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A phylogenetic effect on strontium concentrations in angiosperms

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Abstract

A Residual Maximum Likelihood (REML) procedure was used to compile Sr concentrations in 103 plant species from experiments with Sr concentrations in 66 plant species from the literature. There were 14 species in common between experiments and the literature. The REML procedure $\log_e$-transformed data and removed absolute differences in Sr concentrations arising from soil factors and exposure times to estimate mean relative Sr concentrations for 155 species. One hundred and forty-two species formed a group with a normal frequency distribution in mean relative Sr concentration. A nested hierarchical analysis of variance (ANOVA) based on the most recent molecular phylogeny of the angiosperms showed that plant species do not behave independently for Sr concentration but that there is a significant phylogenetic effect on mean relative Sr concentrations. Concentrations of Sr in non-Eudicots were significantly less than in Eudicots and there were significant effects on Sr concentrations in the dataset down the phylogenetic hierarchy to the family level. Of the orders in the dataset the Cucurbitales, Lamiales, Saxifragales and Ranunculales had particularly high Sr concentrations and the Liliales, Poales, Myrtales and Fabales particularly low Sr concentrations. Mean relative Sr concentrations in 60 plant species correlated with those reported elsewhere for Ca in the same species, and the frequency distribution and some phylogenetic effects on Sr concentration in plants were similar to those reported for Ca. This analysis of mean relative Sr concentrations in 155 plant species across the angiosperm phylogeny might be helpful for modelling ^{90}Sr in food chains, predicting radiological doses to flora, and selecting species for phytomonitoring and phytoremediation of ^{90}Sr.

Keywords: Strontium; Phylogeny; Radioecology; Calcium; Phytoremediation

1. Introduction

^{90}Sr is amongst the most radioecologically significant isotopes released into terrestrial ecosystems (Kliashtorin et al., 1994). It is a chemical analogue of Ca which is accumulated by microbes, plants and animals to fulfil essential physiological functions (White and Broadley, 2003). The 28.8 year half-life and high energy β-emissions of ^{90}Sr mean that it can be a significant long-term radiological hazard to the biosphere. ^{90}Sr is available to the soil solution in almost any mineral soil it contaminates (Frissel, 1992), transport is rapid (Kliashtorin et al., 1994), and transfer to plants high (Ban-nai and Muramatsu, 2002). In the Khyshtym accident zone ^{90}Sr is the most common contaminating radioisotope (Karavaeva et al., 1994; Tikhomirov and Shcheglov, 1994) and in the Chernobyl exclusion zone ^{90}Sr is a significant contributor to radioactive contamination (Anspaug et al., 1988; Kashparov et al., 1999). ^{90}Sr-contaminated land also occurs at some nuclear test sites (e.g. Walker et al., 1997) and nuclear facilities (e.g. Poston et al., 1998). Routine releases from nuclear facilities frequently contain some ^{90}Sr, and there is much ^{90}Sr in nuclear waste. Understanding soil-to-plant transfer of ^{90}Sr is critical to understanding its behaviour in terrestrial ecosystems, and therefore, to environmental assessments of accidental releases, to monitoring regimes, and to environmental impact assessments of nuclear waste disposal programmes. It has also long been clear that increases of two- or three-fold in plant uptake of ^{90}Sr might make it possible to decontaminate soils of ^{90}Sr using plant uptake (Romney et al., 1957; Nishita et al., 1958; Fuhrmann et al., 2002). Soil properties clearly affect soil-to-plant transfer of ^{90}Sr (Abbazov et al., 1978; Roca et al., 1997; Askbrant and Sandalls, 1998) but differences between plant species in uptake from the same soil have also long been known to make a significant contribution to differences in soil-to-plant transfer (Andersen,

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1967; Garret et al., 1971; Veresoglou et al., 1995). Here, we present a phylogenetic analysis of inter-species differences in Sr concentrations in plants.

Molecular phylogenetics and improved algorithms for inter-taxa comparisons are transforming our understanding of the evolutionary history of the living world (Sugden et al., 2003). There are now available new phylogenies of the angiosperms (Soltis et al., 1999; Kuzoff and Gasser, 2000; APGII, 2003). Many inter-species comparisons, and the statistics they are based on, assume that species are independent sampling units (Ackerley, 1999). The mapping of inter-species comparisons to new phylogenies of flowering plants shows that this assumption is frequently violated (Harvey et al., 1996; Ackerley, 1999), i.e. numerous inter-species comparisons reveal a phylogenetic effect on phenotype. Not only have phylogenetic effects been described in plant phenotypes such as photosynthetic pathway (Ehleringer and Monson, 1993), carnivory (Albert et al., 1992), N-fixing symbioses (Doyle, 1998), mycorrhizal symbioses (Fitter and Moyerson, 1996) and ecological traits (Ackerley, 1999), but also in the uptake of $^{134/137}$Cs (Broadley et al., 1999; Willey et al., 2005), heavy metals (Broadley et al., 2001), Al (Jansen et al., 2002), Ca (Broadley et al., 2003) and a range of nutrients (Broadley et al., 2004). It has been noted that phylogenies might be useful to estimating radionuclide transfer to plants (Beresford et al., 2004; Willey et al., 2005). Sr concentrations in different plant species are an inter-species comparison yet to be analysed phylogenetically. Such an analysis might be useful given that post-Chernobyl studies clearly revealed the importance of a range of species in semi-natural ecosystems to dose assessment models (Desmet et al., 1990), there is increasing focus on radiological dose assessments to a range of flora (Strand and Larsson, 2001) and growing interest in finding plant species that might optimise phytoextraction of ^{90}Sr (Willey et al., 2001).

