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REVIEW

Selenium accumulation by plants

Philip J. White[1,2,*]

[1]*Ecological Sciences Group, The James Hutton Institute, Invergowrie, Dundee DD2 5DA, UK and* [2]*Distinguished Scientist Fellowship Program, King Saud University, Riyadh 11451, Kingdom of Saudi Arabia*
* *For correspondence. E-mail philip.white@hutton.ac.uk*

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• **Background** Selenium (Se) is an essential mineral element for animals and humans, which they acquire largely from plants. The Se concentration in edible plants is determined by the Se phytoavailability in soils. Selenium is not an essential element for plants, but excessive Se can be toxic. Thus, soil Se phytoavailability determines the ecology of plants. Most plants cannot grow on seleniferous soils. Most plants that grow on seleniferous soils accumulate <100 mg Se kg^{-1} dry matter and cannot tolerate greater tissue Se concentrations. However, some plant species have evolved tolerance to Se, and commonly accumulate tissue Se concentrations >100 mg Se kg^{-1} dry matter. These plants are considered to be Se accumulators. Some species can even accumulate Se concentrations of 1000–15 000 mg Se kg^{-1} dry matter and are called Se hyperaccumulators.

• **Scope** This article provides an overview of Se uptake, translocation and metabolism in plants and highlights the possible genetic basis of differences in these between and within plant species. The review focuses initially on adaptations allowing plants to tolerate large Se concentrations in their tissues and the evolutionary origin of species that hyperaccumulate Se. It then describes the variation in tissue Se concentrations between and within angiosperm species and identifies genes encoding enzymes limiting the rates of incorporation of Se into organic compounds and chromosomal loci that might enable the development of crops with greater Se concentrations in their edible portions. Finally, it discusses transgenic approaches enabling plants to tolerate greater Se concentrations in the rhizosphere and in their tissues.

• **Conclusions** The trait of Se hyperaccumulation has evolved several times in separate angiosperm clades. The ability to tolerate large tissue Se concentrations is primarily related to the ability to divert Se away from the accumulation of selenocysteine and selenomethionine, which might be incorporated into non-functional proteins, through the synthesis of less toxic Se metabilites. There is potential to breed or select crops with greater Se concentrations in their edible tissues, which might be used to increase dietary Se intakes of animals and humans.

Key words: Arabidopsis, *Astragalus*, ecology, evolution, genetic variation, hyperaccumulation, metabolism, quantitative trait locus (QTL), selenium, *Stanleya*, sulphur.

INTRODUCTION: SELENIUM IN SOILS, PLANTS AND ANIMALS

Selenium (Se) is an essential mineral element for both human and animal nutrition (White and Brown, 2010). In humans, Se deficiency is associated with hypothyroidism, cardiovascular disease, a weakened immune system, male infertility, cognitive decline and increased incidence of various cancers (Fairweather-Tait *et al.*, 2011; Rayman, 2012; Fordyce, 2013). The Institute of Medicine (USA) has proposed a recommended dietary allowance of 55 μg Se d^{-1} for adult humans (Institute of Medicine, 2000). Unfortunately, it is estimated that the diets of as many as 1 billion people might lack sufficient Se for their well-being (Combs, 2001; Fairweather-Tait *et al.*, 2011; Joy *et al.*, 2014; Stoffaneller and Morse, 2015). Since much of the Se in human diets is derived, either directly or indirectly, from edible plants, the lack of Se in human diets is generally attributed to crop production on soils with low Se content or Se phytoavailability (Broadley *et al.*, 2006; White and Broadley, 2009; Chilimba *et al.*, 2011; Fairweather-Tait *et al.*, 2011; Rayman, 2012; Fordyce, 2013; Joy *et al.*, 2015).

Excessive dietary Se intakes can also be harmful to humans and animals (Fairweather-Tait *et al.*, 2011; Rayman, 2012; Fordyce, 2013). The symptoms of mild selenosis in humans include dermatitis, cracking of nails, hair loss and garlicky breath (due to exhalation of dimethylselenide), while severe selenosis can cause acute respiratory distress, myocardial infarction and renal failure. The Institute of Medicine (USA) has suggested a tolerable upper intake of 400 μg Se d^{-1} for adults (Institute of Medicine, 2000). The symptoms of selenosis in animals, which occur when they consume feed with >1–5 mg Se kg^{-1} dry matter (DM), include garlicky breath, hair loss, hoof deformation (in cattle), abnormal posture, lack of vitality, slow growth, anorexia, diarrhoea, reduced reproductive performance, fetal deformities and respiratory failure (Dhillon and Dhillon, 2003; Fordyce, 2013). Plants growing on seleniferous soils have tissue Se concentrations sufficient to cause selenosis in animals (Rosenfeld and Beath, 1964; Brown and Shrift, 1982; Dhillon and Dhillon, 2003; Fordyce, 2013).

Selenium concentrations in plants are directly related to Se phytoavailability in the soil, as witnessed by the larger Se concentrations in (1) plants growing in natural soils with greater Se phytoavailability (Rosenfeld and Beath, 1964; Brown and Shrift, 1982; Ihnat, 1989); (2) plants growing in soils anthropogenically contaminated with Se (Fang and Wu, 2004; Wu, 2004); (3) produce grown on agricultural soils with greater Se phytoavailability (Ihnat, 1989; Broadley *et al*., 2006; Williams *et al*., 2009; Lee *et al*., 2011; Garrett *et al*., 2013; Joy *et al*., 2015); and (4) produce to which soil or foliar Se fertilizers have been applied (Broadley *et al*., 2006; White and Broadley, 2009; Chilimba *et al*., 2012; Fordyce, 2013; Alfthan *et al*., 2015). Indeed, the application of inorganic Se fertilizers has been particularly effective in increasing Se concentrations in edible crops, increasing the Se content of diets and improving the Se status, and health, of both animals and humans (White and Broadley, 2009; Alfthan *et al*., 2015).

The concentration and chemical forms of Se in natural soils are determined primarily by geology (Dhillon and Dhillon, 2003; Broadley *et al*., 2006; White *et al*., 2007*b*; Fordyce, 2013; Pilbeam *et al*., 2015). Selenium concentrations in most soils lie in the range 0·01–2·0 mg Se kg^{-1}, but soils associated with particular geological features can reach concentrations of 1200 mg Se kg^{-1} (Dhillon and Dhillon, 2003; Fordyce, 2013; Pilbeam *et al*., 2015). The Se concentrations in the latter soils are toxic to many plants and they support a unique flora (Rosenfield and Beath, 1964; Brown and Shrift, 1982). Seleniferous soils are widespread in the Great Plains of the USA, Canada, South America, Australia, India, China and Russia (Dhillon and Dhillon, 2003; Fordyce, 2013; Pilbeam *et al*., 2015).

Selenate (SeO_4^{2-}) is the main water-soluble form of Se in oxic soils (pH + pe > 15), which include most cultivated soils, whereas selenite (SeO_3^{2-}) predominates in anaerobic soils with a neutral to acidic pH (pH + pe = 7·5–15), such as paddy soils (Mikkelsen *et al*., 1989; White *et al*., 2007*b*; Fordyce, 2013; Pilbeam *et al*., 2015). Selenide (Se^{2-}) species are stable only under low redox conditions (pH + pe < 7·5) and are rarely present in cultivated soils. Selenate is relatively mobile in the soil solution, but selenite is strongly absorbed by iron and aluminium oxides/hydroxides and, to a lesser extent, by clays and organic matter (Fordyce, 2013; Pilbeam *et al*., 2015). Thus, the addition of selenate to soils facilitates immediate Se accumulation by plants, while selenite provides a longer lasting Se fertilizer (Broadley *et al*., 2006; Fordyce, 2013; Pilbeam *et al*., 2015).

