

Predicting Inter-Taxa Differences in Plant Uptake of Cesium-134/137

Neil J. Willey,* Shirong Tang, and Nicholas R. Watt

ABSTRACT

For $^{134/137}\text{Cs}$, and many other soil contaminants, research into transfer to plants has focused on particular crops and phytoremediation candidates, producing uptake data for a small proportion of all plant taxa. Despite the significance of differences in uptake between plant taxa, the capacity of soil-to-plant transfer models to predict them is currently confined to those taxa for which data exist, there being no method to predict uptake by other taxa. We used residual maximum likelihood (REML) analysis on data from experiments (including 89 plant taxa from China plus 32 phytoremediation candidates) together with data from the literature, to construct a database of relative $^{134/137}\text{Cs}$ concentrations in 273 plant taxa. The REML $^{134/137}\text{Cs}$ concentrations in plants are not normally distributed but significantly clustered. Analysis of variance (ANOVA), coded with a recent ordinal phylogeny for flowering plants, showed that plant taxa do not behave independently for $^{134/137}\text{Cs}$ concentration because 42 and 15% of inter-taxa differences are associated with phylogeny above the species and ordinal level, respectively. In general, Eudicots, and especially the Caryophyllales, Asterales, and Brassicales, have high $^{134/137}\text{Cs}$ concentrations, while the Fabales and Magnoliids, in particular Poales, have low $^{134/137}\text{Cs}$ concentrations. Plants of the stress-tolerant ruderal (S-R) growth strategy *sensu* Grime have, in general, high concentrations of Cs, while those of the competitive (C) and generalist (C-S-R) strategies have low concentrations, although these effects are less pronounced than those of phylogeny. Plant phylogeny and growth strategy might thus be used to predict a significant portion of inter-taxa differences in plant uptake of $^{134/137}\text{Cs}$.

ENVIRONMENTAL MODELS of contaminant behavior are rich in data for staple food crops but also need to account for uptake by diverse plant taxa because of the variety of human diets and the impact of contaminants on ecosystems. For phytoremediation and phytomonitoring, differences between taxa are an exploitable resource, providing a range of candidate species to match to sites, but they have thus far exploited relatively few taxa. A narrow taxonomic scope can, therefore, limit both the usefulness of environmental models in a range of agricultural and natural ecosystems and the efficacy of phytotechnologies at a range of sites.

For ^{137}Cs the further development of soil-to-plant transfer models, decontamination methods, and monitoring technologies is currently desirable not only for the large volumes of soil currently contaminated but

also because (i) decommissioning and decontaminating nuclear licensed sites will be an important part of the nuclear industry in the 21st century as many sites reach the end of their useful lives (Hall and Watt, 2002); (ii) expansion of nuclear power generation is occurring in some countries, for example, China and India (Tang and Willey, 2003), and being mooted in others in response to increasing atmospheric CO_2 (Starr, 2000), widening the potential for release of $^{134/137}\text{Cs}$ into the environment; and (iii) there is an urgent need to solve the problems of locating and monitoring terrestrial radioactive waste repositories. Phytoremediation has been investigated as a decontamination option for radiocesium contaminated land (Lasat et al., 1997, 1998; Dushenkov et al., 1999; Willey et al., 2001; Fuhrmann et al., 2002). There has also been much recent interest in the development of biomonitors (Whital, 2001), especially for radioisotopes, in response to proposed changes in the International Commission on Radiological Protection guidelines to protect not just humans but also flora and fauna from the effects of ionizing radiation (Strand and Larsson, 2001). Data on $^{134/137}\text{Cs}$ concentrations in plants are plentiful but focused on North American and European taxa. If, however, these data can be complemented with taxa from other locations they provide an opportunity to quantify differences in the uptake of a contaminant in a diverse range of plant taxa. Further, the chemical similarity between Cs and the much-researched plant macronutrient K means that the mechanisms implicated in $^{134/137}\text{Cs}$ uptake are being investigated at a level of detail attainable for few other contaminants (Broadley et al., 2001a).

Traits such as plant $^{134/137}\text{Cs}$ uptake, which are products of factors related to plant mineral nutrition, are likely to be controlled by both ancient evolutionary heritage and by more recent adaptations for particular ecological niches. Therefore, to predict differences between plant taxa in such traits the influence of both factors needs to be estimated (Ackerley, 2001). Analyses of variance (ANOVA) coded using recent molecular phylogenies are used to identify "phylogenetic signals" in phenotypes and quantify their location on the phylogeny (Harvey et al., 1996). Residual maximum likelihood (REML) procedures have recently been established that can compile sufficiently diverse databases of relative concentrations of ions in plants for phylogenetically coded ANOVAs to be performed on them (e.g., Broadley et al., 2001b). An obsolete taxonomy, which has now been superceded by molecular phylogenies, initiated such studies using $^{134/137}\text{Cs}$ uptake by 136 plant taxa (Broadley et al., 1999). Phylogenetic signals have now been established in the uptake by plants of a variety of heavy metals (Broadley et al.,

N.J. Willey, Centre for Research in Plant Science, University of the West of England, Frenchay, Bristol BS16 1QY, UK. S. Tang, College of Environmental Science and Engineering, Guangzhou University, Jie Fang Road, Guangzhou 510405, Guangdong Province, P. R. China. N.R. Watt, British Nuclear Group, Berkeley Centre, Berkeley, Gloucestershire, GL13 9PB, UK. Received 30 Nov. 2004. *Corresponding author (Neil.Willey@uwe.ac.uk).

Published in J. Environ. Qual. 34:1478–1489 (2005).
 Technical Reports: Bioremediation and Biodegradation
 doi:10.2134/jeq2004.0454
 © ASA, CSSA, SSSA
 677 S. Segoe Rd., Madison, WI 53711 USA

Abbreviations: ANOVA, analysis of variance; C, competitor; C-S-R, generalist growth strategist; REML, residual maximum likelihood; S-R, stress-tolerant ruderal.

2001b), aluminium (Jansen et al., 2002), calcium (Broadley et al., 2003), and nutrients (Broadley et al., 2004). Grime's plant growth strategy theory has advanced the understanding of plant adaptation to ecological niches and divides plants into three primary and four secondary growth strategies based on their reaction, in the established phase, to environmental stress and disturbance (Grime, 2001). Grime noted that plant strategy theory might be useful in predicting the persistence of ^{134/137}Cs in ecosystems (Grime, 1988) but its usefulness in predicting concentrations in plants has only ever been tested with six taxa (Willey and Martin, 1997). In fact, links between Grime's growth strategies and pollutant behavior in the environment have seldom been explored, and no other phylogenetic signals for ion concentrations in plants have been compared with the effects of ecological adaptations.

Here we report a taxonomically diverse database of ^{134/137}Cs concentrations in 273 plant taxa and use it to test three hypotheses: (i) plant ^{134/137}Cs concentrations are normally distributed, (ii) there is a phylogenetic signal in ^{134/137}Cs concentrations in plants, and (iii) plant growth strategy affects Cs concentrations in plants. This knowledge might be useful for food chain models and for searching for phytoremediation and phytomonitoring candidates, and might provide a useful methodology for other contaminants in the soil-plant system.

MATERIALS AND METHODS

Data on Cs concentration in plant shoots used for statistical analyses were in part produced in the greenhouse and in part derived from the literature. Data from the two sources was relativized using a REML procedure.

Data Produced in the Greenhouse

Taxa were chosen to represent a range of families and to complement the range of data available in the literature. They included 64 taxa from China and 11 phytoremediation candidates whose ¹³⁷Cs uptake had never previously been measured, plus 25 Chinese taxa and 21 phytoremediation candidates with values previously reported in the literature. Five replicate 12-cm-diameter pots with a single individual of each of 121 species were grown in Levington's F1 potting compost with 20% added grit in a greenhouse with 22°C/16 h light–15°C/8 h night. When plants were 5 wk old, they were radiolabeled, in five experimental datasets in a randomized block design, in an arena supplied with supplementary light at 350 μE m⁻¹ s⁻¹, with 50 mL of ¹³⁷CsCl at 3.7 kBq L⁻¹ and 250 μM CaSO₄ applied to the substrate surface of each pot, and harvested after 5 h. Plants at harvest were all in the exponential, established phase of their growth and had not flowered. Plant shoots were dried at 80°C, ground, and counted for ¹³⁷Cs γ-emissions with appropriate blanks, standards, and background correction in an LKB Wallac (Turku, Finland) CompuGamma 1282 γ-counter [NaI(Tl) detector].