^{90}Sr's chemical analogue Ca is a plant macronutrient. Ca is accumulated from the soil solution into shoots through a combination of symplastic pathways mediated by Ca channels (White, 1998) and apoplastic pathways (White, 2001). Angiosperm shoot Ca concentration generally varies between 0.1 and 5% on a dry weight basis (Marschner, 1995). Dicots have long been thought to accumulate Ca to higher concentrations than monocots, at least partly because of the higher cation exchange capacity of their roots (White and Broadley, 2003). Broadley et al. (2003), using a new angiosperm phylogeny, showed that there was a significant phylogenetic effect on angiosperm shoot Ca content and that Eudicots tend to accumulate Ca to higher concentrations than the Commelinid Monocots. Much inter-taxa variation in Ca content occurred at the level of order and above, with the orders Cucurbitales, Brassicales, Malvales and Rosales having with the highest Ca content.

Broadley et al. (2003) demonstrated the importance that phylogenetic effects in the variation of Ca concentration in angiosperms might have for predicting transfer coefficients and managing human dietary intakes of Ca. Given that Ca and Sr are known to behave similarly during soil-to-plant transfer (Andersen, 1967; Veresoglou et al., 1995, 1996), we hypothesised that there is a phylogenetic effect on Sr concentrations in plants and that this might be useful for predicting transfer coefficients, managing dietary intakes and selecting plants for phytoextraction of ^{90}Sr. Here, using the same statistical methods as Broadley et al. (2003), we report an analysis for 103 taxa we grew and 66 taxa from the literature, that quantifies a phylogenetic effect on Sr content of angiosperms and compares it to that of Ca.

2. Methods

Literature reports of inter-species comparisons in Sr concentrations of any isotope were compiled with data we generated for ^{85}Sr using the Residual Maximum Likelihood (REML) procedure of Broadley et al. (1999, 2001, 2003, 2004). Nine publications were identified that reported, without the possibility of foliar contamination, a comparison of concentrations of a Sr isotope in green shoots in two or more plant species growing on the same substrate under identical conditions. In five of these, more than one comparison was reported (e.g. from different soil types or with different levels of additives to soil). These were treated as separate studies in the REML to give 45 studies in total, including 66 species, from the literature (Table 1). Different isotopes of Sr were used in different studies but were all included in the database on the assumption that plants did not discriminate between isotopes of Sr. Plant exposure times to Sr in literature studies varied from days to weeks but might all be classified as 'chronic exposure' although in no instance was it established that uptake had reached steady-state.

One hundred and three species, chosen to complement those in literature studies by increasing the taxonomic spread across comparisons, were radiolabelled with ^{85}Sr. Five replicate pots of each species, with approximately 250 g of Levingtons's F2 (Fisons, Ipswich, UK) per pot, were grown in a greenhouse for approximately 7 weeks in 16 h day and 8 h nights at c. 24 and 16 °C, respectively. Plants were labelled with ^{85}Sr in the exponential phase of their growth and before they flowered, hence some species were slightly younger or older than 7 weeks. Species chosen were primarily fast growing and herbaceous but also included as wide a range of food crops as practicable. Plants were watered on demand up to the day before labelling. Plants were radiolabelled by putting 50 ml of 250 μM $SrCl_2$ (radiolabelled with 1110 kBq l^{-1} ^{85}Sr) evenly onto the substrate surface. This saturated the substrate, ensured homogenous distribution and produced a small volume of excess radiolabelled solution which was prevented from escaping from the pots by saucers. Excess solution in saucers was reabsorbed during the labelling period in all instances. Plants were harvested after 3 h, approximately 1 cm above the substrate surface, weighed fresh, dried for at least 48 h at 80 °C, weighed dry, ground and a weighed amount analysed for ^{85}Sr γ-emissions in an LKB

Table 1
Mean relative concentrations from REML analysis for 155 plant species from 58 studies according to the Angiosperm Phylogeny Group classification (APG, 2003)

Class	Subclass	Group	Superorder	Order	Genus and species	Common name	Mean relative concentration	Study
Non-Eudicots	Magnoliids		Magnoliids	Piperales	*Peperomia hederaefolia*	Ivy Peperomia	4.35	5
					Peperomia rotundifolia	Round-lvd peperomia	3.58	12
					Houttynia cordata	Houttynia	3.01	1
				Magnoliales	*Michelia maudiae*	Michelia	3.30	3
				Laurales	*Calycathus floridus*	Carolina Allspice	2.22	2
					Calycathus occidentalis	Western spice bush	3.74	3
					Chimonanthus praecox	Wintersweet	3.21	4
	Monocots		Non-Commelinids	Asparagales	*Crocosmia masonorum*	Montbretia	1.43	5
					Tigridia pavonia	Peacock flower	−0.01	6
					Asparagus officinalis	Asparagus	2.21	13
				Dioscorales	*Dioscorea japonica*	Yam	4.48	1
				Liliales	*Allium ameloprasum*	Wild Leek	3.08	3
					Allium cepa	Onion	0.62	3, 13, 57
					Allium porrum	Leek	−0.50	57
					Allium scheonoprasum	Chives	−0.35	3, 57
					Allium tuberosum	Garlic chives	2.85	4
			Commelinids	Arecales	*Areca lutescens*	Areca palm	3.41	1
					Phoenix dactylifera	Date	0.57	5
				Commelinales	*Commelina coelestris*	Blue spiderwort	3.87	1
				Poales	*Carex comens*	Bronze sedge	4.95	7
					Carex stricta	Tussock Sedge	1.80	4
					Cyperus 'Zumila'	Cyperus	4.01	1
					Agrostis capillaries	Common Bent	2.96	49–55
					Anthoxanthum odoratum	Sweet Vernal Grass	2.58	44, 46, 48–56
					Avena sativa	Oats	2.55	14, 15, 36–40, 57
					Cynodon dactylon	Bermuda Grass	2.70	14
					Cynosaurus cristatus	Cested Dog's Tail	2.74	36, 38
					Dactylis glomerata	Cock's Foot	2.42	43–57
					Digitaria decumbens	Pangola Grass	3.03	14
					Digitaria sanguinalis	Crab Grass	2.97	14
					Festuca pratense	Meadow Fescue	2.59	57
					Holcus lanatus	Yorkshire Fog	2.44	49, 56
					Hordeum distichum	Spring Barley	2.40	15, 36–40
					Hordeum sativum	Barley	2.17	57
					Lolium perenne	Rye grass	2.92	1, 43–48, 57
					Oryza sativa	Rice	2.04	20–35, 57
					Panicum miliaceum	Common Millet	2.05	57
					Paspalum notatum	Bahia Grass	2.02	14
					Paspalum dilitatum	Dallis Grass	2.55	14
					Pennisetum typhoides	Pearl Millet	1.23	58
					Phleum pratense	Timothy Grass	2.83	36–40, 57
					Secale cereale	Rye	2.38	15
					Sorghum vulgare	Sorghum	1.31	11, 58
					Triticum aestivum	Wheat	2.58	6, 15, 20–35
					Triticum durum	Durum wheat	2.15	6