Selenium is not considered to be an essential element for flowering plants (angiosperms), although it is considered to be a beneficial element since it can stimulate growth, confer tolerance to environmental factors inducing oxidative stress, and provide resistance to pathogens and herbivory (Quinn *et al*., 2007; Pilon-Smits *et al*., 2009; White and Brown, 2010; El Mehdawi and Pilon-Smits, 2012; Feng *et al*., 2013). Angiosperm species have been divided into three ecological types according to their ability to accumulate Se in their tissues (Rosenfeld and Beath, 1964; Brown and Shrift, 1982; White *et al*., 2007*a*). These types are designated non-accumulator, Se-indicator and Se-accumulator species. Most angiosperm species are non-accumulator species. These species cannot tolerate tissue Se concentrations >10–100 µg Se g^{-1} DM and cannot colonize seleniferous soils (Rosenfeld and Beath, 1964; White *et al*., 2004; Dhillon and Dhillon, 2009; Fordyce, 2013). In contrast, Se-indicator species are able to tolerate tissue Se concentrations approaching 1 mg Se g^{-1} DM and colonize both non-seleniferous and seleniferous soils (Rosenfeld and Beath, 1964; Moreno Rodriguez *et al*., 2005). Tissue Se concentration in Se-indicator plants is directly related to Se phytoavailability in the soil and, therefore 'indicates' soil Se phytoavailability (cf. Baker, 1981). The distribution of Se-accumulator species is generally restricted to seleniferous soils, where their leaf Se concentrations can exceed 1 mg Se g^{-1} DM (Table 1; Rosenfeld and Beath, 1964; Brown and Shrift, 1982). These species include several members of the Asteraceae, Brassicaceae and Fabaceae, which accommodate large Se concentrations in leaf trichomes and epidermal cells (Freeman *et al*., 2006, 2010; El Mehdawi and Pilon-Smits, 2012). Several members of the Lecythidaceae family [e.g. Brazil nut (*Bertholletia excelsa* Humb. and Bonpl.), paradise nut (*Lecythis zabucajo* Aubl.), coco de mono (*Lecythis ollaria* Loefl.) and monkeypot nut (*Lecythis minor* Jacq., syn. *Lecythis elliptica* Kunth.)] are also renowned for accumulating large Se concentrations in their fruit and seed (Chang *et al*., 1995; Hammel *et al*., 1996; Dernovics *et al*., 2007). Selenium concentrations can reach 512 µg g^{-1} f. wt, which is equivalent to about 530 µg g^{-1} DM, in Brazil nuts (Chang *et al*., 1995), 5–12 mg g^{-1} DM in seeds of coco de mono (Hammel *et al*., 1996; Ferri *et al*., 2004) and 4–6 mg g^{-1} in monkeypot nuts (Dernovics *et al*., 2007; Németh *et al*., 2013). It is thought that the ability to accumulate Se arose by convergent evolution of appropriate Se transport and biochemical pathways in disparate angiosperm clades during geological periods when seleniferous soils were more widespread than they are today (Brown and Shrift, 1982; White *et al*., 2007*a*; Cappa and Pilon-Smits, 2014). Species are defined as 'Se-hyperaccumulators' if their leaves contain >1 mg Se g^{-1} DM when sampled from the natural environment (Reeves and Baker, 2000; Terry *et al*., 2000), although there is debate as to whether this threshold should be lowered to 100 µg Se g^{-1} DM (Reeves and Baker, 2000; van der Ent *et al*., 2013). Thus, species that hyperaccumulate Se are an extreme sub-set of Se-accumulator species.

SELENIUM UPTAKE, TRANSLOCATION AND METABOLISM IN PLANTS

Plant roots can take up Se as selenate (SeO_4^{2-}), selenite (SeO_3^{2-}; $HSeO_3^-$; H_2SeO_3) or organoselenium compounds, such as selenocysteine (SeCys) and selenomethionine (SeMet), but are unable to take up colloidal elemental Se or metal selenides (White and Broadley, 2009). Selenate uptake by root cells from the rhizosphere is catalysed by high-affinity sulphate transporters (HASTs) homologous to the arabidopsis (*Arabidopsis thaliana* [L.] Heynh.) AtSULTR1;1 and AtSULTR1;2 transporters (Terry *et al*., 2000; White *et al*., 2004, 2007*b*; Sors *et al*., 2005*b*; Shinmachi *et al*., 2010; Gigolashvili and Kopriva, 2014). In arabidopsis, AtSULTR1;1 contributes little to selenate uptake in S-replete plants, but its relative contribution is increased greatly when plants have insufficient S for growth (El Kassis *et al*., 2007; White *et al*., 2007*b*). Phosphate transporters, such as rice OsPT2, catalyse the uptake of $HSeO_3^-$ (Zhang *et al*., 2014), and homologues of the rice aquaporin channel OsNIP2;1 catalyse the uptake of H_2SeO_3 (Zhao *et al*., 2010; Pommerrenig *et al*., 2015).

TABLE 1. *Angiosperm species credited with the appellation of Se-(hyper)accumulator which is formally defined as a species for which plants with shoot Se concentrations >1000 mg Se kg^{-1} dry matter have been sampled from a natural environment*

Species	Authority	Synonyms	Location	Se concentration (mg Se kg^{-1} DM)	Reference
Asteraceae (Asterales)					
Dieteria canescens	(Pursh) Nutt.	*Machaeranthera ramosa*	Midwest USA	1600	Beath *et al.* (1939*a*)
Grindelia squarrosa	(Pursh) Dunal		Lower Brule Reservation, SD, USA	930	Lakin and Byers (1941)
Gutierrezia microcephala	(DC.) A.Gray		Thompson, UT, USA	1287	Beath (1943)
Oonopsis foliosa	Greene	*Haplopappus fremontii* var. *fremontii*	Lascar, CO, USA	3630	Beath *et al.* (1939*b*)
Oonopsis wardii	(A.Gray) Greene	*O. condensata*, *Haplopappus fremontii* var. *wardii*	Albany County, WY, USA	9120	Byers (1935)
Symphyotrichum ascendens	(Lindl.) G.L.Nesom		Soda Springs, ID, USA	4455	Pfister *et al.* (2013)
Symphyotrichum ericoides	(L.) G.L.Nesom	*Aster ericoides*	Pine Ridge, Fort Collins, CO, USA	1378	El Mehdawi *et al.* (2015)
Symphyotrichum lateriflorum	(L.) Á.Löve & D.Löve	*Aster multiflorus*	SD, USA	1800	Moxton *et al.* (1939)
Xylorhiza glabriuscula	Nutt.	*X. villosa*, *Machaeranthera glabriuscula*, *Aster parryi*	Huerfano County, CO, USA	1750	Byers *et al.* (1938)
Xylorhiza parryi	Greene	*Machaeranthera parryi*	Albany County, WY, USA	5390	Byers (1935)
Xylorhiza venusta	(M.E.Jones) A.Heller	*Machaeranthera venusta*	Midwest USA	3486	Rosenfeld and Beath (1964)
Fabaceae (Fabales)					
Acacia cana	Maiden		NW Queensland, Australia	1121	McCray and Hurwood (1963)
Astragalus albulus	Wooton & Standl.		La Ventana, NM, USA	530	Beath *et al.* (1941), listed by Rosenfeld and Beath (1964)
Astragalus asclepiadoides	M.E.Jones				Listed by Brown and Shrift (1982)
Astragalus beathii	C.L.Porter		Cameron, AZ, USA	3135	Beath *et al.* (1940)
Astragalus beckwithii var. *purpureus*	M.E.Jones	*A. artemisarium*	Clark County, NE, USA	970	Lakin and Byers (1941)
Astragalus bisulcatus	(Hook.) A.Gray	*A. bisulcatus* var. *bisulcatus*, *A. diholcus*, *A. scobinatulus*	Pine Ridge, Fort Collins, CO, USA	13 685	Sura-de Jong *et al.* (2015)
Astragalus bisulcatus var. *haydenianus*	(A.Gray) Barneby	*A. haydenianus*	Cuba, NM, USA	2377	Beath *et al.* (1941)
Astragalus bisulcatus var. *nevadensis*	(M.E.Jones) Barneby				Listed by Brown and Shrift (1982)
Astragalus canadensis	L.	*A. carolianus*	Las Vegas, NE, USA	1110	Byers *et al.* (1938)
Astragalus crotalariae	A.Gray	*A. limatus*	Truckhaven, CA, USA	2175	Beath *et al.* (1941)
Astragalus eastwoodiae	M.E.Jones	*A. preusii* var. *eastwoodiae*	Utah, USA	1664	Beath (1943)
Astragalus flavus	Torr. & A.Gray	*A. flavus* var. *flavus*, *A. convertiflorus* var. *flaviflorus*, *A. flaviflorus*	Aztec, NM, USA	1361	Beath *et al.* (1941)
Astragalus flavus var. *argillosus*	(M.E.Jones) Barneby	*A. argillosus*	Greenriver, UT, USA	631	Beath *et al.* (1941), listed by Brown and Shrift (1982)
Astragalus flavus var. *candicans*	A.Gray	*A. convertiflorus*	Thompson, UT, USA	1322	Beath (1943)
Astragalus grayi	S.Watson		Carbon County, WY, USA	4450	Byers (1935)
Astragalus linifolius	(Osterh.) Osterh.				Listed by Brown and Shrift (1982)
Astragalus mokiacensis	A.Gray				Listed by Brown and Shrift (1982)
Astragalus moencoppensis	M.E.Jones				Listed by Brown and Shrift (1982)
Astragalus nelsonianus	Barneby	*A. pectinatus* var. *platyphyllus*			Listed by Brown and Shrift (1982)
Astragalus oocalycis	M.E.Jones				Listed by Brown and Shrift (1982)
Astragalus osterhoutii	M.E.Jones		Kremmling, CO, USA	2678	Beath *et al.* (1940)
Astragalus pattersonii	A.Gray		Thompson, UT, USA	8512	Beath (1943)

