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Effect of the arbuscular mycorrhizal symbiosis upon uptake of cesium and other cations by plants

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Abstract Pot experiments were set up to determine the species-specific uptake of cesium (Cs) by mycorrhizal (AM) and non-mycorrhizal (non-AM) plants. Using stable Cs and K application, side-effects of mineral fertilization (K) on AM development and uptake of Cs and the other cations Na, Ca and Mg were investigated. AM colonization by the fungus *Glomus mosseae* led to a significant decrease in shoot Cs content of *Agrostis tenuis* from the first (4 weeks) to the third harvest (8 weeks). With regard to the root system, statistically significant differences were observed from the first (4 weeks) to the second harvest (6 weeks). Supply of additional K produced a significant decrease in Cs uptake by both AM and non-AM plants over a 10-week period. In the case of AM plant shoots, K fertilization did not very effectively reduce Cs uptake by *A. tenuis*. Cs contents of fertilized AM roots were similar to non-AM controls. Potassium application resulted in an increase in K content and a slight reduction in Na and Mg contents of shoots and roots. Without K fertilization, the Na content of non-AM controls was significantly enhanced over AM shoots. Shoot and root Ca contents were generally higher without than with K addition. Negative side-effects of K fertilization as a countermeasure to Cs uptake were not observed in relation to AM development. The intensity of colonization by *G. mosseae* was not significantly depressed by K treatment. AM development in plants appeared to decrease Cs uptake, at least at moderate nutrient levels. It is possible that Cs is sequestered by AM extraradical fungal hyphae and consequently not transferred to the plant to the extent found in non-AM roots.

Keywords *Glomus mosseae* · *Agrostis tenuis* · Plant cation contents · (Radio)cesium · Soil-plant transfer · Countermeasures

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Introduction

Contamination of the environment by radionuclides has occurred in a number of countries as a result of industrial activities, nuclear weapons production and testings and nuclear accidents. In 1986, the accident at Chernobyl in Ukraine led to contamination of large tracts of land by radiocesium (^{137}Cs). This nuclide has by far the most serious consequences for long-range health, social stress and economic impact. Other radionuclides, most notably ^{90}Sr and ^{239}Pu, are believed to have contributed in a minor way to the doses received (Eisenbud and Gesell 1997).

Since the Chernobyl accident, the soil to plant transfer of various radionuclides, transfer factors and concentration ratios of radionuclides in natural food chains have been the subject of several investigations (see, for example, the review by Haselwandter and Berreck 1994). Most of these studies were concerned with the physical, chemical and (some) biological parameters influencing radionuclide transfer. Despite the notion that mycorrhizal (AM) development substantially affects mineral nutrition of plants, remarkably little research has been carried out on the effect of AM on plant uptake of radionuclides. Few species of either fungus or host plant have been investigated and the results are controversial, some of them inconclusive (McGraw et al. 1979; Rogers and Williams 1986). Some AM species may enhance Cs uptake, whilst others appear to decrease plant Cs content (Haselwandter et al. 1994; Dighton and Terry 1996). Basic knowledge of all potential uptake mechanisms is a prerequisite for the design of countermeasures to reduce the transfer of radionuclides into plants. Thus all potential soil- and plant-based countermeasures (application of fertilizers or chemical binding agents, mechanical/physical soil treatments, crop and land use changes) and their possible side-effects should be evaluated for effects upon AM-mediated plant uptake of radionuclides.

In the present study, pot experiments were carried out on the species-specific uptake of Cs by AM and non-AM plants. Possible side-effects of mineral (K) fertilization

