plant and Soil* **195**, 99–106.
- Lasat MM, Ebbs SD, Kochian LV. 1998. Phytoremediation of a radiocaesium-contaminated soil: evaluation of caesium-137 bioaccumulation in shoots of three plant species. *Journal of Environmental Quality* **27**, 165–169.
- Maathuis FJM, Sanders D. 1994. Mechanism of high-affinity potassium uptake in roots *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences, USA* **91(20)**, 9272–9276.
- Maathuis FJM, Sanders D. 1995. Contrasting roles in ion transport of two K^+ -channel types in root cells of *Arabidopsis thaliana*. *Planta* **197**, 456–464.
- Maathuis FJM, Sanders D. 1997. Regulation of K^+ absorption in plant root cells by external K^+ : interplay of different plasma membrane K^+ transporters. *Journal of Experimental Botany* **48**, 451–458.
- Marschner H, Schimansky CH. 1970. Suitability of using rubidium-86 as a tracer for potassium in studying potassium uptake by barley plants. *Zeitschrift für Pflanzenernahrung und Bodenkunde* **128**, 129–143.
- Menzel RG. 1954. Competitive uptake by plants of potassium, rubidium, caesium, calcium, strontium, and barium from soils. *Soil Science* **77(6)**, 419–425.
- Menzel RG, Heald WR. 1955. Distribution of potassium, rubidium, cesium, calcium, and strontium within plants grown in nutrient solutions. *Soil Science* **78(5)**, 287–293.
- Middleton LJ, Handley R, Overstreet R. 1960. Relative uptake and translocation of potassium and cesium in barley. *Plant Physiology* **35**, 913–918.
- Nisbet AF. 1995. *Effectiveness of soil-based countermeasures: six months to one year after contamination of five diverse soil types with ^{134}Cs and ^{90}Sr* . Contract report to MAFF. NRPB-M546, NRPB, Chilton, UK.
- Nisbet AF, Woodman RFM, Haylock RGE. 1999. *Recommended soil-to-plant transfer factors for radiocaesium and radiostrontium for use in arable systems*. NRPB-R304, NRPB, Chilton, UK.
- Nisbet AF, Woodman RFM. 2000. Soil-to-plant transfer factors for radiocaesium and strontium in agricultural systems. *Health Physics* **78(3)**, 279–288.
- Nishita H, Dixon D, Larson KH. 1962. Accumulation of Cs and K and growth of bean plants in nutrient solution and soils. *Plant and Soil* **17**, 221–242.
- Nissen P. 1991. Uptake mechanisms. In: Waisel Y, Eshel A, Kafkafi U, eds. *Plant roots: the hidden half*. USA: Marcel Dekker Inc.
- Prister BS, Perepelyatnikov GP, Perepelyatnikova IV. 1993. Countermeasures used in the Ukraine to produce forage and animal food products with radionuclide levels below intervention limits after the Chernobyl accident. *The Science of the total Environment* **137**, 183–198.
- Roca MC, Vallejo VR. 1995. Effect of soil potassium and calcium on caesium and strontium uptake by plant roots. *Journal of Environmental Radioactivity* **28**, 141–159.
- Roca MC, Vallejo VR, Roig M, Tent J, Vidal M, Rauret G. 1997. Prediction of cesium-133 and strontium-85 crop uptake based on soil properties. *Journal of Environmental Quality* **26**, 1354–1362.
- Russell RS. 1966. *Radioactivity and human diet*. 1st edn. Pergamon Press, Oxford.
- Sacchi BL, Espen L, Nocito F, Cocucci M. 1997. Cs^+ uptake in subapical maize root segments: Mechanism and effects on H^+ release, transmembrane electric potential and cell pH. *Plant Cell Physiology* **38**, 282–289.
- Sanchez AL, Wright SM, Smolders E, Naylor C, Stevens PA, Kennedy VH, Dodd BA, Singleton DL, Barnett CL. 1999. High plant uptake of radiocaesium from organic soils due to Cs mobility and low soil K content. *Environmental Science and Technology* **33**, 2752–2757.