(continued)

Table 1. *Continued*

Species	Authority	Synonyms	Location	Se concentration (mg Se kg^{-1} DM)	Reference
Astragalus pectinatus	(Hook.) G.Don		Teton County, MT, USA	5170	Williams *et al*. (1940)
Astragalus praelongus	E.Sheld.	*A. pattersoni* var. *praelongus*, *A. recedens*	Leupp, AZ, USA	4835	Beath *et al*. (1941)
Astragalus praelongus var. ellisiae	(Rydb.) B.L.Turner	*A. ellisiae*	Valmont, NM, USA.	656	Beath *et al*. (1941), listed by Brown and Shrift (1982)
Astragalus praelongus var. *longchopus*					Listed by Brown and Shrift (1982)
Astragalus preussii	A.Gray	*A. preussii* var. *preusii*, *A. preussii* var. *latus*	Thompson, UT, USA	4188	Beath (1943)
Astragalus preussii var. *laxiflorus*	A.Gray				Listed by Brown and Shrift (1982)
Astragalus racemosus	Pursh.	*A. racemosus* var. *racemosus*, *A. racemosus* var. *treleasei*	WY, USA	14 920	Knight and Beath (1937)
Astragalus racemosus var. *longisetus*	M.E.Jones				Listed by Brown and Shrift (1982)
Astragalus rafaelensis	M.E.Jones		Jensen, TX, USAA	716	Beath *et al*. (1941), listed by Brown and Shrift (1982)
Astragalus sabulosus	M.E.Jones		Thompson, UT, USA	2210	Beath *et al*. (1941)
Astragalus saurinus	Barneby				Listed by Brown and Shrift (1982)
Astragalus toanus	M.E.Jones		ID, USA	990	Lakin and Byers (1948)
Astragalus urceolatus	(Greene ex Rydb.) Greene ex Ch. Porter				Listed by Beath *et al*. (1940)
Astragalus woodruffi	M.E.Jones				Listed by Brown and Shrift (1982)
Neptunia amplexicaulis	Domin		Richmond, Queensland, Australia	4334	Knott and McCray (1959)
Brassicaceae (Brassicales)					
Cardamine hupingshanensis	K.M.Liu, L.B.Chen, H.F.Bai & L.H.Liu		Yutangba, Enshi, China	1965	Yuan *et al*. (2013)
Stanleya bipinnata	Greene	*S. pinnata* var. *gibberosa*, *S. pinnata* var. *bipinnata*	Laramie, WY, USA	2490	Beath *et al*. (1940)
Stanleya pinnata	(Pursh) Britton	*S. pinnata* var. *pinnata*	Pine Ridge, Fort Collins, CO, USA	>4000	Galeas *et al*. (2007)
Stanleya pinnata var. *integrifolia*	(E. James) Rollins	*S. integrifolia*	Vernal, UT, USA	977	Beath *et al*. (1941)
Amaranthaceae (Caryophyllales)					
Atriplex confertifolia	(Torr. & Frém.) S.Watson		Thompson, UT, USA	1734	Beath (1943)
Atriplex nuttallii	S.Watson		WY, USA	930	Beath *et al*. (1937)
Rubiaceae (Gentianales)					
Coelospermum decipiens	Baill.	*Morinda reticulata*	Cape York Peninsula, Queensland, Australia	1141	Knott and McCray (1959)
Orobanchaceae (Lamiales)					
Castilleja angustifolia var. *dubia*	A.Nelson	*C. chromosa*	Lysite, WY, USA	3460	Beath *et al*. (1941)

For each species the largest tissue Se concentration known to the author, and location of the plant that was analysed, are listed.
Species binomials, authorities and synonyms were consistent with The Plant List (http://www.theplantlist.org/) in July 2015.

Transporters that catalyse the uptake and movement of cysteine and methionine within the plant might transport SeCys and SeMet (Tegeder, 2012).

The arabidopsis genome contains at least 12 genes encoding sulphate transporters, which are divided into four distinct groups that encode proteins with contrasting physiological functions (Gigolashvili and Kopriva, 2014). An equivalent number of genes encoding sulphate transporters are likely to be present in the genomes of other angiosperms, including species that hyperaccumulate Se (Buchner *et al.*, 2004, 2010; Shinmachi *et al.*, 2010; Cabannes *et al.*, 2011; Takahashi *et al.*, 2012; Gigolashvili and Kopriva, 2014). The expression of genes encoding SULTR1;1 and SULTR1;2 generally increases in roots of non-accumulator and Se-indicator species when their growth is restricted by S supply (El Kassis *et al.*, 2007; Rouached *et al.*, 2008; Shinmachi *et al.*, 2010; Schiavon *et al.*, 2015), or when tissue Se concentrations rise (Takahashi *et al.*, 2000; Van Hoewyk *et al.*, 2005; Zhang *et al.*, 2006*a*; Rouached *et al.*, 2008; Hsu *et al.*, 2011; Inostroza-Blancheteau *et al.*, 2013). Roots of Se-hyperaccumulator species have constitutively high expression of these genes, which might account for their large selenate uptake capacity (Freeman *et al.*, 2010; Cabannes *et al.*, 2011; Schiavon *et al.*, 2015). The increased expression of genes encoding HASTs, particularly *SULTR1;1*, results in greater uptake capacity for both sulphate and selenate, and accounts for the greater tissue Se concentrations in S-starved plants compared with S-replete plants (Terry *et al.*, 2000; White *et al.*, 2004, 2007*b*; Hsu *et al.*, 2011). Sulphur-replete arabidopsis mutants lacking SULTR1;2, but not those lacking other sulphate transporters, take up less selenate and exibit greater tolerance to Se in the rhizosphere than wild-type plants (Shibagaki *et al.*, 2002; El Kassis *et al.*, 2007; Barberon *et al.*, 2008). Similarly, the expression of *OsPT2* increases in roots of plants lacking sufficient phosphorus and results in a greater capacity for selenite uptake (Zhang *et al.*, 2014), and rice mutants lacking OsPT2 take up significantly less selenite than wild-type plants (Zhang *et al.*, 2014).

To account for the characteristically greater Se/S quotient in shoots of Se-hyperaccumulator plants than in shoots of other plants growing under the same conditions (Rosenfeld and Beath, 1964; Bell *et al.*, 1992; Feist and Parker, 2001; Galeas *et al.*, 2007; White *et al.*, 2007*b*; Freeman *et al.*, 2010; Cappa *et al.*, 2014; Harris *et al.*, 2014; DeTar *et al.*, 2015; Schiavon *et al.*, 2015), it has been proposed that the complement of HASTs present in the plasma membranes of root cells differs in its selenate/sulphate selectivity between Se-hyperaccumulator and non-accumulator plants (White *et al.*, 2004, 2007*a*). Specifically, it is hypothesized that the dominant HASTs in the plasma membrane of roots of Se-hyperaccumulator plants are selective for selenate, whereas those in other angiosperms are selective for sulphate. Interestingly, Cabannes *et al.* (2011) reported that the amino acid sequence of the SULTR1 transporters cloned from all the *Astragalus* species they studied (the Se-hyperaccumulator species *A. bisulcatus* [Hook.] A. Gray, *A. crotalariae* A. Gray and *A. racemosus* Pursh., and the non-Se-hyperaccumulator species *A. glycyphyllos* L. and *A. drummondii* Hook.) differed from that of other angiosperms. In particular, they identified an alanine residue in the SULTR1 cloned from the *Astragalus* species that corresponded to a conserved glycine residue in all other transporters of the eukaryotic sulphate permease (SulP) family in a position that might determine the selectivity of this transporter. Harris *et al.* (2014) observed that increasing sulphate concentration in the rhizosphere reduced leaf molybdenum (Mo) concentration in the Se-hyperaccumulator species *Stanleya pinnata* (Pursh) Britton but not in the Se-indicator plant Indian mustard [*Brassica juncea* (L.) Czern.] which, they suggested, might reflect different specificities of the complement of selenate/sulphate/molybdate transporters in Se-hyperaccumulator species and those of other angiosperms. Conversely, increasing the molybdate concentration in the rhizosphere had no effect on shoot S concentration in the Se-hyperaccumulator species *Astragalus bisulcatus* and *A. racemosus*, but reduced shoot S concentration in congeneric non-hyperaccumulator species (DeTar *et al.*, 2015).