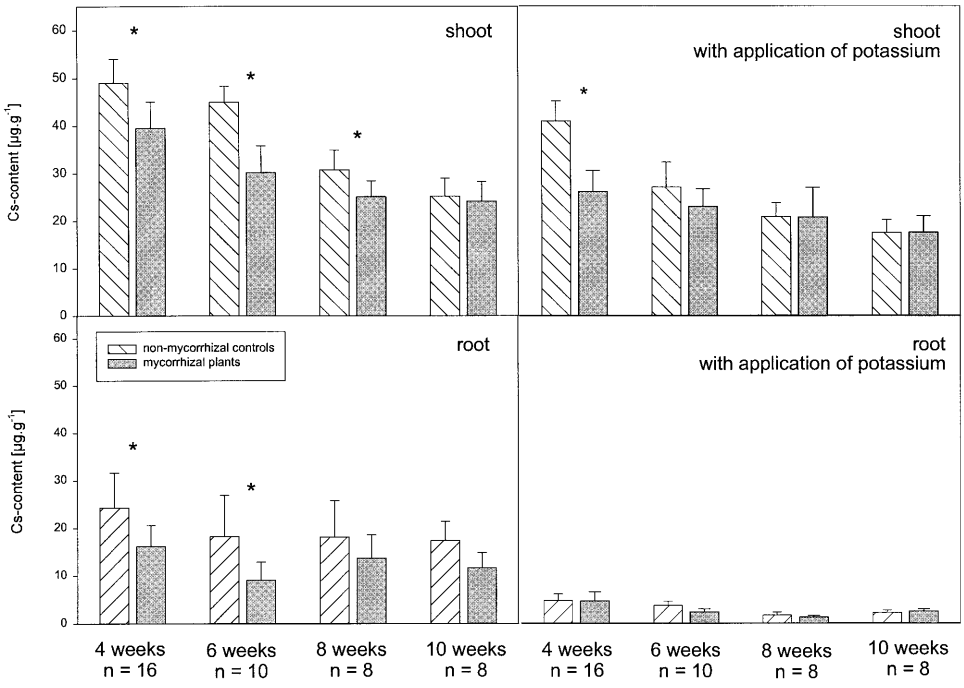

Fig. 1 Cesium (Cs) content (means±SD) of the shoot and the root system of arbuscular mycorrhizal (AM) and non-AM *Agrostis tenuis* harvested after 4, 6, 8 and 10 weeks without and with additional K application (196.3 µg g^{-1} = 100 kg ha^{-1}) (*AM and control means are significantly different at the 5% level)

on plant growth, AM development and uptake of Cs and K were investigated using stable Cs and K. The effects of both mycorrhization and K fertilization on the Na, Mg and Ca contents of the plant biomass were also monitored.

Materials and methods

Plants of the host *Agrostis tenuis* Sibth. (= *A. capillaris*; breed Highland) were grown in pots (∅ 10 cm) filled with 400 g of sterilized (5 h at 160°C) sand (2:1 mixture of quartz sand with grain size 0.8–1.5 mm and 0.1–0.8 mm; Raiffeisen Warenverband Tirol, Innsbruck) under moderate nutrient levels. Nutrients were incorporated into the sand before growth. The P level was adjusted to limit plant growth but promote AM formation and sporulation. Mineral nutrient supplements were provided at the following concentrations (µg per g substrate) KH_2PO_4 21.8 (application every 3–4 weeks, if required for sustaining plant growth); KNO_3 44.5, $Ca(NO_3)_2.2H_2O$ 37.8, NH_4NO_3 27.3 (biweekly addition of a dilute solution), $MgSO_4.7H_2O$ 39.8, FeEDTA (ca. 12% iron) 5, $MnSO_4.H_2O$ 0.12, $ZnSO_4.7H_2O$ 0.08, $CuSO_4.\ 5H_2O$ 0.03, $Na_2MoO_4.2H_2O$ 0.003, H_3BO_3 0.23, $CoCl_2.6H_2O$ 0.005. Cs and additional K were added as a solution to achieve a final concentration of 1.56 ng g^{-1} Cs (0.8 g Cs ha^{-1}) and 196 µg g^{-1} K (100 kg K ha^{-1}).

Plants were inoculated with 5 g of root fragments and substrate including spores from pot cultures of *Festuca ovina* L. mycorrhizal with *Glomus mosseae* (Nicol. & Gerd.) Gerdemann and Trappe, strain MB001Glmo. Plants were grown in a growth chamber at 20°C (15°C during 9 h darkness), 70% humidity (80% during darkness), and a light intensity of 220–260 µmol m^{-2} s^{-1} at 400–700 nm for 15 h in non-draining pots watered with an automatic watering system (Blumat, Telfs, Austria).

Plants were harvested after 4, 6, 8 and 10 weeks, when shoots were detached from roots. The roots were washed with tap water. After drying for 48 h at 80°C, the plant material was pulverized with a mixer mill (MM 2000, Retsch, Germany). For atomic absorption spectrometry, samples were digested in 65% HNO_3 (Suprapure, Merck) in a microwave oven (MLS, Leutkirch, Germany) using the following program: 3 min 250 W, 1 min 0 W, 6 min 250 W, 0,5 min 0 W, 4 min 450 W, and 3 min 550 W. The cation concentrations in the digest were measured with a Hitachi Z 8200 atomic absorption spectrometer using the graphite atomization method. AM fungal colonization intensity of roots was determined by the modified grid line intersect method described by Giovannetti and Mosse (1980).