Table 1 (*Continued*)

Class	Subclass	Group	Superorder	Order	Genus and species	Common name	Mean relative concentration	Study
					Triticum vulgare	Wheat	1.65	57
					Zea mays	Maize	2.03	42, 57
				Zingiberales	*Canna indica*	Canna lily	3.22	4
					Musa ensete	Ethiopian banana	3.20	8
					Zingiber officinale	Ginger	0.58	5
				Alismatales	*Philodendron hastatum*	Elephant's Ear Philodendron	4.88	13
					Scindapsis aureus	Devil's Ivy	0.27	9
EUDICOTS		Basal		Ranunculales	*Papaver pilosum*	Hairy poppy	8.58	9
					Papaver somniferum	Opium poppy	5.67	13
					Pulsatilla vulgaris	Pasque flower	4.28	9, 13
				Proteales	*Grevillea robusta*	Silk oak	6.29	10
		Core		Caryophyllales	*Amaranthus retroflexus*	Redroot Pigweed	1.72	41
					Beta vulgaris	Beet	3.09	1, 8, 57, 36–40, 57
					Spinacia oleracea	Spinach	3.61	37–40
					Fagopyrum esculentum	Buckwheat	3.16	36, 38
					Rheum tartaricum	Rhubarb	2.94	1
					Rumex acetosa	Sorrel	7.33	2
					Rumex crispus	Curled Dock	2.41	43–48
					Rumex sanguineus	Bloodwort	3.27	2
					Dianthus seguiri	Pink	2.73	2
					Dianthus gratinopolis	Cheddar pink	−1.16	3
					Gypsophila elegans	Baby's tears	5.40	10
					Gypsophila paniculata	Baby's Breath	4.02	5
					Silene chalcedonica	Maltese Cross	9.22	8
		Rosids	Basal	Saxifragales	*Bergenia cordifolia*	Heartleaf Bergenia	8.38	13
					Bergenia purpurescens	Bergenia	7.27	6
					Heuchera micrantha	Alum-root	4.77	12
					Heuchera sanguinea	Coral Bells	5.85	2
				Geraniales	*Geranium pyrenaicum*	Pyrenian cranesbill	4.94	8, 12
				Myrtales	*Callistemon subdulatus*	Tonghi bottle-brush	2.70	2
					Clarkia bottea	Farewell-to-Spring	1.51	9
					Oenothera hookeri	Giant Yellow evening primrose	2.24	3
					Oenothera tetragona	Evening primrose	4.41	11
			Eurosid I	Malpighiales	*Hypericum olympicum*	Dwarf St. John's Wort	4.69	5
					Hypericum perforatum	St. John's Wort	−1.86	4
					Linum usitatissimum	Flax	2.94	2, 57
					Passiflora caerulescens	Passion flower	8.19	5
					Viola tricolor	Pansy	3.25	1
				Fabales	*Anthyllis vulneraria*	Kidney Vetch	4.04	57
					Lotus corniculatus	Bird's Foot Trefoil	3.61	43–57
					Lupinus angustifolia	Lupin	3.73	1, 6
					Lupinus luteus	Yellow lupin	2.97	57
					Medicago lupulina	Black medik	0.53	11
					Medicago sativa	Alfalfa	3.51	43–48, 57
					Phaseolus acutifolius	Tepary Beans	4.23	41
					Phaseolus vulgaris	Pinto Beans	2.71	57

Table 1 (*Continued*)