Selenite is rapidly converted to organoselenium compounds in the root, whereas selenate is delivered immediately to the xylem (White *et al.*, 2004; Ximénez-Embún *et al.*, 2004; Li *et al.*, 2008). Sulphate transporters homologous to arabidopsis AtSULTR2;1, AtSULTR2;2 and AtSULTR3;5 have been implicated in the long-distance transport of selenate in the xylem (Takahashi *et al.*, 2000; Gigolashvili and Kopriva, 2014). Selenium is also transported, to a very limited extent, as SeMet and selenomethionine Se-oxide (SeOMet) in the xylem (Li *et al.*, 2008). In arabidopsis, the low-affinity sulphate transporters AtSULTR2;1 and AtSULTR2;2 are thought to catalyse selenate uptake into cells within the stele, whereas AtSULTR3;5 appears to modulate the activity of AtSULTR2;1, but does not catalyse transport itself (Kataoka *et al.*, 2004*a*). The expression of *AtSULTR2;1*, *AtSULTR2;2* and their homologues in other plants is induced both by S starvation and by increasing Se availability (Takahashi *et al.*, 2000; Buchner *et al.*, 2004, 2010; Van Hoewyk *et al.*, 2005; Gigolashvili and Kopriva, 2014). Interestingly, the expression of *SULTR2* genes in roots of S-replete plants of Se-hyperaccumulating *Astragalus* species is greater than in S-replete plants of non-Se-hyperaccumulator *Astragalus* species and S-starved plants of other non-Se-hyperaccumulator species (Cabannes *et al.*, 2011). This might account for the constitutively large Se fluxes from the root to the shoot in *Astragalus* species that hyperaccumulate Se. In addition, the amino acid sequences of SULTR2 and SULTR3;4 from the Se-hyperaccumulator species *A. racemosus* and *A. bisulcatus* differ from those of the congeneric non-Se-hyperaccumulator species *A. drummondii* (Cabannes *et al.*, 2011). *Stanleya pinnata* also exhibits a high constitutive expression of *SpSULTR2;1* (Schiavon *et al.*, 2015).

Selenate is assimilated into organoselenium compounds in plastids (White *et al.*, 2007*b*; Pilon-Smits and LeDuc, 2009; Pilon-Smits, 2012). The sulphate transporter AtSULTR3;1 is localized in the chloroplast membrane (Cao *et al.*, 2013) and might catalyse selenate transport into plastids. Selenate is first activated by adenosine triphosphate sulphurylase (ATPS) to form adenosine 5'-phosphoselenate (APSe), which is then reduced to selenite by adenosine 5'-phosphosulphate reductase (APR) using reduced glutathione (GSH) as the electron donor. There are four genes encoding ATPS and three genes encoding APR in the arabidopsis genome, and equivalent numbers in the genomes of other plant species (Schiavon *et al.*, 2015). In non-accumulator and Se-indicator species, the expression of genes encoding ATPS (*APS*) decreases as S supply is reduced, whereas in Se-hyperaccumulator species, such as *S. pinnata*, they appear to be constitutively expressed (Freeman *et al*., 2010; Schiavon *et al*., 2015). Intriguingly, the expression of *APS* and several *SULTR* genes appears to be co-regulated through the expression of micro RNA (miRNA), such as miRNA395 (Paul *et al*., 2015). The conversion of selenate to selenite appears to be the rate-limiting step in the assimilation of Se into organic compounds (Pilon-Smits *et al*., 2009). Overexpressing genes encoding ATPS or APR in transgenic plants leads to the accumulation of organic Se in their leaves (Pilon-Smits *et al*., 1999*b*; Van Huysen *et al*., 2004; Bañuelos *et al*., 2005*b*; Sors *et al*., 2005*a*). Selenite is reduced to selenide enzymatically by sulphite reductase (Pilon-Smits, 2012) or non-enzymatically by reduced glutathione (Terry *et al*., 2000).

The synthesis of SeCys from serine and selenide is catalysed by cysteine synthase, an enzyme complex containing both serine acetyl transferase (SAT) and *O*-acetylserine (thiol) lyase (OAS-TL) subunits (Birringer *et al*., 2002; Sors *et al*., 2005*b*; White *et al*., 2007*b*; Ogra and Anan, 2012; Pilon-Smits, 2012). Many genes encoding enzymes in the primary S/Se assimilation pathway are upregulated when plant Se supply is increased, and often exhibit constitutively high expression in Se-hyperaccumulator species (Van Hoewyk *et al*., 2005, 2008*b*; Freeman *et al*., 2010). Selenomethionine is synthesized from SeCys and *O*-phosphohomoserine (*O*PHS) through the sequential actions of cystathionine γ-synthase (CγS), which produces selenocystathionine (SeCysta), cystathionine β-lyase (CBL), which produces selenohomocysteine (SeHCys), and methionine synthase (MTR). Selenocysteine is the most abundant form of Se in unselenized garlic (*Allium sativum* L.; Cai *et al*., 1995), and SeMet is often the most abundant form of Se in edible seeds and cereal grains (Smrkolj *et al*., 2005, 2006, 2007; Broadley *et al*., 2006; Kápolna *et al*., 2007; Rayman *et al*., 2008; Thavarajah *et al*., 2008; Zhu *et al*., 2009; Seppänen *et al*., 2010; Hart *et al*., 2011; Fairweather-Tait *et al*., 2011; Shao *et al*., 2014), in seeds of Lecythidaceae (Vonderheide *et al*., 2002; Dumont *et al*., 2006; Ferri *et al*., 2004; Németh *et al*., 2013; da Silva *et al*., 2013) and in potato (*Solanum tuberosum* L.) tubers (Gionfriddo *et al*., 2012). Selenocystathionine appears to be the most abundant form of Se in the non-Se-hyperaccumulator species *Stanleya albescens* M.E. Jones, and is also present at high concentrations in tissues of several Se-hyperaccumulator species (Birringer *et al*., 2002; Ferri *et al*., 2004; Freeman *et al*., 2006, 2010; Németh *et al*., 2013). It is also the main Se compound in cladodes and fruit of selenized prickly pear (*Opuntia ficus-indica* [L.] Mill.; Bañuelos *et al*., 2011). Interestingly, most of the Se in roots and shoots of the Se-hyperaccumulator species *Cardamine hupingshanensis* KM Liu *et al*. is found as selenocystine ($SeCys_2$; Yuan *et al*., 2013), which is also abundant in fruits of Lecythidaceae (Dumont *et al*., 2006; da Silva *et al*., 2013), and Se biofortification of some plants, such as Japanese pungent radish (*Raphanus sativus* L.), results in the formation of selenohomolanthionine from SeHCys (Ogra *et al*., 2007). Selenized brassicas, such as broccoli, cauliflower (*Brassica oleracea* L.) and black mustard (*Brassica nigra* [L.] K.Koch), can also contain large concentrations of seleno-glucosinolates and their Se-aglycons (Matich *et al*., 2012, 2015; Ouerdane *et al*., 2013), and selenosugars, possibly of cell wall origin, have also been reported in appreciable concentrations in selenized plants (Aureli *et al*., 2012).