- Schachtman DP, Schroeder JI, Lucas WJ, Anderson JA, Gaber RF. 1992. Expression of an inward rectifying potassium channel by the *Arabidopsis* KAT1 cDNA. *Science* **258**, 1654–1658.
- Schachtman DP, Schroeder JI. 1994. Structure and transport mechanism of a high-affinity potassium uptake transporter from higher plants. *Nature* **370**, 655–658.
- Sentenac H, Bonneaud N, Minet M, Lacroute F, Salmon JM, Gaynard F, Grignon C. 1992. Cloning and expression in yeast of a plant potassium ion transport system. *Science* **256**, 663–665.
- Shaw G. 1993. Blockade by fertilisers of caesium and strontium uptake into crops: effects on the root uptake process. *The Science of Total Environment* **137**, 119–133.
- Shaw G, Bell JNB. 1991. Competitive effects of potassium and ammonium on caesium uptake kinetics in wheat. *Journal of Environmental Radioactivity* **13**, 283–296.
- Shaw G, Bell JNB. 1994. Plants and radionuclides. In: Farago ME, ed. *Plants and chemical elements: biochemistry, uptake, tolerance and toxicity*. Germany: VCH, 179–220.
- Shaw G, Hewamanna R, Lillywhite J, Bell JNB. 1992. Radiocaesium uptake and translocation in wheat with reference to the transfer factor concept and ion competition effects. *Journal of Environmental Radioactivity* **16**, 167–180.
- Smolders E, Shaw G. 1995. Changes in radiocaesium uptake and distribution in wheat during plant development: a solution culture study. *Plant and Soil* **176**, 1–6.
- Smolders E, Kiebooms L, Buysse J, Merckx R. 1996a. ^{137}Cs uptake in spring wheat (*Triticum aestivum* L. cv. Tonic) at varying K supply. I. The effect in solution culture. *Plant and Soil* **181**, 205–209.
- Smolders E, Kiebooms L, Buysse J, Merckx R. 1996b. ^{137}Cs uptake in spring wheat (*Triticum aestivum* L. cv. Tonic) at varying K supply. II. A potted soil experiment. *Plant and Soil* **181**, 211–220.
- Smolders E, Sweeck L, Merckx R, Cremers A. 1997a. Cationic interaction in radiocaesium uptake from solution by spinach. *Journal of Environmental Radioactivity* **34**, 161–170.
- Smolders E, Vandenbrande K, Merckx R. 1997b. Concentrations of Cs-137 and K in soil solution predict the plant availability of Cs-137 in soil. *Environmental Science and Technology* **31(12)**, 3432–3438.
- Wang TB, Gassmann W, Rubio F, Shroeder JI, Glass ADM. 1998. Rapid up-regulation of HKT1, a high-affinity potassium transporter gene, in roots of barley and wheat following withdrawal of potassium. *Plant Physiology* **118**, 651–659.
- Wauters J. 1994. Radiocaesium in aquatic sediments: sorption, remobilisation and fixation. PhD thesis, Faculty of Agricultural Sciences, KU Leuven, Belgium.
- Wiley NJ, Martin MH. 1997. A comparison of stable caesium uptake by six grass species of contrasting growth strategy. *Environmental Pollution* **95**, 311–317.

- Wolt JD.** 1994. *Soil solutions chemistry: applications to environmental science and agriculture*. New York: John Wiley and Sons, Inc.
- Zhu YG.** 1998. Effect of potassium supply on the uptake of radiocaesium by crops. PhD thesis, The University of London, England.
- Zhu YG, Shaw G, Nisbet AF, Wilkins BT.** 1999. Effect of external potassium supply on compartmentation and flux characteristics of radiocaesium in intact spring wheat roots. *Annals of Botany* **84**, 639–644.
- Zhu YG, Shaw G, Nisbet AF, Wilkins BT.** 2000. Effect of potassium starvation on the uptake of radiocaesium by spring wheat (*Triticum aestivum* cv. Tonic). *Plant and Soil* **220**, 27–34.
- Zhu YG, Shaw G.** 2000. Soil contamination with radionuclides and potential remediation. *Chemosphere* **41**, 121–128.