Class	Subclass	Group	Superorder	Order	Genus and species	Common name	Mean relative concentration	Study
					Pisum sativum	Peas	3.87	36–40, 57
					Trifolium arvense	Hare's foot clover	3.70	8
					Trifolium hybridum	Alsike Clover	3.20	57
					Trifolium repens	White clover	−3.29	3, 11, 14, 43–57
					Trifolium subterranean	Subterranean Clover	3.21	49–56
					Trifolium pratense	Red clover	3.79	6, 10, 36–40, 57
					Vicia sativa	Commen Vetch	3.12	57
				Rosales	*Humulus japonicus*	Japanese hop	5.08	12
					Humulus lupulus	Hop	5.81	6
					Cannabis sativa	Hemp	3.73	57
					Elaeagnus multiflora	Cherry Silverberry	0.74	2
					Maclura pomifera	Osage orange	−0.78	7
					Morus alba	White mulberry	4.32	7
					Fragaria vesca	Strawberry	3.61	1, 3, 7
					Pilea cadierei	Aluminum Plant	5.95	9
				Cucurbitales	*Cucurbita maxima*	Pumpkin 'Blue Hubbard'	6.01	5
					Cucurbita pepo	Marrow	6.63	3, 42
			Eurosid II	Brassicales	*Alyssum montanum*	Mountain Madwort	2.79	2
					Alyssum petraeum	Golden Tuft	5.98	9
					Alyssum saxatile	Basket of Gold	0.25	3
					Armoracia rusticana	Horseradish	2.61	57
					Brassica juncea	Indian Mustard	3.44	41
					Brassica napus	Rape	1.01	57
					Brassica oleracea	Cabbage	2.50	4, 9, 36–40, 57
					Brassica rapa	Chinese Cabbage	3.16	16–19
					Raphanus sativus	Radish	2.68	16–19, 36–40, 57
					Sinapsis alba	White Mustard	3.34	36–40, 57
					Tropaeolum perigrinum	Canary creeper	5.37	5
				Malvales	*Cistus palhinhae*	St. Vincent Cistus	3.29	10
					Althaea rosea	Hollyhock	3.49	1
					Althaea rugosa	Hollyhock	3.26	10
					Malva sylvestris	Common mallow	4.72	4
				Sapindales	*Pistachia chinensis*	Chinese pistachio	6.14	12
					Ruta graveolens	Rue	1.07	7
		Asterids	Basal	Ericales	*Camellia sinensis*	Camelia (Tea)	0.47	10
			Euasterid II	Apiales	*Anethum graveolens*	Dill	2.72	57
					Anthriscus cerefolium	Chervil	3.70	57
					Apium graveolens	Celery	4.45	2, 57
					Coriandrum sativum	Coriander	7.55	12
					Daucus carota	Carrot	3.16	1, 36–40, 57
					Petroselinum crispum	Parsley	3.08	57
					Hedera helix	Ivy	1.59	5
				Asterales	*Centaurea cyanus*	Cornflower	3.87	2
					Cichorum intybus	Chicory	3.67	49–56

Table 1 (*Continued*)

Class	Subclass	Group	Superorder	Order	Genus and species	Common name	Mean relative concentration	Study
					Helianthus annuus	Sunflower	4.62	7, 57
					Helianthus debilis	Sunflower 'Vanilla ice'	5.16	11
					Lactuca sativa	Lettuce	3.79	13, 36–40
					Tithonia rotundifolia	Mexican sunflower	4.79	1, 10
			Euasterid I	Solanales	*Ipomoea purpurea*	Purple morning glory	4.44	6, 7
					Nemophila menziesii	Baby blue eyes	4.02	3
					Lycopersicon esculentum	Tomato	5.03	4, 57
					Nicotiana glauca	Yellow tree tobacco	5.05	3, 4, 6, 7
					Nicotiana sylvestris	Tobacco	3.70	3
					Solanum sisymbrifolium	Sticky Nightshade	4.34	6
					Solanum tuberosum	Potato	3.51	36–40, 57
				Lamiales	*Mentha piperata*	Peppermint	5.26	3, 12
					Mentha spicta	Spearmint	6.72	13
					Salvia officinalis	Sage	3.20	1
					Plantago major	Geater Plantain	4.00	43–56
					Plantago lanceolata	Ribwort Plantain	3.92	43–56
					Antirrhinum majus	Snapdragon	8.71	3
					Digitalis ambigua	Large Yellow foxglove	3.86	3

Study numbers: 1–13; *Experiments for this paper*. 14; Garret et al. (1971). 15; Krouglev et al. (1997). 16–19; Choi et al. (1998), *four treatments*. 20–35; Abbazov et al. (1978), 16 *soil types*. 36–40; Freddricksson and Erikson (1957), *four treatments*. 41, Fuhrmann et al. (2002). 42, Fresquez et al. (1998). 43–49; Veresoglou et al. (1995), *2 × 3 treatments*. 49–56, Veresoglou et al. (1996), *2 × 4 treatments*. 57, Andersen (1967). 58, Sachdev et al. (1998).

Wallac 'Compugamma 1282' with appropriate blanks and background corrections. Experimental plants were, therefore, acutely exposed to ^{85}Sr. Labelling of species took place in 13 batches (each of which was treated as a separate study in the REML analysis) using a randomised block design in an arena with light supplemented to c. 350 $\mu Em^{-1}\,s^{-1}$. Of the 103 species, 14 were also in the 66 species in literature studies. The whole Sr database (Table 1), therefore, included 155 taxa across 58 studies, derived from both the literature and experiment. Many taxa had multiple measurements in the database but some taxa had single measurements (Table 1).

Each of the 58 studies was used as a separate 'block' in the REML analysis and the species unit was used as the 'treatment' in the REML analysis, i.e. even if values for separate varieties were reported for a species they were coded as a single species. REML analysis was run on the statistical package Genstat for Windows 5th Ed. release 4.2 (VSN International, Oxford, UK) (Thompson and Welham, 2001) using the programme of Broadley et al. (1999, 2001, 2003, 2004). Defining blocks and treatments in this way accounts for the absolute differences in values arising from blocks (experimental conditions) to reveal mean relative values for the treatments (species). REML analyses can produce mean relative concentrations that are both positive and negative (Thompson and Welham, 2001). Following REML transformation a nested ANOVA was carried out coded using the updated phylogeny of the Angiosperm Phylogeny Group (2003). The categories 'class', 'subclass', 'group' and 'superorder' (Table 1) were used nominally for units above the level of the order although the relationship between the Linnaean hierarchy they derive from and higher groups on recent phylogenies is contentious. Normality statistics used an Anderson–Darling test on Minitab 13.0 for Windows, in which standardised residual tests, correlation and linear regressions were also performed.