Selenium toxicity has been attributed to the non-specific replacement of cysteine and methionine in proteins by SeCys and SeMet (Brown and Shrift, 1982; Van Hoewyk, 2013). The magnitude of this appears to be related to the tissue Se/S quotient, rather than the Se content alone (White *et al*., 2004; El Kassis *et al*., 2007). In particular, the replacement of cysteine with SeCys prevents the formation of disulphide bridges, which are essential for protein structure and function, and the replacement of cysteine with SeCys in the active site of enzymes impairs catalytic activity (Brown and Shrift, 1982; Van Hoewyk, 2013). Thus, the conversion of SeCys and SeMet to non-toxic or volatile Se metabolites can increase plant Se tolerance (Sors *et al*., 2005*b*; White *et al*., 2007*b*; Pilon-Smits and LeDuc, 2009; Van Hoewyk, 2013). Selenocysteine methyltransferase (SMT) catalyses the methylation of SeCys to Se-methylselenocysteine (SeMSeCys), and *S*-adenosyl-methionine:methionine methyl transferase (MMT) catalyses the methylation of SeMet to Se-methylselenomethionine (SeMSeMet; Sors *et al*., 2005*b*; White *et al*., 2007*b*; Pilon-Smits and LeDuc, 2009; Van Hoewyk, 2013). Genes encoding functional SMT are not thought to exist in plants with little Se tolerance, such as arabidopsis (Lyi *et al*., 2005; Van Hoewyk, 2013; Zhao *et al*., 2015), and there is only a single gene encoding MMT in the arabidopsis genome (Tagmount *et al*., 2002). The expression of *BoSMT* increases upon exposure of broccoli to selenate and correlates with the accumulation of SeMSeCys (Lyi *et al*., 2005), while differences among *Astragalus* and *Stanleya* species in their ability to accumulate Se appear to be directly correlated with SMT activity (Sors *et al*., 2005*a*, 2009; Freeman *et al*., 2010). The *AbSMT* gene appears to be expressed constitutively in *Astragalus bisulcatus* (Pickering *et al*., 2003). SeMSeCys is the most abundant form of Se in roots and shoots of Se-hyperaccumulator species, such as *A. bisulcatus* and *Stanleya pinnata* (Birringer *et al*., 2002; Pickering *et al*., 2003; Sors *et al*., 2005*a*; Freeman *et al*., 2006, 2010; Lindblom *et al*., 2013; Alford *et al*., 2014), in allium (chive, garlic, leek, onion) and brassica (broccoli, Brussels sprouts, cabbage, cauliflower, Chinese cabbage, kale) crops fertilized with either selenate or selenite (Birringer *et al*., 2002; Sugihara *et al*., 2004; Rayman *et al*., 2008; Zhu *et al*., 2009; Fairweather-Tait *et al*., 2011; Kápolna *et al*., 2012; Ávila *et al*., 2014; Thosaikham *et al*., 2014), and in leaves of other vegetable crops fertilized with selenite (Sugihara *et al*., 2004; Mazej *et al*., 2008). It is also present in large concentrations in tubers of selenized potato (Gionfriddo *et al*., 2012) and seeds of selenized legumes (Smrkolj *et al*., 2007; Shao *et al*., 2014). Selenocysteine can also be converted to alanine and elemental Se by a SeCyslyase (cpNifS) located in the chloroplast (van Hoewyk *et al*., 2008*a*; Pilon-Smits and Leduc, 2009). Although elemental Se is not commonly observed in leaves, significant amouts of elemental Se have been found in stems, nodules and roots of Se-hyperaccumulator plants grown in the presence of appropriate endosymbiotic bacteria and fungi (Valdez Barillas *et al*., 2012; Lindblom *et al*., 2013; Sura-de Jong *et al*., 2015). It is also noteworthy that plant genomes contain genes encoding putative Se-binding proteins (SBPs) that might contribute to Se tolerance in plant tissues (Agalou *et al*., 2005; Dutilleul *et al*., 2008). In the arabidopsis genome, there are three genes encoding SBPs. The expression of *AtSBP1*, and its homologues in other plants, is upregulated in response to S starvation (Hugouvieux *et al*., 2009; Byrne *et al*., 2010).

Both SeMSeCys and SeMSeMet can be conjugated with glutamate to form γ-glutamyl-SeMSeCys (γ-Glu-SeMSeCys) or γ-glutamyl-SeMSeMet (γ-Glu-SeMSeMet), or converted to dimethyldiselenide (DMSe) or dimethylselenide (DMDSe) and volatilized (Sors *et al*., 2005*b*; White *et al*., 2007*b*; Pilon-Smits and LeDuc, 2009; Ogra and Anan, 2012; Van Hoewyk, 2013). SeMSeMet can also be converted to dimethylselenonium propionate and thence to DMSe (Grant *et al*., 2004). Many Se-hyperaccumulator species, such as *A. bisulcatus* (Freeman *et al*., 2006; Alford *et al*., 2014), and allium crops (garlic, leek, onion) grown on Se-rich soils accumulate significant concentrations of γ-glutamyl-SeMeSeCys (Sugihara *et al*., 2004; Ogra *et al*., 2005; Broadley *et al*., 2006; White *et al*., 2007*b*; Rayman *et al*., 2008; Fairweather-Tait *et al*., 2011; Kápolna *et al*., 2012). In *A. bisulcatus*, the formation of γ-glutamyl-SeMeSeCys appears to be promoted by rhizobial symbiosis, which has been attributed to a greater supply of glutamate in nodulated plants (Alford *et al*., 2014). The Se compound γ-glutamyl-Secystathionine has also been reported in some Se-hyperaccumulator plants (e.g. monkeypot nuts; Dernovics *et al*., 2007). In general, Se is volatilized as DMSe in non-hyperaccumulator species and as DMDSe in Se-hyperaccumulator species (Pilon-Smits and LeDuc, 2009). There is considerable variation among angiosperms in their ability to volatilize Se (Terry *et al*., 1992; Pilon-Smits *et al*., 1999*a*; de Souza *et al*., 2000), and the production of these volatiles appears to be determined by the conversion of SeCys to SeMet, and transgenic plants overexpressing CγS volatilize more Se than untransformed plants (Pilon-Smits and LeDuc, 2009).

Selenium concentrations tend to be greatest in the younger leaves of plants and generally increase to a maximum during seedling growth, then decline before, or upon, flowering, when Se is translocated from leaves to reproductive organs (Rosenfeld and Beath, 1964; Turakainen *et al*., 2004; Galeas *et al*., 2007; White *et al*., 2007*b*; Cappa *et al*., 2014; Harris *et al*., 2014). This is consistent with transcriptional analyses suggesting that Se/S assimilation occurs predominantly in younger leaves and especially the first leaves a plant produces (White *et al*., 2007*b*). Selenium is readily redistributed in the phloem as both selenate and the organoselenium compounds SeMet and SeMSeCys (Carey *et al*., 2012). In arabidopsis, the HAST AtSULTR1;3 is thought to catalyse selenate uptake into the phloem and the expression of *AtSULTR1;3* is increased in S-deficient plants (Yoshimoto *et al*., 2003).

Most plant cells can accumulate selenate in their vacuoles. When non-accumulator plants are fertilized with selenate, much of this is translocated to the shoot and sequestered in the vacuoles of cells within the vasculature and leaf meophyll (Ximénez-Embún *et al*., 2004; Mazej *et al*., 2008). Sulphate transporters homologous to AtSULTR4;1 and AtSULTR4;2 are present in the tonoplast of plant cells and are thought to catalyse the efflux of selenate from the vacuole (Kataoka *et al*., 2004*b*; Gigolashvili and Kopriva, 2014). The expression of *AtSULTR4;1* and *AtSULTR4;2* increases both upon S starvation and when plants are exposed to Se (Van Hoewyk *et al*., 2005; Gigolashvili and Kopriva, 2014). The expression of both *SULTR4;1* and *SULTR4;2* is greater in shoots of the Se-hyperaccumulator species *Stanleya pinnata* than in the congeneric Se-indicator species *S. albescens* when grown in the presence of selenite (Freeman *et al*., 2010). Increased expression of *TaSULTR4;1* has been linked to greater grain Se concentrations in S-starved wheat than in S-replete wheat (Shinmachi *et al*., 2010). The expression of a number of genes encoding ABC transporters is increased in roots and leaves of perennial ryegrass (*Lolium perenne* L.) upon exposure to Se, and it has been suggested that some of these might be involved in the transport of Se compounds within the plant (Byrne *et al*., 2010), although there is presently no direct evidence to support this hypothesis.

THE EVOLUTION OF SELENIUM HYPERACCUMULATION

There can be considerable variation in shoot Se concentration among angiosperm species growing in the same environment (Rosenfeld and Beath, 1964; Brown and Shrift, 1982; Ihnat, 1989; White *et al*., 2004, 2007*a*; Bitterli *et al*., 2010). However, little of this variation can be attributed to systematic differences between angiosperm orders, and it is thought to reflect species-specific adaptations (White *et al*., 2004; Watanabe *et al*., 2007). In general, Se concentration in leaf tissues declines in the order Se-accumulator > Se-indicator > non-accumulator species. Differences in Se accumulation between species are most pronounced within genera containing Se-accumulator or Se-indicator plants, such as *Astragalus* and *Stanleya* (White *et al*., 2004).