Data Derived From the Literature

Data were found from 30 studies that had inter-taxa comparisons (at least two taxa) of concentrations of any Cs isotope in aboveground green shoots after exposure to a single set of conditions. Only studies in which foliar contamination was absent and which had taxa in common with at least one other

study were included. This provided data for 198 taxa. The 121 taxa from five experimental datasets together with the 198 taxa from 30 literature datasets (with 46 overlapping taxa) gave 273 taxa in all.

Statistical Analysis

Statistical analyses followed two phases: REML analysis to relativize Cs concentration data and ANOVA to identify phylogenetic signals. As for studies with heavy metals (Broadley et al., 2001b), Ca (Broadley et al., 2003), and nutrient ions (Broadley et al., 2004) a REML program on log_e transformed data was used to relativize data for species across the 30 literature datasets and the five experimental datasets by treating datasets as blocks, and their 273 taxa as treatments. This was run in the statistical package Genstat for Windows Fifth Edition Release 4.2 (VAG International, 2000) with units and nomenclature of original authors, and can produce relative concentrations for taxa that are either positive or negative (Thompson and Welham, 2001). Blocking datasets in this way removes the absolute differences in values arising from different experimental conditions to reveal relative values for the treatments (taxa).

A Kolmogorov–Smirnov test was run in Minitab 13.32 for Windows (Minitab, 2000) to test for normality of REML transformed data for the 273 taxa under study. Grubb's test was used to identify outliers. Cluster analysis was run in SPSS 10.0 for Windows (SPSS, 1999) with between-groups linkage, the interval-squared Euclidean-distance method, and a Euclidean distance of 7.5 on REML transformed data for the 273 taxa. The REML transformed data were coded using a recent ordinal phylogeny published for comparative experiments in biology (Soltis et al., 1999). Analysis of variance was run on REML transformed data in Genstat for Windows Fifth Edition Release 4.2. The relationship between the Linnean hierarchy and phylogenetic groups above the Ordinal level is contentious so here we use "Class," "Subclass," "Group," and "Superorder" in a nominal sense only. The REML transformed data included values for 61 exemplar species of Grime et al.'s (1988) growth strategies, which were averaged for the three primary strategies and four secondary strategies and contour plotted using Minitab 13.32 for Windows.

RESULTS AND DISCUSSION

Inter-Taxa Differences in Cesium-134/137 Concentration

Residual maximum likelihood analysis of shoot ^{134/137}Cs concentrations provided, from 949 concentration values, a database of relative ^{134/137}Cs concentrations in 273 taxa of flowering plants (Table 1)—twice as large as any previously reported (Broadley et al., 1999). One-way ANOVA of the 89 taxa from China (Datasets 31, 32, and 34 in Table 1), the most thorough single experimental comparison of inter-taxa differences in plant radio-caesium concentrations yet reported, confirmed that there can be large and significant differences in this phenotype ($F = 23.5$, $P < 0.001$). The complete REML database (Table 1) suggests that inter-taxa differences in ^{134/137}Cs concentrations for flowering plants (with log_e REML values of 4.62 to $-0.2 = 4.82$, which gives $e^{4.82} = 123.9$ on a linear scale) are of about two orders of magnitude. This confirms that ^{134/137}Cs concentration in plants is a diverse trait that needs to be accommodated in soil-

Table 1. Average residual maximum likelihood (REML) values of radiocesium, cluster analysis groupings, and growth strategies (GS) for 273 taxa of flowering plants from original experiments and the literature.

Genus	Species	REML	Group	GS†	Reference‡
Amaranthus	caudatus	4.62	1		15
Brassica	oleracea (sprouts)	4.58	1		10
Polygonum	microcephalum D. Don	4.62	1		31
Amaranthus	cruentus L.	4.09	2		15, 31, 34
Amaranthus	cruentus L. cv. myronivka	3.2	2		15
Amaranthus	paniculatus L.	4.26	2		31
Amaranthus	retroflexus cv. aureus	3.65	2		15
Amaranthus	retroflexus cv. belozernii	3.44	2		15
Beta	vulgaris Mangold	3.23	2		2
Beta	vulgaris L. var. "Hongtiancai"	3.57	2		32
Beta	vulgaris L. var. "Lutiancai"	3.8	2		30
Brassica	juncea Coss var. folia Bailey	3.42	2		31
Brassica	napus (Swede)	3.27	2		2
Brassica	napus (turnip)	3.21	2		16
Centaurea	cyanus L.	3.7	2		30, 31
Cerastium	fontanum	3.17	2	R/CSR	27
Chenopodium	album Linn. var. centrорubrum	3.45	2		32
Chenopodium	quinoa Willd	3.28	2		32
Chrysanthemum	coroarium L.	4.26	2		31
Datura	stramonium L.	3.68	2		32
Gomphrea	globosa L. var. alba	3.77	2		31
Gypsophila	oldhamiana Miq.	3.5	2		31
Melandrium	apricum (Turcz.) Rohrb	3.33	2		31
Nicotiana	tabacum Samsun	3.86	2		32
Rumex	hastatus	3.52	2		31
Rumex	sanguineus	3.211	2		34
Secale	cereale (winter rye)	4.01	2		3
Silene	latifolia	3.27	2		34
Valerianella	locusta	3.2	2	SR	10
Zinnia	elegans Jacq.	3.49	2		31
Agropyron	crisatum	1.72	3		16
Amaranthus	bicolor L.	2.57	3		15
Amaranthus	mangostanus	1.78	3		17
Amaranthus	tricolour L.	2.79	3		31
Amaranthus	cruentus L. cv. paniculatus	2.34	3		15
Amaranthus	graecizans	2.83	3		34
Amaranthus	retroflexus	2.66	3		21, 34
Amaranthus	retroflexus L. cv. Antey	3.04	3		15
Amaranthus	retroflexus L. cv. PT-95	3.04	3		15
Aquilegia	viridiflora Pall	1.68	3		32
Armoracia	rusticana	1.7	3	C/CR	2
Artemisia	annua L.	2.33	3		31
Atriplex	patula	2.19	3	R	7
Bellis	perennis L.	2.73	3	R/CSR	31
Beta	vulgaris (beetroot)	3.08	3		2, 7
Beta	vulgaris (cylindra)	2.5	3		7
Beta	vulgaris (chard)	2.91	3		7, 17
Beta	vulgaris (sea beet)	2.62	3		7
Beta	vulgaris (spinach beet)	2.52	3		2, 7
Beta	vulgaris (spinach beet)	2.52	3		7
Beta	vulgaris (sugar beet)	2	3		3
Beta	vulgaris	2.17	3		34
Bidens	pilosa L.	2.24	3		31
Brassica	juncea Coss. var. tumida	1.72	3		31
Brassica	napus	1.93	3		22
Brassica	nigra	1.86	3		7
Brassica	oleracea (cabbage)	2.45	3		2, 7, 16, 20
Brassica	oleracea (cauliflower)	2.51	3		16, 20
Brassica	oleracea (kohlrabi)	2.99	3		10
Brassica	oleracea (red cabbage)	2.15	3		10
Brassica	oleracea (savoy cabbage)	2.93	3		10
Brassica	oleracea (white cabbage)	2.34	3		10
Brassica	juncea (L.) Czern	2.52	3		20, 21, 29
Calendula	officinalis L.	2.14	3		31
Calluna	vulgaris	2.68	3	SC	11, 19, 24, 25, 27
Campanula	yunnanensis Hong	2.03	3		32
Cannabis	sativa	2.41	3		2
Capsella	bursa-pastoris	1.92	3	R	7
Capsicum	annuum	1.76	3		22
Carex	pillulifera	1.96	3	S	25
Carex	spp.	2.79	3		13, 19
Carthamus	tinctorius L.	2.93	3		30, 31
Celosia	argentea L.	2.83	3		31
Celosia	crisata L.	2.9	3		32
Chenopodium	album	2.33	3	R/CR	34
Chenopodium	amaramtricolor	1.99	3		32
Chenopodium	ficifolium	1.86	3		34
Chenopodium	spp.	1.89	3		32
Cicer	arietenum	2	3		4

Continued next page.

Table 1. Continued.