3. Results

Table 1 shows the mean relative concentrations of Sr in 155 species derived from REML analysis. There was significant inter-species variation overall, and in the 103 species labelled under similar conditions in experiments ($P < 0.005$ for One-way ANOVAs). Mean relative concentrations for the 155 species failed the Anderson–Darling test for normality ($A^2 = 1.718$; $P < 0.001$; Fig. 1). However, as indicated by their large standardised residuals, removing seven species with distortingly large values (*Silene chalcedonica*, *Antirrhinum majus*, *Papaver somniferum*, *Bergenia cordifolia*, *Passiflora caerulescens*, *Coriandrum sativum*, *Rumex sanguineus*) and six points with distortingly small values (*Allium tuberosum*, *Allium schoenoprasum*, *Maclura pomifera*, *Dianthus seguiri*, *Hypericum olympicum*, *Trifolium arvense*) produced a core data set for 142 taxa with a normal distribution ($A^2 = 0.648$;

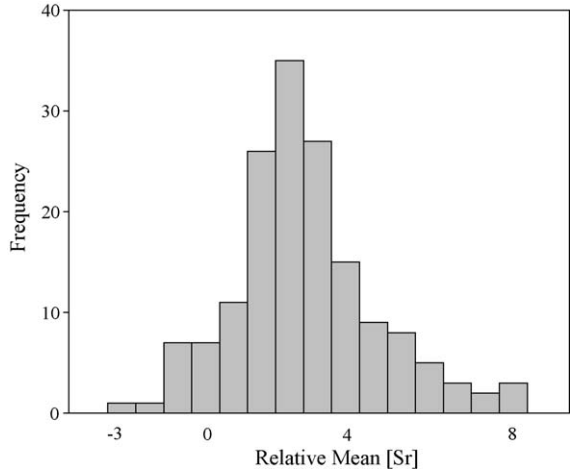

Fig. 1. The frequency distribution of mean relative Sr concentrations in 155 angiosperm species (15 divisions used, approximate mean relative Sr concentrations across divisions marked on *x*-axis).

$P = 0.089$). All data were included in subsequent analysis because ANOVA is relatively robust to the assumption of normality.

There was a significant phylogenetic effect in the mean relative concentrations for Sr at all levels of the phylogenetic hierarchy down to the family (Table 2). There was a significant difference between non-Eudicots and Eudicots (Fig. 2a; Table 2), and the Monocots had the lowest mean relative Sr concentration of any 'Group' (Fig. 2b; Table 2). The mean relative Sr concentrations in the Commelinid monocots were significantly less than those of the Eudicots ($T = 3.66$, d.f. = 135, $P < 0.001$). Of the orders represented in the dataset the Cucurbitales, Lamiales, Saxifragales and Ranunculales had high mean relative Sr concentrations whilst the Asparagales, Liliales, Poales, Myrtales and Fabales had low mean relative Sr concentrations (Fig. 2c). Overall, the analysis indicated that about 15% of inter-taxa variation in Sr concentrations in plants was at the level of the order or above, 28% at the family or above, and a particularly large proportion of the variation (47%) at the level of genus (Table 2).

The inter-species variation in Sr concentrations in plants is significantly related to inter-species variation in Ca concentration. There are 60 species in the database reported here

Table 2
Percent variation in Sums of Squares of Sr concentrations in plants and significance of ANOVA down the updated APG (2003) phylogeny

	SS × 10^6	%SS	Cumulative%	*F*-ratio	*P*-value
Class	5.3	2.48	2.52	17.52	<0.001
Subclass	8.6	4.02	6.50	9.18	<0.001
Group	3.17	1.48	7.98	7.22	<0.001
Superorder	8.21	3.84	11.81	6.14	<0.001
Order	8.2	3.83	15.64	2.19	0.002
Family	28.5	13.32	28.96	1.56	0.029
Genus	100	46.73	75.69	1.28	0.192
Species	37	17.29	100.00		
Total	214				