When grown in the same environment, Se concentrations in leaves of Se-hyperaccumulating species are significantly greater than those of other angiosperms (Rosenfeld and Beath, 1964; Brown and Shrift, 1982; White *et al*., 2007*b*), suggesting that these species might have distinct physiological adaptations enabling this trait. Since Se-hyperaccumulating species occur in several unrelated families (Table 1; Fig. 1A), it is thought that the traits of Se tolerance and accumulation arose by convergent evolution of appropriate biochemical pathways in several angiosperm clades (Brown and Shrift, 1982; White *et al*., 2004; Cappa and Pilon-Smits, 2014). The ability to accumulate Se appears to have evolved independently in the core eudicot families Amaranthaceae (Caryophyllales), Asteraceae (Asterales), Brassicaceae (Brassicales), Fabaceae (Fabales), Orobanchaceae (Lamiales) and Rubiaceae (Gentianales). The Fabaceae contains the greatest number of species known to hyperaccumulate Se. The ability to hyperaccumulate Se appears to have evolved several times within the Asteraceae, Brassicaceae and Fabaceae (Table 1). Indeed, it even appears to have evolved several times among North American *Astragalus* (Fabaceae): in the Homaloboid Phalanx within the seleniferous Homalobi, for which it can be used as a taxonomic character (Barneby, 1964), and the Preussiani (Fig. 1B), and also within the Piptoloboid and Ceridothrix Phalanxes. The evolution of Se hyperaccumulation in *Stanleya* (Brassicaceae) has also been studied in some detail (Fig. 1C; Cappa *et al*., 2014, 2015). Cappa *et al*. (2015) have observed that Se hyperaccumulation is restricted to the *S. bipinnata*/*pinnata* clade and is likely to have evolved once and then been lost in various ecotypes, such as those described as *S. pinnata* var. *inyoensis* and *S. pinnata* var. *texana*. Cappa *et al*. (2014) reported that *S. pinnata* ecotypes differed markedly in their ability to hyperaccumulate Se and observed that the trait was restricted to populations on the east side of the continental divide. They suggested that Se hyperaccumulation could have

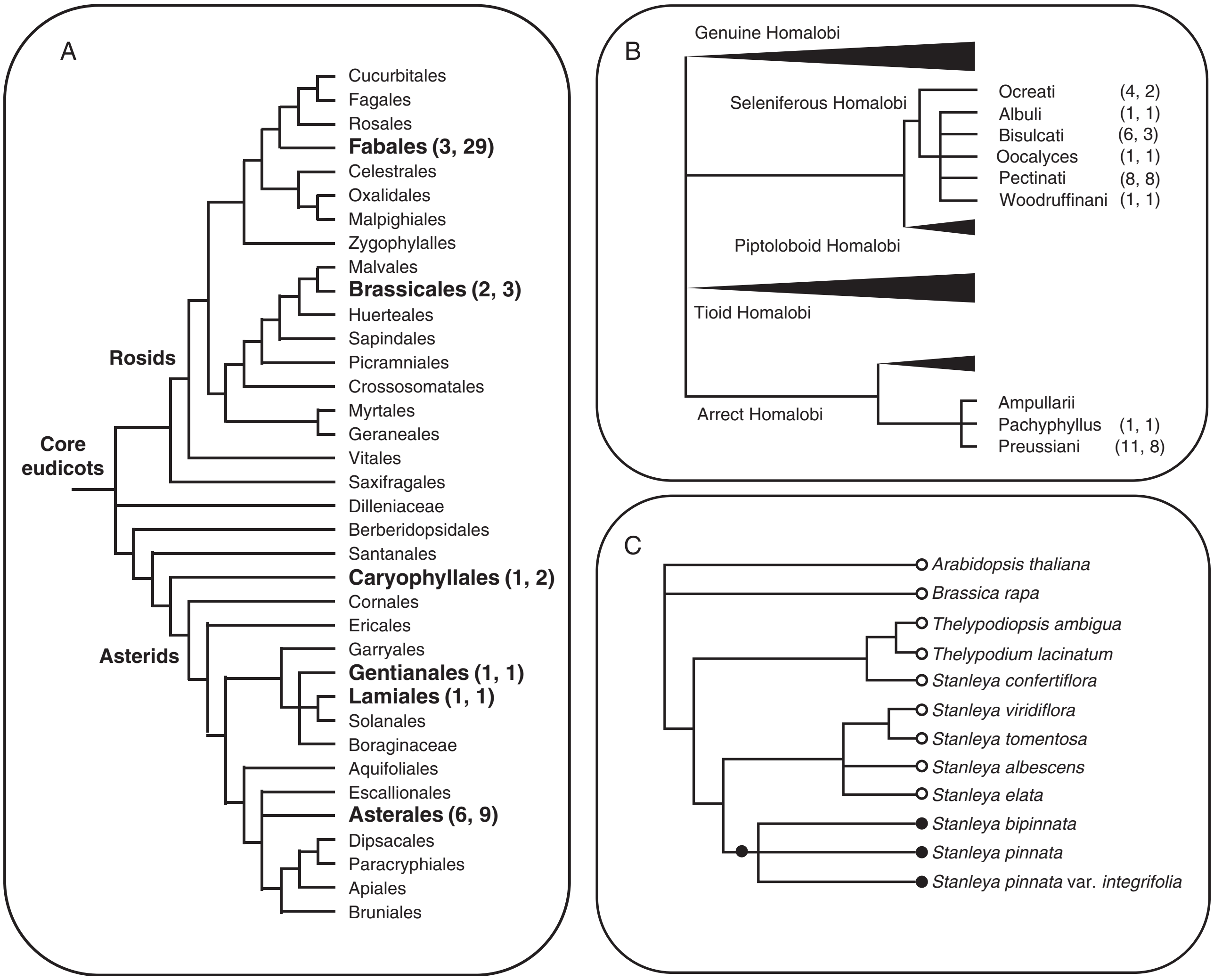

Fig. 1. (A) Distribution of proposed Se-hyperaccumulating species among angiosperm orders. Phylogenetic relationships between the angiosperm orders are reproduced from the Angiosperm Phylogeny Group (2009). The number of Se-hyperaccumulating genera and Se-hyperaccumulating species in each order are given in parentheses based on data presented in Table 1. (B) Distribution of proposed Se-hyperaccumulating taxa among sections of the Homaloboid astragali of North America. Taxonomic relationships are derived from Barneby (1964). The number of Se-hyperaccumulating taxa and Se-hyperaccumulating species in each section are given in parentheses based on data presented in Table 1. (C) Distribution of proposed Se-hyperaccumulating taxa among Brassicaceae indicating a single origin of Se hyperaccumulation (filled circles) in the *Stanleya pinnata*/*bipinnata* clade (Cappa *et al*., 2015).

evolved in eastern USA and either (*a*) the Rocky Mountains formed a geographical barrier for gene flow to the west; (*b*) a reproductive barrier prevented gene flow because of ploidy differences among populations in the east and west; or (*c*) there is a greater cost to Se hyperaccumulation in the west. Evidence suggests that the ability to tolerate large tissue Se concentrations evolved earlier than the trait of Se hyperaccumulation in *Stanleya* and might have been a necessary predisposition enabling Se hyperaccumulation (Cappa *et al*., 2015).

Several hypotheses have been proposed for the evolution of Se hyperaccumulation in plants. First, there is a clear evolutionary advantage in being one of a few stress-tolerant plant species able to colonize seleniferous soils (Brown and Shrift, 1982). This character might have occurred through the evolution of mechanisms for Se exclusion by roots, tissue Se tolerance or Se volatilization. However, although Se exclusion by roots allows non-accumulator plants to survive greater rhizosphere Se concentrations, it does not confer the ability to colonize seleniferous soils (Rosenfeld and Beath, 1964; Brown and Shrift, 1982). In contrast, the ability to accumulate Se in non-toxic forms, and to remove Se by volatilization, are characteristics shared by many Se-indicator and Se-accumulator plants that colonize seleniferous soils, and there is considerable variation in the expression of these between and among plant species (Terry *et al*., 2000; Bañuelos *et al*., 2005*a*; White *et al*. 2007*b*; Pilon-Smits and LeDuc, 2009). Since the colonization of seleniferous soils by angiosperm species appears to require the ability to tolerate Se in their tissues, it is unsurprising that biochemical pathways that restrict the incorporation of selenoamino acids into proteins through the production of non-toxic Se metabolites appear to have evolved before those of Se hyperaccumulation (Cappa *et al*., 2015). The accumulation of Se in plant tissues protects them against pathogens and herbivores (Quinn *et al*., 2007; Pilon-Smits *et al*., 2009; El Mehdawi and

Pilon-Smits, 2012), and it has been proposed that this might be the primary ecological driver for the evolution of Se hyperaccumulation (Quinn *et al.*, 2007; El Mehdawi and Pilon-Smits, 2012). It is also possible that the deposition of leaf litter with large Se concentrations around Se-hyperaccumulator plants could prevent competition by species with less tolerance of Se in the rhizosphere (El Mehdawi *et al.*, 2011).

In addition to their exceptional ability to accumulate Se, Se-hyperaccumulator species have several other characteristics that appear to distinguish them from Se-indicator and non-accumulator species. When compared with other angiosperms, Se-hyperaccumulator species (1) constitutively express genes encoding sulphate transporters (Cabannes *et al.*, 2011; Schiavon *et al.* 2015); (2) have significantly greater leaf Se/S quotients (Bell *et al.*, 1992; Feist and Parker, 2001; Galeas *et al.*, 2007; White *et al.*, 2007*a*; Freeman *et al.*, 2010; Cappa *et al.*, 2014; Harris *et al.*, 2014; DeTar *et al.*, 2015); (3) exhibit reduced Mo accumulation with increasing rhizosphere sulphate or selenate concentrations (Harris *et al.*, 2014); (4) restrict the incorporation of selenoamino acids into proteins through greater expression of appropriate genes (see 'Selenium Uptake, Translocation and Metabolism in Plants'); and (5) accumulate Se in leaf trichomes and epidermal cells (Freeman *et al.*, 2006, 2010; El Mehdawi and Pilon-Smits, 2012). These traits have been proposed as additional diagnostic characteristics for species that hyperaccumulate Se (White *et al.*, 2007*a*; El Mehdawi and Pilon-Smits, 2012; Harris *et al.*, 2014).