Genus	Species	REML	Group	GS†	Reference‡
Cirsium	japonicum (DC.) Maxim.	2.23	3		31
Citrus	sinensis	1.78	3		28
Claytonia	perfoliata	1.32	3		34
Claytonia	sibirica	2.34	3		34
Cucumis	sativus	2.11	3		22
Cucurbita	maxima	2.07	3		22
Cucurbita	pepo	1.85	3		22
Daucus	carota L.	1.81	3	SR/CSR	2
Descurania	sophia (L.) Webb	1.55	3		9
Dianthus	barbatus L.	1.48	3		31
Dianthus	spp.	2.17	3		31
Erica	tetralix	1.95	3	S	11
Elsholtzia	haichowensis Sun ex C.H. Hu	1.72	3		32
Galium	saxatile	1.89	3	S	24
Helianthemum	nummularium	2.19	3	S	7
Helianthus	annuus	1.86	3		2, 8, 12, 15, 17, 23, 29
Helianthus	tuberosum L.	1.75	3		15
Helianthus	tuberosum L. × Helianthus annuus L.	2.29	3		15
Kniphofia	varia Hook	2.04	3		31
Lactuca	sativa L. (lettuce)	1.935	3		14
Lactuca	sativa L.	3.011	3	CR	22
Lactuca	sativa L. var. "Woju"	2.18	3		31
Lotus	corniculatus	2.47	3	S/CSR	2
Lupinus	luteolus	2.95	3		16
Luzula	campestris	1.91	3	S/CSR	13, 24
Lychnis	coronata Thunb	2.94	3		31
Lychnis	senno Sieb. Et Zucc	2.24	3		31
Lycopersicon	esculentum	1.75	3		1, 2, 6, 16, 17, 22
Maianthemum	bifolium	1.91	3		18
Malva	sinensis Cavan	1.82	3		32
Matricaria	spp.	1.85	3		17
Medicago	sativa	1.86	3	C/CSR	2, 9, 16, 23
Melilotus	(L.) (white sweetclover)	0.6	3		16
Melilotus	officinales (L.) Lam (sweetclover)	1.78	3		12
Melilotus	officinales (L.) Lam (yellow sweetclover)	0.68	3		16
Mirabilis	jalapa	1.79	3		34
Molinia	caerulea	1.81	3	SC	11, 19
Nicotiana	tabacum	2.37	3		2, 12, 16, 23, 32
Olea	europaea	1.31	3		28
Panicum	italicum	1.72	3		33
Panicum	miliaceum	1.67	3		2, 22, 33
Papaver	rheas L.	1.66	3	R	22, 32
Pentapetes	phoeniceae L.	2.12	3		32
Petroselinum	crispum	2.29	3		2
Pharbitis	nil	1.68	3		17
Phaseolus	acutifolius	2.29	3		20
Phaseolus	vulgaris (haricot bean)	1.76	3		33
Phaseolus	vulgaris (kidney bean)	1.83	3		1, 2, 6, 33
Phytolacca	acinosa Roxb	1.51	3		31
Portulaca	oleracea	1.94	3		34
Potentilla	erecta	1.77	3	CSR	24
Pyrethrum	pulchrum Ledeb	0.86	3		31
Raphanus	sativus	2.05	3		2, 22
Rheum	rhaponticum	2.38	3		22
Rumex	acetosa	1.96	3	CSR	34
Rumex	acetosella	2.2	3	SR/CSR	27, 34
Rumex	crispus	3.21	3	R/CR	34
Rumex	maritimus	1.06	3		34
Rumex	obtusifolius	2.07	3	CR	34
Salsola	kali	1.92	3		12
Salvia	farinacea Benth.	1.87	3		32
Senecio	vulgaris	2.31	3	R	7
Silene	dioica	2.83	3	CSR	34
Silene	noctiflora	0.98	3		34
Silene	nutans	2.33	3		34
Silybum	marianum (L.) Gaertn	1.96	3		30
Sinapsis	alba	2.16	3		12
Solanum	tuberosum	2.15	3		2
Tetragonia	tetragonoides	1.94	3		34
Trichophorum	caespitosum	1.79	3		11, 19
Trifolium	hybridum	2.22	3	CSR	2
Trifolium	repens cv. Icerat vroege rode	1.9	3	CR/CSR	26, 27
Trifolium	repens	1.785	3		16, 26, 27
Urtica	dioica	0.69	3	C	7
Vicia	faba	1.97	3		12, 14
Vicia	hybrida	1.75	3	R/CSR	20
Vicia	sativa spp. nigra	1.752	3		2
Abelmoschus	esculentus	0.9	4		17
Aeschynomene	indica L.	0.69	4		32
Agropyron	desertorum	1.57	4		16

Continued next page.

Table 1. Continued.

Genus	Species	REML	Group	GS†	Reference‡
Agrostis	stolonifera	1.07	4	CR	7, 35
Agrostis	tenuis	1	4		20
Agrostis	capillaris	0.76	4	CSR	25
Allium	porrum	1.42	4		2, 10
Allium	cepa	0.82	4		2, 16
Allium	schoenoprasum	0.7	4		2
Amaranthus	hybridus L.	1.59	4		15
Amaranthus	hypochondriacus	1.54	4		34
Amaranthus	palmeri	0.95	4		34
Anethum	graveolens	1.3	4		2, 22
Anthoxanthum	odoratum	1.53	4	SR/CSR	7
Anthriscus	cerefolium	1.55	4		2
Anthyllis	vulneraria	1.39	4	S/SR	2
Antirrhinum	majus	0.61	4		17
Antirrhinum	namum	0.87	4		22
Apium	graveolens	1.29	4		2, 16, 17
Astragalus	sinicus L. var. "Changde species"	1.48	4		32
Astragalus	sinicus L. var. "Zhezi No. 84"	1.26	4		32
Astragalus	sinicus L. var. "Zhezi No. 5"	0.87	4		32
Atriplex	hortensis	1.16	4		7, 12
Avena	sativa	1.31	4		2, 12, 16, 22, 33
Beta	vulgaris var. Detroit globe	1.11	4		22
Borago	officinales	1.62	4		22
Brassica	campestris	0.81	4		10, 31
Brassica	campestris L. (hinona turnip)	1.36	4		17
Brassica	campestris L. (komatsuna turnip)	1.46	4		17
Brassica	campestris L. (kyona)	0.81	4		17
Brassica	juncea Coss. var. napiformis Pall. Et Bols	1.63	4		31
Brassica	napus (rape)	1.3	4		2
Brassica	oleracea (broccoli)	1.1	4		17, 20
Bromus	erectus Huds	0.7	4	SC/CSR	7
Bromus	inermis Leyss	0.88	4		7, 16
Bromus	lanceolatus Roth.	0.58	4		7
Bromus	sterilis L.	0.63	4	R/CR	7
Bromus	tectorum L.	1.48	4		9
Campanula	medium	1.13	4		17
Cassia	occidentalis Linn.	1.29	4		32
Centaurea	nigra L.	1.35	4	S/CSR	7
Coriandrum	sativum	1.52	4		22
Dactylis	glomerata L.	1.24	4	C/CSR	2
Danthonia	spicata (L.)	0.97	4		7
Deschampsia	flexuosa	2.65	4	S/SC	18, 25
Dianthus	caryophyllus	1.42	4		17
Dianthus	armeria	2.62	4		34
Eriophorum	vaginatum	1.29	4	S/SC	13
Eschscholtzia	californica Cham	1.46	4		17
Festuca	elatior L.	0.83	4		7
Festuca	gigantea (L.) Vill.	0.87	4	CSR	7
Festuca	juncifolia St.-Amans	0.76	4		7
Festuca	ovina L.	1.08	4	S	7
Festuca	pratensis Huds.	1.41	4	CSR	2
Festuca	rubra L.	1.03	4	CSR	7, 16, 20, 26, 27
Festuca	trachyphylla (Hack.) Kr	0.86	4		7
Glycine	max (L.) Merr.	1.32	4		7, 16, 17, 22
Glycine	max (L.) merr. Var. "Aijiaohan"	1.12	4		32
Glycine	max (L.) merr. Var. "Xiangxi No. 119"	1.41	4		32
Glycine	max (L.) merr. Var. "Xiangxi No. 3"	0.73	4		32
Helianthus	annuus L.	1.51	4		29
Holcus	lanatus	1.5	4	CSR	7
Holcus	mollis	1.25	4	C	26, 27
Hordeum	vulgare	0.67	4		1–6, 9, 14, 16, 33
Ipomea	batatas	1.53	4		17
Juncus	effusus	1.43	4	C/SC	13, 19
Juncus	squarrosus	0.55	4	S	11, 13, 19, 24
Kochia	scoparia L. (Schrad)	1.58	4		20
Koeleria	macrantha (Ledeb.) Schrad.	3.01	4		7
Lactuca	sativa L.	0.66	4		10, 22, 30
Leontodon	hispidus	0.64	4	S	7
Linum	usitatissimum	0.96	4		2, 16, 22
Lolium	perenne	2.53	4	CR/CSR	2, 7, 26, 27, 32
Nardus	stricta	2.82	4	S	13, 19, 24
Nigella	damascena L.	1.13	4		32
Oxalis	acetosella	1.09	4	S/CSR	18
Papaver	naudicale	1.01	4		17
Phalaris	arundinaceae	1.3	4		16, 20
Phaseolus	vulgaris	3	4		22
Phleum	pratense	1.53	4	CSR	2, 16
Picris	echioides	1.3	4		35
Pinnacle	spp.	1.54	4		17
Pisum	sativum L.	1.24	4		2, 4, 12, 15–17, 22, 33

Continued next page.