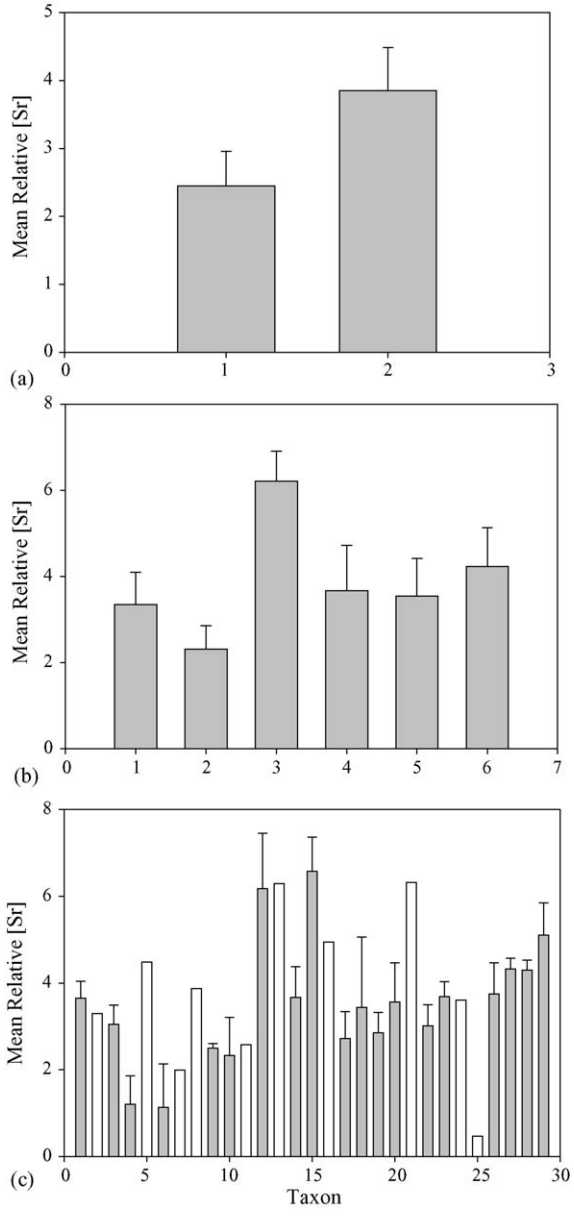

Fig. 2. Relative mean Sr concentrations in 'classes' (a), 'groups' (b) and orders (c) of flowering plants according to APG (2003) classification [(a) 'Classes' 1: non-Eudicots ($n = 53$), 2: Eudicots (102) (with 3× standard error). (b) 'Groups': 1: Magnoliids (7), 2: Monocots (46), 3: Basal Eudicots (4), 4: Core Eudicots (13), 5: Eurosids (56), 6: Euasterids (29) (with 3× standard error). (c) Orders: 1: Piperales (3), 2: Magnoliales (1), 3: Laurales (3), 4: Asparagales (3), 5: Dioscorales (1), 6: Liliales (6), 7: Arecales (2), 8: Commelinales (1), 9: Poales (28), 10: Zingiberales (3), 11: Alismatales (2), 12: Ranunculales (3), 13: Proteales (1), 14: Caryophyllales (13), 15: Saxifragales (4), 16: Geraniales (1), 17: Myrtales (4), 18: Malpighiales (5), 19: Fabales (15), 20: Rosales (8), 21: Curcurbitales (2), 22: Brassicales (11), 23: Malvales (4), 24: Sapindales (2),. 25: Ericales (1), 26: Apiales (7), 27: Asterales (6), 28: Solanales (8), 29: Lamiales (7) (with 1× standard error). Unshaded bars for orders where $n = 1$ or 2].

that are included in Broadley et al.'s (2003) dataset of relative mean values for 206 species in the literature. Fig. 3a shows that there is a significant relationship between the relative mean Ca and relative mean Sr concentrations in these taxa

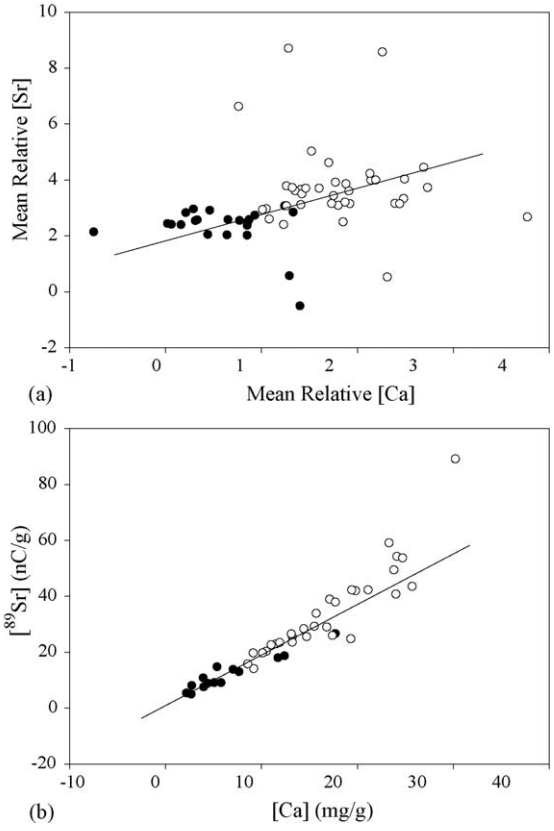

Fig. 3. (a) The relationship between mean relative Sr and mean relative Ca concentrations in 60 angiosperm taxa using Sr from Table 1 and Ca from Broadley et al.'s (2003) literature dataset (closed dots: non-Eudicots, open dots: Eudicots. $R^2 = 36.5\%$, $F = 4.14$, $P = 0.046$). (b) The relationship between Sr and Ca concentrations in 44 angiosperm taxa from Andersen's (1967) dataset (closed dots: non-Eudicots, open dots: Eudicots).

($R^2 = 36.5\%$, $F = 4.14$, $P = 0.046$). *Cucurbita maxima*, *Antirrhinum majus* and *Papaver somniferum* have distortingly high Sr to Ca ratios and *Allium schoenopraesum* and *Zingiber officinale* particularly low ones; removing these five points that have large standardised residuals improved the relationship ($R^2 = 56\%$, $F = 29.7$, $P = 0.000$). The relationship between Ca and Sr in Fig. 3a is similar to but not as close as that previously reported (e.g. Andersen, 1967 for 44 species, Fig. 3b). Fig. 3a, however, includes more diverse species than any previous inter-species comparison of Ca:Sr ratios and the variety of conditions used to produce the data may have increased variability. Fig. 3b highlights that although Ca:Sr ratios in non-Eudicots and Eudicots are similar they take up these elements to different concentrations.

4. Discussion

Much research subsequent to the accident at Chernobyl demonstrated the importance of plant species other than staple crops to assessments of radiation doses to humans (Desmet et al., 1990). There is also increased interest in estimating radiological impacts to flora because of proposals to reform assessments which assume that if humans are adequately protected then so are all other organisms (Strand and Larsson, 2001). Further, phytoremediation is increasingly being considered as a component of decontamination and decommissioning procedures and is more nearly possible for ^{90}Sr than other radioecologically significant isotopes (Willey et al., 2001; Fuhrmann et al., 2002). In all these instances, knowledge of Sr concentrations in a wide range of species is desirable. Table 1 is the most comprehensive inter-species comparison of Sr concentrations in plants yet reported. Care must be taken, however, in interpreting the mean relative Sr concentrations because of both the numerous variables that might effect relative Sr concentrations in plants and the sampling biases in species represented. For example, REML analysis, using absolute concentrations for species in different datasets, statistically accounts for the effects of different exposure conditions and estimates relative mean concentrations for each species in the datasets – in effect a rank order – but the actual rank order of species might not be identical under all conditions. This is because there might be interactions between rank order and, for example, ecological variables (Ehlken and Kirchner, 1996), growth phase at the time of Sr application (Choi et al., 1998), mycorrhizal status (Riesen and Brunner, 1996) or exposure times to Sr. So, the relative mean values in Table 1 represent a general estimate for relative mean Sr concentrations in plants across a variety of conditions and exposures (probably at 'steady-state' uptake and not) rather than for any specific set of uptake conditions. There is also sampling bias because although we attempted to increase the phylogenetic spread of data by complementing that reported in the literature (which was not collected with phylogenetic analysis in mind) with species in our experiments, the availability of fast growing herbs and a wish to try to include significant food crops meant that the dataset is not phylogenetically balanced as it does not reflect exactly the actual number of species in the different phylogenetic groups.