VARIATION IN SELENIUM ACCUMULATION WITHIN PLANT SPECIES

In addition to the considerable variation between species in their ability to accumulate Se in their tissues, there is often significant variation among genotypes of a particular species in this character. It has been observed, for example, that ecotypes of the Se-hyperaccumulator species *Stanleya pinnata* (Feist and Parker, 2001; Cappa *et al.*, 2014) and *Symphyotrichum ericoides* (L.) G.L.Nesom (El Mehdawi *et al.*, 2015) differ significantly in their leaf Se concentrations when grown in the same environment. Ecotypes collected from seleniferous soils generally have greater leaf Se concentrations and leaf Se/S quotients than ecotypes collected from soils with less Se in common garden experiments (Feist and Parker, 2001; Cappa *et al.*, 2014; El Mehdawi *et al.*, 2015). Significant genetic variation in shoot Se concentration has also been reported among tall fescue (*Festuca arundinacea* Schreb.) genotypes (McQuinn *et al.*, 1991; Wu, 1998), and it would appear that there is a negative correlation between shoot Se concentration and shoot yield in this plant species (Wu, 1998).

Arabidopsis accessions differ both in their tolerance of Se in the rhizosphere and in their shoot Se concentration when grown in the same environment (Zhang *et al.*, 2006*a*, *b*, 2007; Tamaoki *et al.*, 2008; Chao *et al.*, 2014). However, there appears to be no correlation between tolerance of Se in the rhizosphere and relative shoot Se concentration among arabidopsis accessions (Zhang *et al.*, 2007). Analyses of crosses between arabidopsis accessions suggest that a single major gene controls selenite tolerance in this species, but that at least three chromosomal quantitative trait loci (QTLs) control selenate tolerance (Zhang *et al.*, 2006*a*, *b*, 2007). Selenite tolerance in arabidopsis has been correlated with concentrations of non-protein thiols (e.g. cysteine, glutathione, phytochelatins) in roots, and tolerance to both selenate and selenite has been correlated with shoot SeCys and $SeCys_2$ concentrations (Zhang *et al.*, 2006*a*). In addition, it has been noted that the shoot S concentration of a selenite-tolerant accession of arabidopsis (Col-0) was greater than that of a selenite-sensitive accession (Ws-2) when they were exposed to selenite (Tamaoki *et al.*, 2008). This has been attributed to greater expression of genes encoding SULTR2;2, SURTR3;1 and SULTR3;5, together with several genes involved in S assimilation, in the selenite-tolerant accession than in the selenite-sensitive accession, which is consistent with the hypothesis that upregulation of the S transport and assimilation pathways is one mechanism to increase selenite tolerance (Tamaoki *et al.*, 2008). Chao *et al.* (2014) failed to identify any QTLs affecting leaf Se concentration in arabidopsis when they applied genome-wide association mapping techniques to a diverse set of 349 accessions, despite most of the variation in leaf Se concentration being accounted for by genotype (heritability 0·68) in their experiments. However, *AtAPR2* was inferred to influence leaf Se accumulation in a population of arabidopsis derived from an accession with a large leaf Se concentration (Hodonín) and the Col-0 accession using extreme array mapping (Chao *et al.*, 2014). The influence of *AtAPR2* on leaf Se accumulation was further confirmed by phenotyping mutants lacking AtAPR2 and accessions with contrasting AtAPR2 activities (Chao *et al.*, 2014). A single amino acid substitution apparently led to the loss of function of AtAPR2 and Se accumulation in leaves in the Hodonín accession (Chao *et al.*, 2014).

There also appears to be sufficient genetic variation to breed for crops that can accumulate more Se in their edible tissues (White and Broadley, 2009). Genetic variation in grain Se concentration has been reported for a number of cereals (Table 1). Although several studies have suggested little genetic variation in grain Se concentration among bread wheat (*Triticum aestivum* L.) genotypes (Table 2; Lyons *et al.*, 2005*a*; Zhao *et al.*, 2009; Lee *et al.*, 2011; Nelson *et al.*, 2011), other studies have reported significant genetic variation in this trait (Garvin *et al.*, 2006; Murphy *et al.*, 2008; Rodríguez *et al.*, 2011; Pu *et al.*, 2014). It is evident that the expression of this trait in bread wheat is strongly dependent upon weather conditions, crop husbandry and Se fertilization (Lyons *et al.*, 2005*a*; Garvin *et al.*, 2006; Zhao *et al.*, 2009; Lee *et al.*, 2011; Nelson *et al.*, 2011). In addition, there appears to be a negative relationship between grain Se concentration and grain yield among genotypes of bread wheat (Zhao *et al.*, 2007; Fan *et al.*, 2008; Murphy *et al.*, 2008), although this is not always observed (Lyons *et al.*, 2005*a*; Zhao *et al.*, 2009). No genetic variation has been observed to date in the distribution of Se within wheat grain (Lyons *et al.*, 2005*b*). Significant genetic variation in grain Se concentration has been observed in other cereals including durum wheat (*Triticum turgidum* L.; Rodríguez *et al.*, 2011), barley (*Hordeum vulgare* L.; Ilbas *et al.*, 2012; Mangan *et al.*, 2015), wild barley (*Hordeum spontaneum* K.Koch; Yan *et al.*, 2011), oat (*Avena sativa* L.; Eurola *et al.*, 2004) and rice (*Orzya sativa* L.; Zhang *et al.*, 2006*c*; Norton *et al.*, 2010, 2012).

Chromosomal loci (QTLs) influencing grain Se concentration have been identified in wheat (Yang *et al.*, 2013; Pu *et al.*,

TABLE 2. *Examples of the variation in selenium concentrations in edible tissues among genotypes of common crops grown under the same conditions*