Table 1. Continued.

Genus	Species	REML	Group	GS†	Reference‡
Poa	annua	1.63	4	R	7, 35
Poa	pratensis	1.6	4		17, 27
Poa	spp.	2.55	4		26
Polygonum	fagopyrum	0.64	4		7, 12, 22, 33
Raphanus	sativus L. cv. Tripolo	0.83	4		8
Rumex	obtusifolius	1.38	4		7
Rumex	patientia X.R. tianschanicus Rumex K-1	2.62	4		31
Rumex	conglomeratus	2.57	4	CR	34
Salsola	komarovii	0.92	4		17
Secale	cereale (spring rye)	1.14	4		2
Senecio	jacobea	2.99	4	R/CR	7
Silene	vulgaris	0.95	4	CSR	34
Solanum	melongena	0.87	4		17
Sorghum	vulgare var. french	1.27	4		22
Sorghum	vulgare var. Red French	1.3	4		22
Spinacia	oleracea L.	0.72	4		16, 32
Stipa	viridula	2.6	4		16
Thlipsis	alpestre	1.44	4		7
Trifolium	pratense	0.83	4	CSR	2, 7, 16
Triticum	aestivum	1.55	4		2, 4, 5, 14, 16, 17, 23, 33
Tussilago	farfara	2.68	4		35
Vaccinium	myrtillus	2.64	4	SC	11, 18, 19, 24
Zea	mays L.	1.06	4		2, 5, 8, 12, 14, 15
Zea	mays L. cv. Caro	1.55	4		8
Agrostis	canina	0.21	5		25
Allium	tuberosum	-0.2	5		17
Brassica	campestris L. (Chinese cabbage)	0.36	5		17
Erica	cinerea	0.2	5		11, 19, 24
Leontodon	autumnalis	0.42	5	R/CSR	7
Oryza	sativa	0.01	5		2, 17
Phaseolus	acutifolius A. Gray	-0.12	5		21
Rumex	crispus	0.3	5		7
Secale	cereale	0.13	5		16
Vigna	radiata	-0.2	5		17

† Plant growth strategies and intermediates *sensu* Grime. C, competitor; R, ruderal; S, stress tolerator; CSR, generalist strategy.

‡ 1, Birkle et al. (1965, Experiment a); 2, Andersen (1967); 3, Andersson and Lonsjo (1988); 4, Antonopoulos-Domis et al. (1990a); 5, Antonopoulos-Domis et al. (1990b); 6, Birkle et al. (1965, Experiment b); 7, Broadley and Willey (1997); 8, Buysse et al. (1996); 9, Cline and Rickard (1972); 10, Clooth and Aumann (1990); 11, Colgan et al. (1990); 12, Collander (1941); 13, Coughtrey et al. (1989); 14, Demirel et al. (1994); 15, Dushenkov et al. (1999); 16, Evans and Dekker (1968); 17, Gouthu et al. (1997); 18, Henrich et al. (1990); 19, Horrill et al. (1990); 20, Lasat et al. (1997); 21, Lasat et al. (1998); 22, Experimental Dataset 1; 23, Papanicolaou et al. (1990); 24, Salt and Mayes (1991); 25, Salt et al. (1992); 26, Salt and Mayes (1993); 27, Salt and Mayes (1990); 28, Skarlou et al. (1999); 29, Tang and Wang (2002); 30, Tang and Willey (2003); 31, Experimental Dataset 2; 32, Experimental Dataset 3; 33, Tikhomirov et al. (1981); 34, Experimental Dataset 4; 35, Experimental Dataset 5.

to-plant transfer models and that might be exploited by phytotechnologies.

Caution is necessary in interpreting the values in Table 1. Residual maximum likelihood analysis across different datasets using taxa they have in common accounts for differences in absolute concentration arising from different experimental conditions. It reveals, therefore, relative concentrations in taxa. It takes no account, however, of any statistical interactions arising between, for example, relative concentrations in taxa and experimental conditions. It is very likely that there are such interactions and the database in Table 1 does not, therefore, contain a definitive listing of relative concentrations in taxa but predicted average relative ^{134/137}Cs concentrations across a variety of conditions. Further, data from experiments reported here are from short-term exposures while much of the literature data was from chronic exposure, and exposure time and relative concentrations in taxa might also interact. However, data in Table 1 are likely to relate reasonably well to relative concentrations after long-term exposures because, as an analogue of K, ^{134/137}Cs is primarily taken up during the exponential phase of plant growth (Weaver et al., 1981), which is when taxa in the experiments reported here were exposed. It has been obvious for almost half a century that clay and K contents of different soils affect ^{134/137}Cs

transfer to plants (Nishita et al., 1958). It is notable, however, that the differences in ^{134/137}Cs concentrations reported from a single plant taxon grown on markedly different soils (e.g., Abbazov et al., 1978; Mascanzoni, 1989) are similar in magnitude to those between taxa in Table 1. We therefore suggest that, for example, low soil-to-plant transfer of ^{134/137}Cs can be produced either by high clay/K or, despite ^{134/137}Cs being available in the soil solution, plants such as those in Category 5 in Table 1 that have low uptake. Clearly, if ^{134/137}Cs is poorly available in the soil, Category 1 plants will not produce high soil-to-plant transfer but we predict that they will produce higher transfer than Category 5 plants in such circumstances. We conclude, therefore, that the implications of inter-taxa differences are significant and supplementary to the long-established factors that control ^{134/137}Cs availability in soil. With the provisos outlined above, the values in Table 1 might be directly useful for soil-to-plant transfer models and phytoremediation and phytomonitoring of radiocesium but they also include sufficient species to allow further analyses.

The ^{134/137}Cs REML values in plant taxa included in the database are not normally distributed ($p < 0.01$ for Kolmogorov–Smirnov test; Fig. 1), no simple transformations to achieve normality could be found, and Grubb's test identified no significant outliers that could

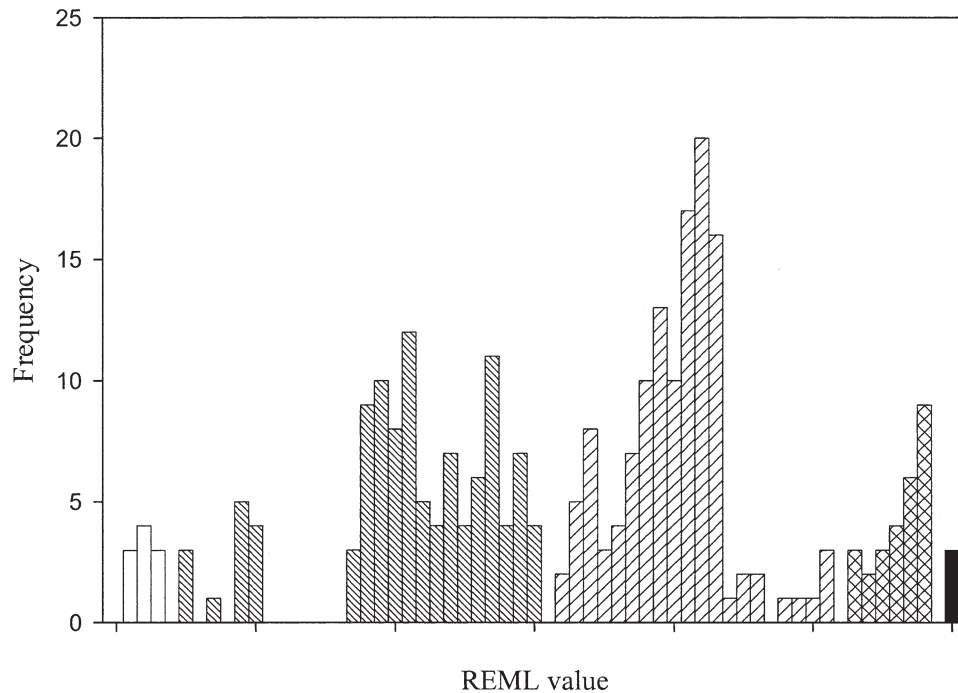


Fig. 1. Frequency distribution for residual maximum likelihood (REML) values of Cs concentrations in plants. Shading indicates five significant groupings identified using cluster analysis with a Euclidean distance of 7.5.

be removed to achieve normality. This contrasts with reports that the concentration of other ions such as Ca is normally distributed across taxa (Broadley et al., 2003). Cluster analysis showed that there are significantly different categories of plant taxa with respect to Cs concentration (Fig. 1; $P < 0.05$). Categories 1, 4, and 5 were not normally distributed but the large Categories 2 and 3 were. This categorization of ion concentration in plants using frequency distributions of relative values might provide a more useful description of the ion concentration trait than, for example, the absolute concentration thresholds used to define hyperaccumulators (Baker, 1981), especially if the constraints on these categories can be identified.