The effects of some of these potentially confounding factors can, however, be estimated. First, it is possible to investigate preliminarily the significance of exposure time by comparing concentrations between species in a dataset of acute exposure (such as the experiments reported here) and a dataset of chronic, 'steady-state', exposure. The dataset of chronic exposure with the most species in common with the experiments reported here is that of Andersen (1967). Following $\log_{10}$-transformation of absolute values to account for the wide range of concentrations, for nine species in common (*Allium cepa*, *Allium schoenopraesum*, *Beta vulgaris*, *Trifolium repens*, *Trifolium pratense*, *Brassica oleracea*, *Daucus carota*, *Lactuca sativa*, *Lycopersicon esculentum*) there is a positive correlation ($r = 0.714$, $P = 0.008$) between concentrations after acute (experiments reported here) and chronic (steady-state) exposures (Andersen, 1967). If acute exposure is in the exponential growth phase (as it was in our experiments), because much Sr uptake occurs during this

phase (Weaver et al., 1981) the relative concentrations it produces might be expected to be related to those following chronic exposures. Second, Broadley et al. (2003) tested whether or not phylogenetic sampling bias affected the detection of a phylogenetic effect in Ca concentrations in plants. They were able to find, with a taxonomically unbalanced literature data set of 206 taxa, phylogenetic effects in Ca concentrations in plants that were the same as those found in a phylogenetically-balanced experimentally-derived set of Ca concentrations in 117 species. The Sr data set reported here includes 155 taxa spread across the higher taxonomic groups and, therefore, seems likely to reveal phylogenetic effects at least at the higher taxonomic levels. Differences in Sr concentration have previously been related only to taxonomy at the family level (Andersen, 1967; Breulmann et al., 1999). The analysis presented here is, therefore, the first scientific attempt to describe phylogenetic effects on Sr concentrations in plants and Table 1 provides a general estimate of relative mean Sr concentrations relativised across a variety of conditions and exposures that is suitable for investigating phylogenetically. Specific investigations under particular conditions or exposures might not produce the same relative concentrations as in Table 1 and are likely to be less useful for investigating the general effects of phylogeny.

In comparison to other studies of ion concentrations in plants down to the ordinal level, the phylogenetic effect for Sr of 14.5% is greater than that for P (6.8%) and N (3.3%) (Broadley et al., 2004), similar to that for Cs (15%) (Willey et al., 2005) approaching that for Pb (20%), Cr (23%), Cu (24%), Cd (27%) (Broadley et al., 2001) and Na (23%) (Broadley et al., 2004), but significantly less than that for Zn (44%), Ni (46%) (Broadley et al., 2001), Ca (63%) (Broadley et al., 2003) and K (49%) (Broadley et al., 2004). For Sr there are significant differences in mean relative concentration between non-Eudicots and Eudicots (Figs. 2a and 3a), and between the Commelinid monocot and Eudicots, just as for Ca there were differences between the Commelinid monocots and Eudicots (Broadley et al., 2003). For Ca such differences have been ascribed to differences in root cation exchange capacities (e.g. White and Broadley, 2003) and the Sr patterns described here are consistent with this, and with Nisbet and Woodman's (2000) finding that cereals (Poales in the Commelinid monocots) have particularly low transfer factors for ^{90}Sr. Testing whether or not root cation exchange capacity is related to differences in Sr concentrations might, therefore, be a fruitful avenue of research for attempts to elucidate the controlling mechanisms on ^{90}Sr concentrations in plants. There are further significant phylogenetic effects down to the family level (Table 2). Specific tests between groups at each level necessitate more extensive sampling than is often present in Table 1, but of the orders represented in the dataset the Cucurbitales, Lamiales, Saxifragales and Ranunculales had high mean relative Sr concentrations (Fig. 2c). This indicates that these plants might merit particular attention in assessments of doses to flora and in the search for plants suitable for phytoremediation and phytomonitoring of ^{90}Sr. The Asparagales, Liliales, Poales, Myrtales and Fabales had low mean relative Sr concentrations (Fig. 2c) and might be a source of 'safe crops' for ^{90}Sr contaminated soil. Broadley et al. (2003) noted that concentrations of Ca in the Cucurbitales were high and in the Poales and Myrtales were low, relative to the other orders in their dataset.

Sr and Ca are chemically closely related and there are numerous reports that they behave as chemical analogues in a variety of plants (e.g. Andersen, 1967; Bauer et al., 1998; Knoblauch et al., 2001). This accounts for the fact that Sr, like Ca, is often located apoplastically in plants, is found in the highest concentrations in leaves (Von Firks et al., 2002) and is transported primarily in the xylem (Herren and Feller, 1997). The phylogenetic signal for Sr has clear similarities with that of Ca, including essentially normal frequency distributions, differences between non-Eudicots and Eudicots, and between some orders. Further, if the literature-derived relative mean concentrations of Broadley et al. (2003) for Ca are plotted, for the 60 species in common, against those for Sr reported here there is a clear positive relationship (Fig. 3a). This relationship is similar to that reported by Andersen (1967) for 44 species, which is the most extensive direct comparison of Sr:Ca concentrations reported and which has recently been a basis for discussions of Sr:Ca uptake mechanisms (White, 2005). In fact, Andersen's data, if classified into non-Eudicots and Eudicots, shows the same phylogenetic differences as the REML-derived relative mean Sr and Ca values (Fig. 3b). Although Andersen's data contributed to the REML analysis it contained only 16 of the 60 species in Fig. 3a. Overall, given the enormous variety of experimental conditions, including acute and chronic doses, that Fig. 3a is based on, the somewhat greater variation than in Fig. 3b is not perhaps surprising and lends support to the known strong relationship between Ca and Sr in plants. Direct comparisons of relative means for orders reported here for Sr and by Broadley et al. (2003) for Ca cannot be made because of the different orders used in the different REML procedures but Broadley et al. (2003) noted the highest Ca uptake in the Cucurbits and the lowest in the Ericales, as was the case for Sr here. Given that there were few representatives from these orders in either the dataset reported here for Sr or that of Broadley et al. (2003) for Ca, their uptake of Sr and Ca might usefully be investigated further. Broadley et al. (2003) reported low Ca in the Poales and Myrtales, as was the case for Sr here. We suggest that, in instances when plants with particularly low Sr uptake are important, it might be worth further investigating Sr uptake in these orders. In the Sr data reported here relative mean concentrations in the Fabales and Brassicales, in particular, are lower than those reported for Ca by Broadley et al. (2003). Investigations of Ca:Sr in the Fabales and Brassicales might help to establish if these differences are real or the effects on rank order of the different species in the datasets.