Statistical analyses were performed by ANOVA/ANCOVA using software packages SPSS 9.0 and Statistica 99, taking AM colonization and K fertilization as experimental factors and harvest time as covariate. Significance of difference between means was evaluated by a Tukey-B-test.

Results and discussion

AM colonization of roots of *A. tenuis* by *G. mosseae* led to a decrease in Cs content of plants from the first to the third harvest. In general, Cs in shoots was at a higher concentration than in roots. The difference in Cs content of AM and non-AM plants was highly significant, at least during the first 6–8 weeks of growth (Fig. 1, Table 1). The reduction in shoot Cs content was in the range of 18.1–32.8%. For the root tissue, there was a reduction in the range of 33.5–50.3%. These results agree with those from an earlier experiment with radioactive ^{137}Cs in which the amount of Cs added was 30 times smaller in order to simulate the highest ^{137}Cs contamination level reached in the Chernobyl zone (Grodzinskaya et al. 1995). In that experiment, shoot tissue radioactivity of AM *F. ovina* plants dropped to about half that of the non-AM controls at the first and second harvest after 3 and 5 weeks, respectively (Haselwandter and Berreck 1994).

Potassium application led to a significant decrease in Cs uptake by both AM and non-AM *A. tenuis* over a growth period of 10 weeks (Fig. 2, Table 1). Potassium-fertilized, non-AM shoots contained 55.7–77.5% of the Cs concentration of the non-fertilized, non-AM plants. In the case of AM plants, K fertilization was slightly less

Table 1 Summary of ANOVA: effects of arbuscular mycorrhizae (AM) and potassium fertilization on Cs contents of the shoot and root systems of the grass *Agrostis tenuis* (harvest time as covariate)

ANOVA		*df* effect	MS effect	*df* error	MS error	*F*	*P* level
Shoot system	AM 1	1*	2225.649*	163*	27.78902*	80.0909*	0.000000*
	Potassium fertilization 2	1*	5807.805*	163*	27.78902*	208.996*	0.000000*
	Combination of 1 and 2	1	53.020	163	27.78920	1.9080	0.169081
Root system	AM 1	1*	561.584*	163*	19.60017*	28.6520*	0.000000*
	Potassium fertilization 2	1*	7814.381*	163*	19.60017*	398.6895*	0.000000*
	Combination of 1 and 2	1*	531.349*	163*	19.60017*	27.10942*	0.000010*

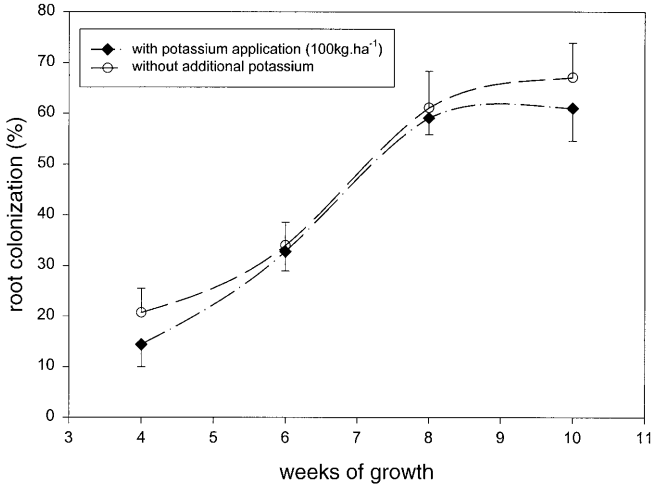

Fig. 2 Effect of K fertilization (196.3 µg g^{-1}=100 kg ha^{-1}) on AM development in *A. tenuis* by *Glomus mosseae* (means±SD, *n*=8–16)

efficient in reducing Cs uptake by *A. tenuis*. However, AM plants in general accumulated lower amounts of Cs than non-AM controls, especially during the first 6–8 weeks of growth. Fertilized AM plant shoots contained Cs at 61.2–70.4% of the concentration in non-fertilized AM plants. Potassium fertilization led to a substantial decrease in root Cs contents of both AM and non-AM plants (see Fig. 1).