Effects of Phylogeny

Analysis of variance on REML-transformed data for 273 taxa using a recent ordinal flowering plant phylogeny (Soltis et al., 1999) identified a significant phylogenetic signal in $^{134/137}\text{Cs}$ concentrations in plants (Fig. 2; Table 2). Magnoliids had significantly lower $^{134/137}\text{Cs}$ concentrations than Eudicots (Fig. 2 and Table 2 "Classes": $P = 0.01$). Within the Eudicot "Groups," the Caryophyllid clade had significantly higher REML values than the Asterid or Rosid clades (Fig. 2 and Table 2). It has previously been suggested, using a now obsolete taxonomy, that Caryophyllids have high uptake of $^{134/137}\text{Cs}$ (Broadley et al., 1999). Data presented here (Table 1; Fig. 2) support the contention that this phenotype is characteristic of the whole Caryophyllid clade, extending the range of taxa that might display it to families such as the Caryophyllaceae, Cactaceae, and Phytolacaceae. In total there are about 10 000 species on the clade including numerous food crops (e.g., beets, amaranths,

buckwheat) and taxa adapted to a wide variety of environments (e.g., *Chenopodium* spp., *Rumex* spp.) (Cuénoud et al., 2002). Within the Asterid and Rosid clades there were differences in $^{134/137}\text{Cs}$ uptake at the ordinal level, with the Asterales, Solanales, and Brassicales having relatively high uptake (Fig. 2). The Asterales, one of the most numerous orders of flowering plants (Hickey and King, 1988), have not previously been noted to have high $^{134/137}\text{Cs}$ uptake but this does accord with recent reports from China that some taxa in the Asteraceae have higher uptake than chenopods of known high uptake (Tang and Willey, 2003). Taxa in the Solanales might be worth further investigation because the few taxa in Table 1 indicate that uptake might be high and there are numerous food crops in this order (e.g., potatoes, tomatoes, aubergines). The relatively high $^{134/137}\text{Cs}$ uptake has not previously been ascribed to the order Brassicales, although high uptake in some brassica species has been noted (Frissel et al., 2002), so given the extensive sampling in the database of this order, plants on this clade might merit special attention in food chain models and the search for phytoremediators and phytomonitors. The Fabales and Poales, two orders that are well represented in Table 1, have low uptake of $^{134/137}\text{Cs}$, and provide many of the world's staple food crops, including legumes and cereals, respectively. This suggests that radiation doses from $^{134/137}\text{Cs}$ in diet calculated using values for staple crops might underestimate doses from less widely used crops, especially if they are from the Caryophyllids, Asterales, Solanales, or Brassicales. The Poales and Fabales are unlikely to be a good source of phytoremediators or phytomonitors. Taxa on the Caryophyllid clade were significant contributors to Categories

Reproduced from Journal of Environmental Quality. Published by ASA, CSSA, and SSSA. All copyrights reserved.

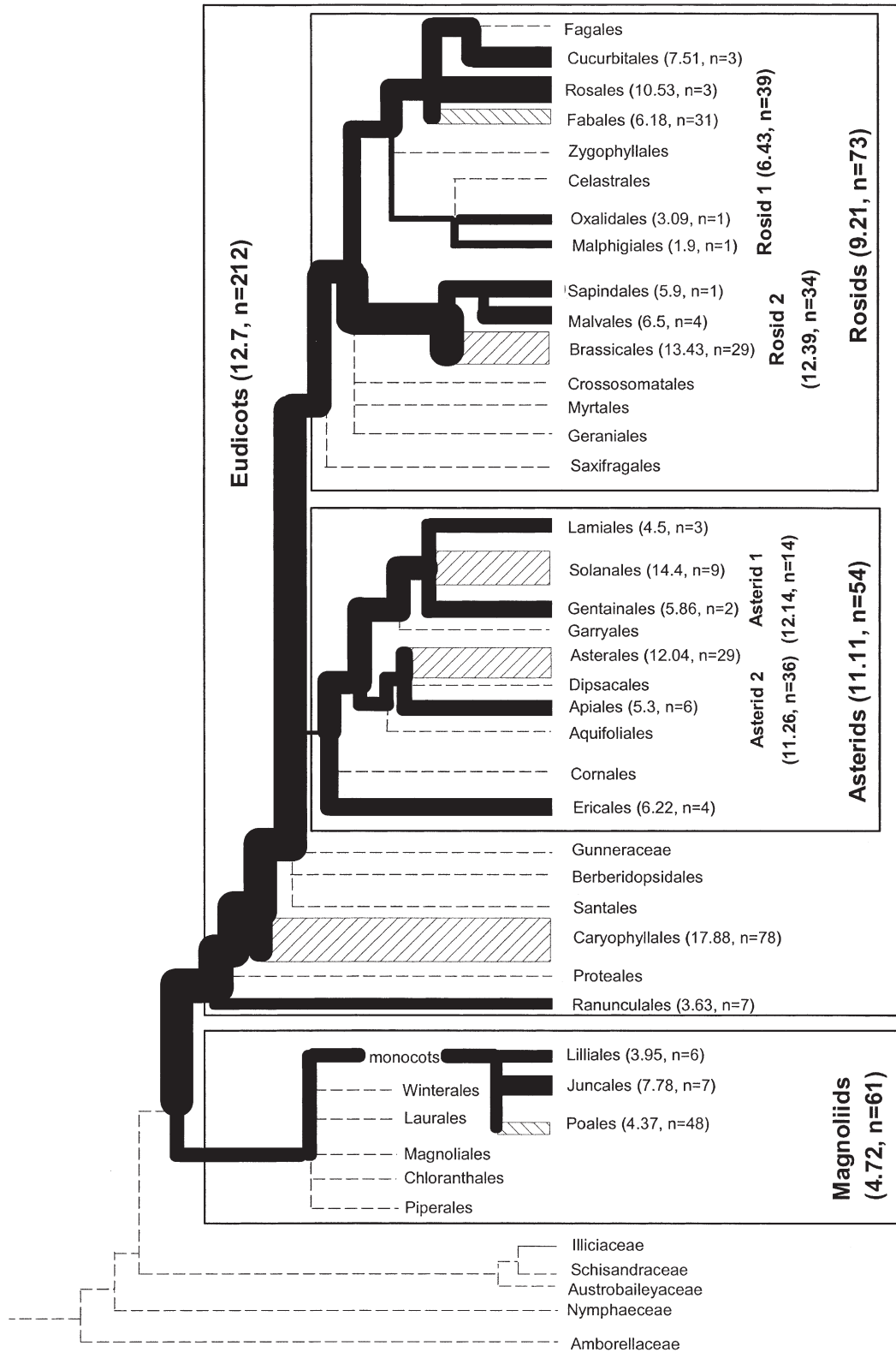


Fig. 2. The phylogeny of residual maximum likelihood (REML) Cs values in flowering plants down to the ordinal level using the phylogeny of Soltis et al. (1999). Thickness of lines denotes average ANOVA values. The ANOVA values and number of replicates per Order are shown in brackets. Orders with unusually high and low uptake of Cs are shaded. Dashed lines = unsampled.

1, 2, and 3, while those in the Poales and Fabales were significant contributors to Categories 4 and 5 (Table 1). Plant phenotypes that are not phylogenetically con-

strained (e.g., phosphorus concentration) display inter-taxa variation that resides entirely at the species level (Broadley et al., 2004). Approximately 42% of the sum

Table 2. Results of analysis of variance (ANOVA) for residual maximum likelihood (REML) Cs concentrations in 273 flowering plant taxa using phylogeny of Soltis et al. (1999).