The results reported here for Sr, though similar to, are not, as might have been expected, identical to those for Ca. There are several reasons why this might be the case. First, the acute

Sr exposures used in experiments here produce related but not identical relative concentrations to chronically exposed plants. During acute exposures, it is less likely, for example, that uptake has reached 'steady-state' in all species. Efforts were made to ensure homogenous ^{85}Sr exposure of roots, and acute exposure occurred during the exponential phase but there is no *a priori* reason why concentrations arising from acute exposures should be identical to those arising from chronic exposures. It is notable, however, that acute exposures to Sr are of radioecological significance in their own right, particularly during immediate responses to releases of radioisotopes, and produce concentrations that are positively related to those from chronic exposure. Second, there might also be differences between Sr and Ca because of the fact that the REML process accounts for differences due to species and study but not differences arising from their interaction. Ca:Sr ratios in plants in general reflect Ca:Sr ratios in soil solution (rather than total Ca:Sr in soil), and this ratio can vary significantly with soil type even when the same total amounts are present (Veresoglou et al., 1996). Thus, interactions between soil variables such as Ca:Sr in solution and species rank order would need to be accounted for before concluding definitively that the phylogenetic signals of Ca and Sr are not identical. However, given the much wider taxonomic spread in Fig. 3a (Fig. 3b is derived primarily from four families), and especially in Table 1, compared with any previously published Sr data, and that the orders with high and low relative mean Sr concentrations were not all the same as those noted for Ca by Broadley et al. (2003), we suggest that it is worth considering a third possibility that Ca:Sr discrimination might not be identical in all plants. There are reports, primarily from the biogeochemical literature, that Sr isotopes are not exact chemical analogues of Ca in ecosystems. This is borne out by reports that discrimination between Sr and Ca can differ with trophic level (Blum et al., 2000) and that in forest cycling of Sr and Ca differences can be detected (Poswa et al., 2000). White and Broadley (2003) have recently shown that different ratios of symplast/apoplast uptake between Sr/Ca might produce different concentration ratios of Sr/Ca in plant shoots. Differences in discrimination have also been reported, for example, between other chemically similar elements such as Cs and K in different orders of plants (Broadley and Willey, 1999).

5. Conclusion

Sr concentrations in plants are essentially normally distributed but because in the REML procedure used here raw values are $\log_e$-transformed, Fig. 1 offers support to the conclusion that Sr concentrations in plant species are, more specifically, $\log_e$normally distributed (e.g. Sheppard and Evenden, 1997). The characteristics of this distribution might be useful in parametric models intended for numerous plant species. Significant differences in Sr concentrations have been reported from a single species grown on different substrates (e.g. Andersen, 1967; Abbazov et al., 1978) but we conclude that inter-species differences in Sr uptake from a single substrate are also significant. This is consistent with the findings of Nisbet and Woodman (2000) who, in an extensive review of ^{90}Sr transfer factors, noted that ^{90}Sr transfer factors differed by an order of magnitude between soil types and by a greater amount between species. Modellers of ^{90}Sr availability in soil such as Roca et al. (1997) have also noted that, in addition to soil factors, plant factors might be important to predicting soil-to-plant transfer. The mean relative concentrations reported here might provide a starting point for integrating the differences between all plant species in uptake of ^{90}Sr with the differences in ^{90}Sr availability in soils and should enable radioecological models to incorporate a wider range of plant taxa than has previously been possible for ^{90}Sr, in particular, for acute exposures.

Analysis using a recent phylogeny clearly showed that plant species not only take up Sr to different concentrations but that uptake by each species is not independent because it is linked through phylogeny. In soil-to-plant transfer models it should, therefore, be assumed neither that plant species just reflect soil ^{90}Sr availability nor that they behave independently. The phylogenetic effect suggests which plant species might merit particular attention in food production systems and be useful in assessing doses to flora from ^{90}Sr. Species with high uptake of ^{90}Sr might be useful sentinels in biomonitoring, perhaps particularly in food production systems, but the frequency distribution in Fig. 1 indicates that almost any of the species in Table 1 might be used as biomonitors to collect data for parametric models. The high uptake noted in particular orders and species of plants might help increase phytoremediation rates for ^{90}Sr as many species in these groups have not previously been assessed and the increases in soil-to-plant transfer necessary to make phytoremediation viable, at two- or three-fold, are less than for other radioisotopes such as ^{137}Cs (Fuhrmann et al., 2002). Alternatively, the low uptake of other orders might be useful in identifying safe crops for contaminated soils. Given the potential sources of variation between studies, the Sr phylogenetic signal reported here is similar to that previously reported for Ca, but we conclude that Ca:Sr ratios in uptake in a number of orders for which few data have previously been reported, might be worth further investigation—to at least put the assumption of identical behaviour of Sr and Ca in plants on a more certain phylogenetic foundation. Overall, the results reported here for Sr suggest that it might be useful for radioecologists to investigate phylogenetic effects in plant concentrations of other radioisotopes.

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