The results of both experiments showed unexpectedly high concentrations of Cs in the shoot system of both AM and non-AM plants. Although no detectable Cs was extractable from the growth substrate by ammonium acetate (Page et al. 1989), substrate-borne Cs could have been partly and for a short time accessible to plants. Further investigations using neutron activation analysis of the substrate revealed Cs concentrations between 0.03 µg (quartz sand, Merck No. 7536) and 1.57 µg (quartz sand, Raiffeisen Warenverband Tirol) per g dry weight of sand (Lettner, personal communication). In all samples tested, Cs inherent to the substrate exceeded the concentration of Cs added to the substrate by orders of magnitude. This should be considered in every Cs-uptake experiment using either stable or radioactive Cs and coarse sand as substrate.

Potassium fertilization has been shown to be efficient in reducing ^{137}Cs availability to crops growing in contaminated soils in pot experiments (see, for example, Belli et al. 1995; Smolders et al. 1996a, b) and in the field (Rosèn 1992; Lönsjö and Haak 1996). In comparative studies on countermeasures, K fertilization was generally more efficient than liming (see, for example, Mitchell et al. 1990). Unfortunately, none of these studies considered the AM status of the host plants and potential effects of AM on cation uptake. In the present investigations, K application generally resulted in a higher K content in the plants (Tables 2, 3). In the experiment with no added K, the K content was below 1.2% relative to dry weight, thus rendering the plants K-deficient according to Fink (1991) after a growth period of 6 weeks until the end of the experiment (10 weeks). Hence K must be considered to be a growth-limiting factor in the experiment without K fertilization, and K appeared to become diluted in the tissue with increasing plant growth. In the experiment with added K, the supply was sufficient (2–4% K relative to dry weight) with no symptoms of tissue dilution over a growth period of 10 weeks (Table 2).

Negative side-effects of K fertilization as a countermeasure to Cs uptake were not observed in terms of AM colonization of the host plants. AM development by *G. mosseae* was not significantly reduced by the K treatment at the beginning or the end of the growth period (Fig. 2). Positive effects of increasing K level on AM colonization ratings of cassava (*Manihot esculenta*) and pasture legumes were reported by Howeler (1980). The effect was much less pronounced in grasses and only in *Brachiaria humidicola* was root colonization increased by application of 20 kg K ha^{-1} (Saif 1986). In the present experiment, K was applied at a rate of 100 kg ha^{-1} in order to reach the level recommended as a countermeasure after Cs contamination of grassland (Schechtner and Henrich 1990; Konoplev et al. 1993; Segal 1993).

Potassium application (without additional N and P fertilization) as a potential countermeasure to Cs uptake did not significantly increase yields (biomass) of AM and non-AM *A. tenuis* (Tables 2, 3). Increased shoot dry weight was only observed in the early stage of the growth period (after 4 weeks). After 10 weeks, control plants reached a significantly higher biomass than AM plants in both experiments, with and without K fertilization. Pot effects and/or imbalances of other nutrients (N/P ratio) can depress growth rates of AM plants (Mosse 1973).

Table 2 Shoot dry weights and cation contents of AM and nonAM *Agrostis tenuis* plants harvested after 4, 6, 8 and 10 weeks without and with application of potassium (K) (100 kg ha^{-1}) (* mycorrhizal and control means are significantly different at the 5% level, *n* number of pots harvested)