	Degrees of freedom	Sum of squares	% Sum of squares	Mean square	Variance ratio
“Class”	1	3 019	5.20	3019	11.79
“Group”	2	2 391	4.12	1195.6	4.67
“Superorder”	4	2 060	3.55	515	2.01
Order	12	924.6	1.59	77.1	0.3
Family	17	2 947	5.07	173	0.68
Genus	99	13 015	22.41	131.5	0.51
Species	79	18 876	32.49	238.9	0.93
Residual	58	14 855	25.57	256	
Total	271	58 089			

of squares in inter-taxa differences in Cs uptake occurred above the level of the species and 15% at the ordinal level and above (Table 2). This confirms a significant phylogenetic signal in Cs concentrations in plants, with a similar distribution among taxonomic levels as the obsolete taxonomy of Cronquist (Broadley et al., 1999), following the reorganization of higher taxonomic levels in the new phylogeny used here. Table 2 suggests that, although the species unit is almost always that chosen for soil-to-plant transfer studies of $^{134/137}\text{Cs}$ and other contaminants, other taxonomic units might often be at least as appropriate. In comparison with ANOVAs of other plant ion concentrations down to the ordinal level, the phylogenetic signal for Cs is greater than that for P (6.8%) and N (3.3%) (Broadley et al., 2004), approaching that for Pb (20%), Cr (23%), Cu (24%), Cd (27%), (Broadley et al., 2001b), and Na (23%) (Broadley et al., 2004), but less than that for Ca (63%) (Broadley et al., 2003) and K (49%) (Broadley et al., 2004).

The $^{134/137}\text{Cs}$ dataset reported here is not strictly phylogenetically balanced (i.e., the sample numbers on each clade are not proportional to the number of taxa on each clade). This is because literature datasets we used were not designed with phylogenetic analyses in mind, although we did ameliorate the imbalance through taxa chosen for our experiments. Broadley et al. (2003) compared analyses for Ca concentrations on balanced and

unbalanced sampling and found that with 206 taxa at the ordinal level, the phylogenetic signals revealed were indistinguishable. It seems likely, therefore, that there is a phylogenetic signal in $^{134/137}\text{Cs}$ concentrations in plants and that Fig. 2 and Table 2 provide its most thorough description so far.

Effects of Plant Growth Strategy *sensu* Grime

Of the 281 species used by Grime et al. (1988) to exemplify, through screening experiments, plant growth strategies, 61 occur in Table 1. Figure 3 shows, using the triangular representation of strategy types established by Grime et al. (1988), that taxa of the stress-tolerant ruderal strategy have the highest Cs concentrations and that there is an upward trend from C (competitor) strategists toward the S-R (stress-tolerant ruderal) and C-S-R (generalist) strategists. Grime et al. (1988) suggested that Region A of the growth strategy triangle includes plants that maximize the utilization of resources captured rather than maximizing the capture of resources (Region D). If Grime is correct in asserting that mineral nutrition is a primary axis of ecological specialization (Grime, 2001), then it is not perhaps surprising that as an analogue of a nutrient ion $^{134/137}\text{Cs}$ uptake is affected by growth strategy. However, competitive plants generally contain the highest concentration of N and the con-

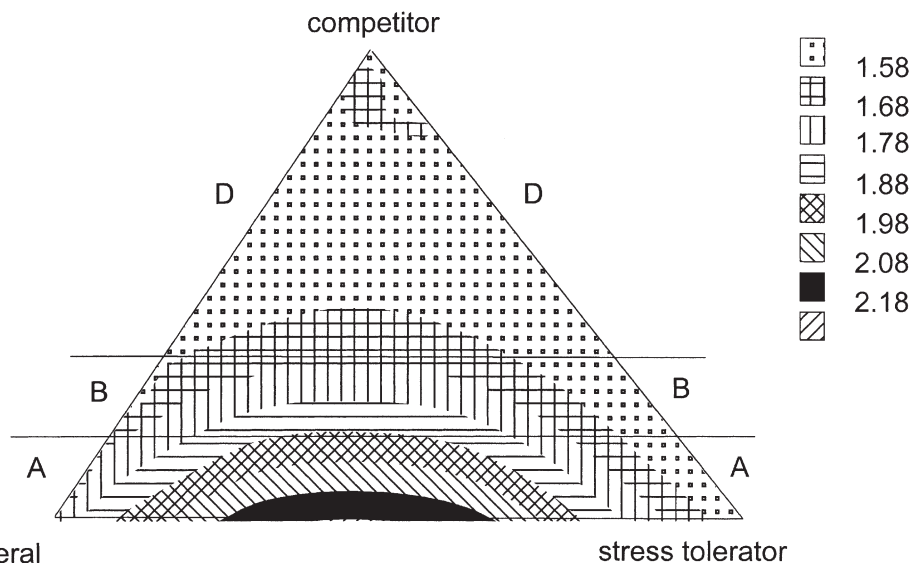


Fig. 3. The average residual maximum likelihood (REML) Cs values across Grime's plant growth strategies based on 61 species. Letters A, D, and B are floristic elements: A, plants of disturbed conditions that maximize utilization of captured resources; D, dominant plants that maximize capture of resources; B, subordinates.

centration of K tends to correlate with that of N in plants (Grime, 2001). Figure 3 suggests that, under comparative conditions, C strategy species will not take up $^{134/137}\text{Cs}$ to concentrations as high as will S-R strategists. The discrimination between Cs and K during uptake is a key determinant of $^{134/137}\text{Cs}$ concentrations in plants (Broadley and Willey, 1997) and Fig. 3 might reflect a greater discrimination against Cs by competitive plants than stress-tolerant ruderals. The significance of differences between all Grime's seven primary and secondary strategies in the established phase can only really be established with a more extensive data set but it is notable that across Fig. 3 there are no differences of the magnitude of those between Magnoliids and Eudicots. Grime's plant growth strategy theory was designed to predict vegetation processes and ecosystem properties; Fig. 3 provides the strongest empirical support thus far that it might be of general use for predicting the behavior of $^{134/137}\text{Cs}$ in ecosystems.

CONCLUSIONS

Here we have shown that the concentration to which different plant taxa take up $^{134/137}\text{Cs}$ differs significantly and that molecular phylogenies (reflecting ancient evolutionary heritage) and plant growth strategies (reflecting adaptations for particular niche types) can be used to predict a portion of this difference. This shows, most importantly, that plant taxa are not independent units with respect to $^{134/137}\text{Cs}$ concentration but have discernable patterns of variation in this trait. This has a variety of consequences for modeling soil-to-plant transfer of $^{134/137}\text{Cs}$ and for selecting taxa for phytoremediation or phytomonitoring. Models for $^{134/137}\text{Cs}$ behavior in the soil-plant system should assume neither that plant taxa all have uptake that just reflects soil processes nor that each taxon has independent uptake characteristics. This is particularly important for interpreting the effects of soil variables on plant uptake of $^{134/137}\text{Cs}$ based on experiments with a few plant taxa.

The analysis reported here shows that the frequency distribution of this phenotype is not normal but clustered, and that phylogeny and growth strategy help to explain this clustering. Rather than just focusing on staple crops or utilizing the few plants shown to have high uptake at contaminated sites, it might now be possible to phylogenetically expand environmental models and target taxon selection for phytoremediation. This avoids exhaustive experiments with all plant taxa because it makes general predictions of plant uptake of $^{134/137}\text{Cs}$ by large taxonomic units or growth strategies. For example, food chain models might utilize data from Table 1 to predict high uptake by grain amaranths, although there are few actual values for $^{134/137}\text{Cs}$ uptake by the great number of varieties utilized around the world. Certainly, it suggests that grain amaranths might not be modeled by a dietary category like "cereal" that includes plants in the Poales with, in general, significantly lower $^{134/137}\text{Cs}$ concentrations. Similarly, if phytoremediation candidates for $^{134/137}\text{Cs}$ are being sought, taxa in the clades identified in Fig. 2 as having high $^{134/137}\text{Cs}$ uptake and whose product

of concentration \times biomass is greatest have the greatest potential for phytoremediation of $^{134/137}\text{Cs}$. Clearly, $^{134/137}\text{Cs}$ is poorly available in many soils but in soils in which it can be available (like Oxisols, Histosols, and Andosols) if phytoremediation is attempted then the data reported here might aid taxon selection for any location. It has recently been suggested that rehabilitation of land contaminated with $^{134/137}\text{Cs}$ might best be achieved with safe crops that have very low $^{134/137}\text{Cs}$ uptake (www.strategy-ec.org.uk; verified 28 Apr. 2005). Data reported here might aid the selection of such safe crops. It is unlikely that plant taxa with the highest or lowest uptake of $^{134/137}\text{Cs}$ are included in Table 1. The analysis reported here does, however, allow us to predict that they might be in the Caryophyllales and Poales, respectively—considerably narrowing the search for them.