	Cultivation time	No added K		Added K	
		Non-AM controls	AM plants	Non-AM controls	AM plants
Dry weight (mg per pot)	4 weeks (*n*=16)	235±28	202±49	328±65	232±59
	6 weeks (*n*=10)	503±34*	398±81	445±90	369±79
	8 weeks (*n*=8)	650±88	589±79	689±137	610±89
	10 weeks (*n*=8)	927±92*	730±140	840±105*	701±55
K content (mg 100 mg^{-1} shoot dry wt.)	4 weeks (*n*=16)	1.49±0.28	1.35±0.20	2.65±0.27	2.45±0.30
	6 weeks (*n*=10)	1.12±0.11	1.05±0.07	2.62±0.54	2.37±0.29
	8 weeks (*n*=8)	0.87±0.10	0.75±0.04	3.13±0.41*	2.50±0.28
	10 weeks (*n*=8)	0.71±0.05	0.66±0.18	2.98±0.42	2.55±0.45
Na content (µg mg^{-1} shoot dry wt.)	4 weeks (*n*=16)	1.14±0.21*	0.84±0.16	0.81±0.35	0.85±0.15
	6 weeks (*n*=10)	1.34±0.36*	0.74±0.15	0.73±0.21	0.91±0.18
	8 weeks (*n*=8)	1.38±0.20*	0.86±0.14	1.00±0.18	1.17±0.18
	10 weeks (*n*=8)	1.44±0.12*	1.16±0.39	0.85±0.15	1.17±0.30
Ca content (µg mg^{-1} shoot dry wt.)	4 weeks (*n*=16)	2.39±0.79	2.29±0.82	1.40±0.29	1.23±0.30
	6 weeks (*n*=10)	3.75±0.81	3.39±0.62	1.49±0.23	1.25±0.30
	8 weeks (*n*=8)	4.09±0.78*	3.21±0.37	1.34±0.30	1.05±0.45
	10 weeks (*n*=8)	5.33±0.62	5.08±1.36	1.38±0.30	1.38±0.18
Mg content (µg mg^{-1} shoot dry wt.)	4 weeks (*n*=16)	1.16±0.18	0.94±0.07	0.98±0.28	0.92±0.18
	6 weeks (*n*=10)	1.16±0.06	1.09±0.09	0.90±0.06	0.91±0.23
	8 weeks (*n*=8)	1.29±0.18	1.22±0.14	0.90±0.06	0.95±0.06
	10 weeks (*n*=8)	1.60±0.36	1.44±0.17	0.80±0.17*	1.11±0.31

Table 3 Root dry weights and cation contents of AM and non-AM *Agrostis tenuis* plants harvested after 4, 6, 8 and 10 weeks without and with application of K (100 kg ha^{-1}) (*mycorrhizal and control means are significantly different at the 5% level, *n* number of pots harvested)

	Cultivation time	No added K		Added K	
		Non-AM controls	AM plants	Non-AM controls	AM plants
Dry weight (mg per pot)	4 weeks (*n*=16)	379±75	355±87	455±103*	288±83
	6 weeks (*n*=10)	524±123	409±106	447±134*	264±51
	8 weeks (*n*=8)	604±115*	446±58	469±137	359±67
	10 weeks (*n*=8)	549±67	439±82	545±125*	380±45
K content (mg 100 mg^{-1} root dry wt.)	4 weeks (*n*=16)	1.13±0.27	1.09±0.21	1.61±0.28	1.90±0.53
	6 weeks (*n*=10)	0.33±0.11*	0.56±0.09	1.21±0.30*	2.05±0.20
	8 weeks (*n*=8)	0.35±0.05	0.45±0.04	0,98±0.30	1.03±0.20
	10 weeks (*n*= 8)	0.26±0.05	0.32±0.04	1.02±0.20	1.24±0.20
Na content (µg mg^{-1} root dry wt.)	4 weeks (*n*=16)	0.24±0.09*	0.32±0.01	0.12±0.03*	0.07±0.01
	6 weeks (*n*=10)	0.13±0.05*	0.21±0.03	0.07±0.01	0.06±0.01
	8 weeks (*n*=8)	0.10±0.01	0.12±0.01	0.07±0.01*	0.04±0.01
	10 weeks (*n*=8)	0.08±0.02	0.12±0.05	0.07±0.01*	0.04±0.00
Ca content (µg mg^{-1} root dry wt.)	4 weeks (*n*=16)	4.09±1.44	3.36±0.49	2.44±0.48	2.37±0.37
	6 weeks (*n*=10)	2.95±0.32	3.48±0.45	3.41±0.80	3.12±0.46
	8 weeks (*n*=8)	2.74±0.35*	4.31±0.47	3.47±1.65	2.72±0.93
	10 weeks (*n*=8)	3.52±0.46*	5.22±0.75	1.84±0.59	2.03±0.22
Mg content (µg mg^{-1} root dry wt.)	4 weeks (*n*=16)	2.13±0.62	1.74±0.55	1.18±0.30	1.12±0.25
	6 weeks (*n*=10)	1.49±0.45	1.11±0.20	1.09±0.15	1.03±0.15
	8 weeks (*n*=8)	0.98±0.25	0.87±0.07	1.22±0.20	1.02±0.13
	10 weeks (*n*=8)	0.98±0.20	0.63±0.06	1.09±0.42	1.01±0.33