Interest in the biomonitoring of environmental contaminants, and the potential contribution of biotechnology to it, is increasing (Whital, 2001). For radionuclides this is especially so with the possibility of a change to International Commission on Radiological Protection guidelines to protect flora and fauna from the effects of radioactive contaminants (Strand and Larsson, 2001). However, no methodology for selecting the most suitable taxa for biomonitoring has been proposed. Taxa currently used in biomonitoring of pollutants have been selected in much the same way as those used in bioremediation—they have been noted to have high uptake in surveys of contaminated sites. The probabilistic models that data from biomonitors can be fed into frequently assume normal distributions. The non-normal, clustered data reported here for $^{134/137}\text{Cs}$ concentrations in plants suggests that care must be taken in selecting taxa for its biomonitoring. Clearly, taxa in category 1 (Table 1) or on the Caryophyllid clade might be useful sentinels for monitoring maximum $^{134/137}\text{Cs}$ concentrations in flora. In agricultural systems, crop plants on this clade might be suitable sentinel species for Cs. However, using biomonitoring data to predict $^{134/137}\text{Cs}$ concentrations in groups of plants, or in ecosystems, might be most securely performed by selecting taxa in Categories 2 and 3 to represent groups that have normal distributions.

Recent advances in the molecular understanding of K uptake in the model plant *Arabidopsis thaliana* have shown that important K uptake systems such as the AKT1 transporter are not implicated in $^{134/137}\text{Cs}$ uptake (Broadley et al., 2001a). Electrophysiological models have suggested that $^{134/137}\text{Cs}$ enters plants through voltage independent cation channels (White and Broadley, 2000), although recent research into $^{134/137}\text{Cs}$ uptake is also focusing on other uptake systems (C. Hampton, personal communication, 2004). The Caryophyllid clade is a well-established monophyletic group of flowering plants with numerous distinguishing features (Cuénoud et al., 2002), including poor discrimination between K and Cs uptake (Broadley and Willey, 1997). The Asterales is also a clearly defined monophyletic clade (Angiosperm Phylogeny Group II, 2003). The mechanisms of monovalent cation uptake in the Caryophyllid and Asterales clades are less well known than those of model plant species such as *Arabidopsis* (Brassicales), wheat, and rice (Poales)

for which identities of numerous cation transport proteins are becoming available (Mäser et al., 2001). If advanced molecular techniques are applied to the problems of $^{134/137}\text{Cs}$ in the soil–plant system the data reported here might direct the search for useful transporters and their genes among taxonomic groups.

There is increasing evidence that differences in plant concentrations of a number of elements include a phylogenetic signal (Broadley et al., 1999, 2001b, 2003, 2004). Here, we have provided for $^{134/137}\text{Cs}$ concentrations in plants the first rigorous analyses of phylogenetic effects based on a recent molecular phylogeny, and of plant growth strategy effects based on Grime (2001), both of which were designed for just such analyses. There are numerous edaphic factors well-established to affect $^{134/137}\text{Cs}$ concentrations in plants. We conclude that phylogenetic and growth strategy factors should be added to them. It seems likely that phylogeny and growth strategy might also be important in the behavior of other contaminants in the soil–plant system.

ACKNOWLEDGMENTS

We would like to thank Judy Brown for help with radioanalysis, the Leverhulme Trust for funding Shirong Tang's visit to UWE, Bristol, UK, British Nuclear Fuels for a Ph.D. studentship for Nick Watt, and the UK Food Standards Agency for supporting this work.

REFERENCES

- Abbazov, M.A., I.D. Dergunov, and R.G. Mikulin. 1978. Effect of soil properties on the accumulation of strontium-90 and cesium-137 in crops. *Pochvovedenie* 2:25–29.
- Ackerley, D.D. 2001. Comparative plant ecology and the role of phylogenetic information. p. 391–414. *In* M.C. Press et al. (ed.) *Physiological plant ecology*. Blackwell Sci., Oxford.
- Andersen, A.J. 1967. Investigations on the plant uptake of fission products from contaminated soils. 1. Influence of plant species and soil types on the uptake of radioactive strontium and caesium. Rep. 170. Riso, Denmark.
- Andersson, I., and H. Lonsjö. 1988. Transfer of Cs-137 in two farm ecosystems. *Swed. J. Agric. Res.* 18:195–206.
- Angiosperm Phylogeny Group II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. *APG II. Bot. J. Linn. Soc.* 141:399–436.
- Antonopoulos-Domis, M., A. Clouvas, and A. Gagianas. 1990a. Derivation of soil to plant transfer factors of radiocesium in Northern Greece after the Chernobyl accident, and comparison with greenhouse experiments. *Environ. Pollut* 68:119–128.
- Antonopoulos-Domis, M., A. Clouvas, and A. Gagianas. 1990b. Soil to plant transfer of radiocesium: Application to the Chernobyl accident. p. 591–597. *In* G. Desmet, P. Nassimbeni, and M. Belli (ed.) *Transfer of radionuclides in natural and semi-natural environments*. Elsevier Appl. Sci., London.
- Baker, A.J.M. 1981. Accumulators and excluders—Strategies in the response of plants to heavy metals. *J. Plant Nutr.* 3:643–654.
- Birkle, D.E., J. Letey, N.T. Coleman, and W.K. Richardson. 1965. Uptake by plants of Cs-137, Ce-144 and Y-91 as influenced by rhizosphere oxygen treatments. *Soil Sci.* 99:93–97.
- Broadley, M.R., H.C. Bowen, H.L. Cotterill, J.P. Hammond, M.C. Meacham, A. Mead, and P.J. White. 2003. Variation in the shoot calcium content of angiosperms. *J. Exp. Bot.* 54:1–16.
- Broadley, M.R., H.C. Bowen, H.L. Cotterill, J.P. Hammond, M.C. Meacham, A. Mead, and P.J. White. 2004. Phylogenetic variation in the shoot mineral concentration of angiosperms. *J. Exp. Bot.* 55:321–336.
- Broadley, M.R., A.J. Escobar-Gutiérrez, H.C. Bowen, N.J. Willey, and P.J. White. 2001a. Influx and accumulation of Cs^+ by the *akt1* mutant of *Arabidopsis thaliana* (L.) Heynh. lacking a dominant K^+ transport system. *J. Exp. Bot.* 52:839–844.
- Broadley, M.R., and N.J. Willey. 1997. Differences in root uptake of radiocesium by 30 plant taxa. *Environ. Pollut.* 97:11–17.
- Broadley, M.R., N.J. Willey, and A. Meade. 1999. A method to assess taxonomic variation in Cs concentrations among flowering plants. *Environ. Pollut.* 106:341–349.
- Broadley, M.R., N.J. Willey, J.C. Wilkins, A.J.M. Baker, A. Mead, and P.J. White. 2001b. Phylogenetic variation in heavy metal accumulation in angiosperms. *New Phytol.* 152:9–27.
- Buyse, J., K. Brande, and R. Merckx. 1996. Genotypic differences in the uptake and distribution of radiocesium in plants. *Plant Soil* 178:265–271.
- Cline, J.F., and W.H. Rickard. 1972. Radioactive strontium and cesium in cultivated and abandoned field plots. *Health Phys.* 23:317–324.
- Clooth, G., and D.C. Aumann. 1990. Environmental transfer parameters and radiological impact of the Chernobyl fallout in and around Bonn (FRG). *J. Environ. Radioact.* 12:97–119.
- Colgan, P.A., E.J. McGee, J. Pearce, J.G. Cruickshank, N.E. Mulvany, J.H. McAdam, and B.W. Moss. 1990. Behaviour of radiocesium in organic soils—Some preliminary results on soil-plant transfers from a semi-natural ecosystem in Ireland. p. 341–354. *In* G. Desmet, P. Nassimbeni, and M. Belli (ed.) *Transfer of radionuclides in natural and semi-natural environments*. Elsevier Appl. Sci., London.
- Collander, R. 1941. Selective absorption of cations by higher plants. *Plant Physiol.* 16:691–720.
- Coughtrey, P.J., J.A. Kirton, N.G. Mitchell, and C. Morris. 1989. Transfer of radioactive caesium from soil to vegetation and comparison with potassium in upland grasslands. *Environ. Pollut.* 62:281–315.
- Cuénoud, P., V. Savolainen, L.W. Chatrou, M. Powell, R.J. Grayer, and M.W. Chase. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbcL*, *atpB* and *matK* DNA sequences. *Am. J. Bot.* 89:132–144.
- Demirel, H., I. Özer, I. Çelenk, M.B. Halitligil, and A. Özmen. 1994. Uptake of cesium-137 by crops from contaminated soils. *J. Environ. Qual.* 23:1280–1285.
- Dushenkov, S., A. Mikheev, A. Prokhnevsky, M. Ruchko, and B. Sorochinsky. 1999. Phytoremediation of radiocesium contaminated soil in the vicinity of Chernobyl, Ukraine. *Environ. Sci. Technol.* 33:469–475.
- Evans, E.J., and A.J. Dekker. 1968. Comparative Cs-137 content of agricultural crops grown in a contaminated soil. *Can. J. Soil Sci.* 48:45–53.
- Fuhrmann, M., M.M. Lasat, S.D. Ebbs, L.V. Kochian, and J. Cornish. 2002. Uptake of cesium-137 and strontium-90 from contaminated soil by three plant species: Application to phytoremediation. *J. Environ. Qual.* 31:904–909.
- Frissel, M.J., D.L. Deb, M. Fathony, Y.M. Lin, A.S. Mollah, N.T. Ngo, I. Othman, W.L. Robison, V. Skarlou-Alexiou, O. Topocouluo, J.R. Twining, S. Uchida, and M.A. Wasserman. 2002. Generic values for soil-to-plant transfer factors of radiocesium. *J. Environ. Radioact.* 58:113–128.
- Goutho, S., T. Arie, S. Ambe, and I. Yamaguchi. 1997. Screening of plant species for comparative uptake abilities of radioactive Co, Rb, Sr and Cs from soil. *J. Radioanal. Nucl. Chem.* 222:247–251.
- Grime, J.P. 1988. Appendix 39. Memorandum submitted from NERC Unit of Comparative Plant Ecology. p. 399–403. *In* *Chernobyl: The government's reaction*. Vol. II. Minutes of Evidence and Appendices. HMSO, London.
- Grime, J.P. 2001. Plant strategies, vegetation processes and ecosystem properties. 2nd ed. John Wiley, Chichester, UK.
- Grime, J.P., J.G. Hodgson, and R. Hunt. 1988. *Comparative plant ecology*. Unwin Hyman, Chichester, UK.
- Hall, S., and N. Watt. 2002. The potential of phytoextraction to remediate caesium-137 contaminated ground on nuclear licensed sites. *Nucl. Eng.* 43:27–31.
- Harvey, P.H., A.J.L. Brown, J. Maynard-Smith, and S. Nee. 1996. New uses for new phylogenies. Oxford Univ. Press, Oxford.
- Henrich, E., M. Friedrish, W. Haider, K. Kienzl, E. Heisel, A. Boisits, and G. Hekerle. 1990. The contamination of large Austrian forest systems after the Chernobyl nuclear reactor accident: Studies 1988 and further. p. 217–227. *In* G. Desmet, P. Nassimbeni, and M.