Improved uptake of nutrients such as K, Ca, Na, Mg, Mn and heavy metals as trace elements has often been implicated in mycorrhiza-assisted nutrition but results are generally variable. In most investigations, K was at a lower concentration in the tissues of AM than non-AM plants. In general, accumulation of K is strongly influenced by the form of N source available (NO_3^- or NH_4^+) as well as by other cations, particularly Ca^{2+} and Na^+. In AM plants, the K content may also be influenced by the synthesis and storage of polyphosphate (Smith and Read 1997). There exists an antagonism in ion uptake among K^+, Na^+, Ca^{2+}, Mg^{2+} and NH_4^+ (Gauch 1972; Amberger 1983), which also seems to be applicable to Cs^+ (see Fig. 1). The Cs content of shoot and root systems was significantly lower with K fertilization than without.

In the present experiments, K application had strong effects on Ca uptake but only slight effects on Na and Mg uptake (Table 2). Potassium-fertilized plant shoots contained 55–26% of the Ca concentration of the non-fertilized plants. Grass well supplied with nutrients contains 5–20 µg Ca mg^{-1} dry weight (Fink 1991). Hence, in the experiment with K application, both AM and non-AM plants must be considered to have been Ca deficient. Due to the competitiveness of Ca with ^{90}Sr, positive side-effects of K fertilization on ^{90}Sr uptake could be expected, at least in sandy soils, where the availability and mobility of Sr are high (Ivanov et al. 1997). With the exception of enhanced Na uptake by shoots of AM *A. tenuis* in the treatment with added K and enhanced Ca uptake by AM roots in the treatment without added K (Tables 2, 3), cation uptake was generally reduced under moderate nutrient levels, when comparing AM seedlings to non-AM controls.

The results of experiments with both stable Cs and radiocesium application clearly demonstrate that AM colonization of *A. tenuis* and *F. ovina* can decrease Cs uptake, at least under moderate nutrient levels and growth chamber conditions. One possible explanation is that Cs is sequestered by the extraradical fungal hyphae and is not transferred to the plant to the same extent as in non-AM roots. Accumulation of radiocesium in fungal structures has been demonstrated by Witkamp (1968), Haselwandter et al. (1988), Dighton et al. (1991), and Dighton and Terry (1996).

Element energy loss spectroscopy has shown higher accumulation of trace elements in fungal structures than in the plant root cells (Turnau et al. 1993). Polyphosphate granules, which are formed in the apical part of the extramatrical mycelium and are then transported by cytoplasmatic streaming, have been found to contain elements such as Fe, Mn, S, Mg, N, Al and Cl (Turnau et al. 1993). The sequestration of potentially toxic elements by polyphosphate granules may be considered a filter mechanism. Such findings make it clear that interactions with P nutrition and other aspects of AM physiology must be taken into account in studies of the accumulation and tolerance of heavy metals and other toxic elements (Haselwandter et al. 1994; Leyval et al. 1997). A filter mechanism for Cs has not been described.

Results of investigations are not always consistent between plant and fungal species. McGraw et al. (1979) reported that AM colonization of *Paspalum notatum* by two out of ten AM fungi species led to a twofold increase in radioactivity in leaf tissue. Rogers and Williams (1986) found a marked increase in ^{137}Cs in AM *Melilotus officinalis*, while in the case of *Sorghum sudanense* the Cs content was not significantly different between the AM and the control grass. Dighton and Terry (1996) determined the radiocesium uptake by *F. ovina* and *Trifolium repens* from labeled soil. In *Festuca*, AM infection resulting from the use of non-sterilized soil as inoculum did not enhance plant growth. Shoots showed a higher concentration of radiocesium than roots and, similar to an experiment with heather (*Calluna vulgaris*), translocation of Cs to shoots increased in the presence of AM. In the case of *Trifolium*, however, AM plants took up less radiocesium than non-AM plants. There appeared to be no increased translocation of Cs to the shoot.

In the present study, the reduction in Cs uptake by AM plants relative to controls was rather underestimated because of the greater biomass of control plants (Tables 2 and 3). Thus AM fungi have a definite potential to reduce radionuclide transfer from soil to plants and could act as a low-cost biological countermeasure. However, the screening of a large number of species of both AM fungi and host plants is required.

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