- Belli (ed.) Transfer of radionuclides in natural and semi-natural environments. Elsevier Appl. Sci., London.
- Hickey, M., and K. King. 1988. 100 Families of flowering plants. 2nd ed. Cambridge Univ. Press, Cambridge.
- Horrill, A.D., V.H. Kennedy, and T.R. Harwood. 1990. The concentrations of Chernobyl derived radionuclides in species characteristic of natural and semi-natural ecosystems. p. 27–39. *In* G. Desmet, P. Nassimbeni, and M. Belli (ed.) Transfer of radionuclides in natural and semi-natural environments. Elsevier Appl. Sci., London.
- Jansen, S., M.R. Broadley, E. Robbrecht, and E. Smets. 2002. Aluminium hyperaccumulation in angiosperms: A review of its phylogenetic significance. *Bot. Rev.* 68:235–269.
- Lasat, M.M., M. Fuhrmann, S.D. Ebbs, J.E. Cornish, and L.V. Kochian. 1998. Phytoremediation of a radiocaesium contaminated soil: Evaluation of cesium-137 bioaccumulation in the shoots of three plant species. *J. Environ. Qual.* 27:165–169.
- Lasat, M.M., W.A. Norvell, and L.V. Kochian. 1997. Potential for phytoextraction of ¹³⁷Cs from a contaminated soil. *Plant Soil* 195: 99–106.
- Mascanzoni, D. 1989. Plant uptake of activation and fission products in a long-term field study. *J. Environ. Radioact.* 10:233–249.
- Mäser, P., S. Thomine, J.I. Schroeder, J.M. Ward, K. Hirschi, H. Sze, E. Tallen, A. Amtmann, F.J. Maathuis, D. Sanders, J.F. Harper, J. Tchiew, A. Gribskovsky, M.W. Persans, D.E. Salt, S.A. Kim, and M.L. Guerinot. 2001. Phylogenetic relationships within cation transporter families of Arabidopsis. *Plant Physiol.* 126:1646–1667.
- Minitab. 2000. Minitab 13.32 for Windows. Minitab, State College, PA.
- Nishita, H., A.J. Steen, and K.H. Larson. 1958. The release of Sr-90 and Cs-137 from Vina loam upon prologued cropping. *Soil Sci.* 86:195–201.
- Papanicolaou, E.P., C.G. Apostolakis, V. Skarlou, and S. Synetos. 1990. Soil to plant transfer of radioactive cesium as determined in field samples in the Mediterranean region. p. 626–633. *In* G. Desmet, P. Nassimbeni, and M. Belli (ed.) Transfer of radionuclides in natural and semi-natural environments. Elsevier Appl. Sci., London.
- Salt, C.A., and R.B. Mayes. 1990. Seasonal patterns of Cs-134 uptake into hill pasture vegetation. p. 344–350. *In* G. Desmet, P. Nassimbeni, and M. Belli (ed.) Transfer of radionuclides in natural and semi-natural environments. Elsevier Appl. Sci., London.
- Salt, C.A., and R.W. Mayes. 1991. Seasonal variations in radiocaesium uptake by reseeded hill pasture grazed at different intensities by sheep. *J. Appl. Ecol.* 28:947–962.
- Salt, C.A., R.W. Mayes, and D.A. Elston. 1992. Effects of season, grazing intensity and diet composition on the radiocaesium intake by sheep on a reseeded hill pasture. *J. Appl. Ecol.* 29:378–387.
- Salt, C.A., and R.W. Mayes. 1993. Plant uptake of radiocaesium on heather moorland grazed by sheep. *J. Appl. Ecol.* 30:235–246.
- Skarlou, V., C. Nobeli, J. Anoussis, C. Haidouti, and E. Papanicolaou. 1999. Transfer factors of ¹³⁴Cs for olive and orange trees grown on different soils. *J. Environ. Radioact.* 45:139–147.
- Soltis, P.S., D.E. Soltis, and M.W. Chase. 1999. Angiosperm phylogeny inferred from multiple genes as a research tool for comparative biology. *Nature (London)* 402:402–404.
- SPSS. 1999. SPSS 10.0 for Windows. SPSS, Chicago.
- Starr, C. 2000. Powerful reactions. Millennium essay. *Nature (London)* 406:679.
- Strand, P., and C.-M. Larsson. 2001. Delivering a framework for the protection of the environment from ionising radiation. p. 131–145. *In* F. Brechignac and B. Howard (ed.) Radioactive pollutants—Impact on the environment. EDP Sciences, France.
- Tang, S.R., and X.C. Wang. 2002. Interaction between copper and radiocaesium in Indian mustard and sunflower grown in the hydroponic solution. *J. Radioanal. Nucl. Chem.* 252:9–14.
- Tang, S., and N.J. Willey. 2003. The uptake of Cs by species of Amaranthaceae and Asteraceae from two Chinese soils. *Plant Soil* 250: 75–81.
- Thompson, R., and S.J. Welham. 2001. REML analysis of mixed models. p. 413–503. *In* R.W. Payne (ed.) The guide to Genstat—Part 2. Statistics. VSN Int., Oxford.
- Tikhomirov, F.A., I.T. Moiseev, and R.M. Aleksakhin. 1981. Fundamental principles of the behaviour of Cs-137 in the soil and its migration into agricultural crops. *Biol. Bull.* 8:59–64.
- VAG International. 2000. Genstat for Windows Fifth Edition Release 4.2. VAG Int., Oxford, UK.
- Weaver, C.M., N.D. Harris, and L.R. Fox. 1981. Accumulation of strontium and caesium by kale as a function of plant age. *J. Environ. Qual.* 10:95–98.
- White, P.J., and M.R. Broadley. 2000. Mechanisms of caesium uptake by plants. *New Phytol.* 147:241–256.
- Whital, J. 2001. Biomonitoring. *Nature (London)* 411:989–990.
- Willey, N.J., S.C. Hall, and A. Mudiganti. 2001. Assessing the potential of phytoextraction at a site in the UK contaminated with ¹³⁷Cs. *Int. J. Phytorem.* 3:321–333.
- Willey, N.J., and M.H. Martin. 1997. A comparison of caesium uptake by six grass species of contrasting growth strategy. *Environ. Pollut.* 95:311–317.