Crop	Plant species	Tissue	Trial	Details	Selenium (mg Se kg^{-1} DM)	Genotypes	Reference
Wheat	*Triticum aestivum* L.	Grain	Field trial, Sonora, Mexico		0·045 (0·010–0·130)	$n = 100$	Lyons *et al.* (2005*a*)
Wheat	*Triticum aestivum* L.	Grain	Field trial, Sonora, Mexico		0·076 (37-120)	$n = 40$	Lyons *et al.* (2005*a*)
Wheat	*Triticum aestivum* L.	Grain	Field trial, Manhattan, KS, USA		0·045 (0·039–0·055) ns	$n = 14$	Garvin *et al.* (2006)
Wheat	*Triticum aestivum* L.	Grain	Field trial, Hutchinson, KS, USA		0·36 (0·28–0·48)***	$n = 14$	Garvin *et al.* (2006)
Wheat	*Triticum aestivum* L.	Grain	Field trial, Pullman, WA, USA		0·015 (0·002–0·030)***	$n = 63$	Murphy *et al.* (2008)
Wheat	*Triticum aestivum* L.	Grain	Field trial, Martonvásár, Hungary		0·099 (0·033–0·238)	$n = 150$	Zhao *et al.* (2009)
Wheat	*Triticum aestivum* L.	Grain	Six field trials, Europe		0·070 (0·032–0·091) ns	$n = 26$	Zhao *et al.* (2009)
Spring wheat	*Triticum aestivum* L.	Grain	Two field trials, SD, USA		0·832 (0·730–0·940) ns	$n = 10$	Lee *et al.* (2011)
Winter wheat	*Triticum aestivum* L.	Grain	Two field trials, SD, USA		0·418 (0·370–0·460) ns	$n = 8$	Lee *et al.* (2011)
Wheat	*Triticum aestivum* L.	Grain	Three field trials, Edmonton, Canada	Conventional agronomy	0·023 (0·020–0·028) ns	$n = 5$	Nelson *et al.* (2011)
Wheat	*Triticum aestivum* L.	Grain	Three field trials, Edmonton, Canada	Organic cultivation	0·131 (0·115–0·151) ns	$n = 5$	Nelson *et al.* (2011)
Wheat	*Triticum aestivum* L.	Grain	Field trial, Canary Islands		0·072 (0·032–0·130)*	$n = 11$	Rodríguez *et al.* (2011)
Wheat	*Triticum aestivum* L.	Grain	Hydroponics	10 μM Na_2SeO_4	0·232 (0·190–0·300)	$n = 20$	Souza *et al.* (2014)
Durum wheat	*Triticum turgidum* L.	Grain	Field Trial, Martonvásár, Hungary		0·081 (0·039–0·146)	$n = 10$	Zhao *et al.* (2009)
Durum wheat	*Triticum turgidum* L.	Grain	Field trial, Canary Islands		0·079 (0·031–0·154)*	$n = 8$	Rodríguez *et al.* (2011)
Einkorn wheat	*Triticum monococcum* L.	Grain	Field Trial, Martonvásár, Hungary		0·279 (0·179–0·440)	$n = 5$	Zhao *et al.* (2009)
Emmer wheat	*Triticum dicoccon* (Schrank) Schübl.	Grain	Field Trial, S. Italy		0·028 (0·018–0·035)	$n = 10$	Piergiovanni *et al.* (1997)
Emmer wheat	*Triticum dicoccon* (Schrank) Schübl.	Grain	Field Trial, Martonvásár, Hungary		0·229 (0·151–0·326)	$n = 5$	Zhao *et al.* (2009)
Spelt wheat	*Triticum spelta* L.	Grain	Field Trial, S. Italy		0·039 (0·019–0·058)	$n = 10$	Piergiovanni *et al.* (1997)
Spelt wheat	*Triticum spelta* L.	Grain	Field trial, Martonvásár, Hungary		0·209 (0·125–0·244)	$n = 5$	Zhao *et al.* (2009)
Barley	*Hordeum vulgare* L.	Grain	Field trials on loess soil, China		0·045 (0·000–0·144)	$n = 10$	Yan *et al.* (2011)
Barley	*Hordeum vulgare* L.	Grain	Field trial, Moldova	No Se fertilizer	0·111 (0·084–0·142) ns	$n = 3$	Ilbas *et al.* (2012)
Barley	*Hordeum vulgare* L.	Grain	Field trial, Moldova	12·5 g ha^{-1} Na_2SeO_3	0·218 (0·154–0·252)*	$n = 3$	Ilbas *et al.* (2012)
Wild barley	*Hordeum spontaneum* K.Koch	Grain	Field trial on loess soil, China		0·045 (0·000–0·387)	$n = 92$	Yan *et al.* (2011)
Oat	*Avena sativa* L.	Grain	Field trials, 8–10 sites × 3 years, Finland	Se fertilizer	0·110 (0·110–0·140)***	$n = 6$	Eurola *et al.* (2004)
Oat	*Avena sativa* L.	Grain	Six field trials, ND, USA		0·380 (0·310 - 0·412) ns	$n = 18$	Doehlert *et al.* (2013)
Rice	*Oryza sativa* L.	Brown grain	Field trials, Wuxi City, China		0·057 (0·029–0·103)*	$n = 151$	Zhang *et al.* (2006*c*)
Common bean	*Phaseolus vulgaris* L.	Seed	Twelve field trials, Saskachewan, Canada		0·430 (0·381–0·500) ns	$n = 9$	Ray *et al.* (2014)
Common bean	*Phaseolus vulgaris* L.	Seed	Glasshouse soil	No Se fertilizer	0·052 (0·046–0·081) ns	$n = 4$	Smrkolj *et al.* (2007)
Common bean	*Phaseolus vulgaris* L.	Seed	Glasshouse soil	Foliar Se fertilizer	2·081 (1·892–2·379) ns	$n = 4$	Smrkolj *et al.* (2007)
Field pea	*Pisum sativum* L.	Seed	Twelve field trials, Saskachewan, Canada		0·457 (0·373–0·519) ns	$n = 17$	Thavarajah *et al.* (2010)
Chickpea	*Cicer arietinum* L.	Seed	Field trials, ND, USA		0·333 (0·153–0·563)*	$n = 10$	Thavarajah and Thavarajah (2012)
Chickpea	*Cicer arietinum* L.	Seed	Ten field trials, Saskachewan, Canada		0·732 (0·629–0·846)**	$n = 8$	Ray *et al.* (2014)
Lentil	*Lens culinaris* Medik.	Seed	Sixteen field trials, Saskachewan, Canada		0·523 (0·425–0·672)	$n = 19$	Thavarajah *et al.* (2008)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Tel Hadya, Syria (2008)		0·020 (0·016–0·024)*	$n = 10$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Tel Hadya, Syria (2009)		0·025 (0·016–0·044)*	$n = 17$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Surkhet, Nepal		0·439 (0·277–0·577) ns	$n = 17$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Nawalpur, Nepal		0·064 (0·036–0·117)*	$n = 17$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Annacuur, Morocco		0·015 (0·008–0·023)*	$n = 20$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Sidi ElAidi, Morocco		0·042 (0·025–0·063)*	$n = 16$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Pullman, WA, USA		0. 026 (0·09–0·028) ns	$n = 72$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Horsham, Australia		0·255 (0·172–0·287) ns	$n = 17$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Melton, Australia		0·041 (0·027–0·063)*	$n = 17$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Diyarbakir, Turkey (2008)		0·049 (0·035–0·065)*	$n = 11$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Field trial, Sanliufa, Turkey (2009)		0·045 (0·030–0·067)*	$n = 10$	Thavarajah *et al.* (2011)
Lentil	*Lens culinaris* Medik.	Seed	Four field trials, Saskachewan, Canada		1·180 (0·970–1·637)**	$n = 18$	Ray *et al.* (2014)
Mung bean	*Vigna radiata* (L.) R.Wilczek	Seed	Field, ICRISAT, India (2012)		0·502 (0·210–0·910)**	$n = 20$	Nair *et al.* (2015)
Soybean	*Glycine max* (L.) Merr.	Seed	Field	0·111 mg Se kg^{-1} soil; Se fertilizer	6·923 (6·355–7·491)**	$n = 2$	Yang *et al.* (2003)
Indianmustard	*Brassica juncea* (L.) Czern.	Leaves	Hydroponics	2 mg L^{-1} Na_2SeO_4	707 (501–1092)*	$n = 9$	Bañuelos *et al.* (1997)
Indian mustard	*Brassica juncea* (L.) Czern.	Leaves	Field trial	Se-laden soil	543 (407–769)*	$n = 9$	Bañuelos *et al.* (1997)
Rapid-cycling Brassica	*Brassica oleracea* L.	Leaves	Hydroponics	E1: 2 mg L^{-1} Na_2SeO_4	604 (120–988)	$n = 219$	Kopsell and Randle (2001)
Rapid-cycling Brassica	*Brassica oleracea* L.	Leaves	Hydroponics	E2: 2 mg L^{-1} Na_2SeO_4	341 (152–531)**	$n = 190$	Kopsell and Randle (2001)
Broccoli	*Brassica oleracea* L. (Italica Group)	Floret	Greenhouse soil	Non-saline irrigation	0·5 (0·4–0·7) ns	$n = 4$	Bañuelos *et al.* (2003)
Broccoli	*Brassica oleracea* L. (Italica Group)	Leaves	Greenhouse soil	Non-saline irrigation, no Se	0·3 (0·2–0·5) ns	$n = 4$	Bañuelos *et al.* (2003)
Broccoli	*Brassica oleracea* L. (Italica Group)	Floret	Greenhouse soil	Non-saline irrigation, 250 μg Se L^{-1}	48 (43-51)*	$n = 4$	Bañuelos *et al.* (2003)
Broccoli	*Brassica oleracea* L. (Italica Group)	Leaves	Greenhouse soil	Non-saline irrigation, 250 μg Se L^{-1}	29 (26-31)*	$n = 4$	Bañuelos *et al.* (2003)

(continued)

TABLE 2. *Continued*

Crop	Plant species	Tissue	Trial	Details	Selenium (mg Se kg^{-1} DM)	Genotypes	Reference
Broccoli (hybrid)	*Brassica oleracea* L. (Italica Group)	Floret	Three field trials, SC, USA		0·068 (0·053–0·085)**	$n = 20$	Farnham *et al.* (2007)
Broccoli (inbreds)	*Brassica oleracea* L. (Italica Group)	Floret	Three field trials, SC, USA		0·063 (0·049–0·080) ns	$n = 15$	Farnham *et al.* (2007)
Broccoli	*Brassica oleracea* L. (Italica Group)	Leaves	Hydroponics	20 μM Na_2SeO_4	1100 (801–1798)	$n = 38$	Ramos *et al.* (2011*b*)
Onion	*Allium cepa* L.	Bulb	Hydroponics	2 mg L^{-1} Na_2SeO_4	0·085 (0·060–0·113)***	$n = 16$	Kopsell and Randle (1997)
Lettuce	*Lactuca sativa* L.	Leaves	Hydroponics	15 μM Na_2SeO_4	5·28 (2·76–7·20)	$n = 30$	Ramos *et al.* (2011*a*)
Lettuce	*Lactuca sativa* L.	Leaves	Hydroponics	15 μM Na_2SeO_3	2·87 (1·67–5·33)	$n = 30$	Ramos *et al.* (2011*a*)
Chicory	*Cichorium intybus* L.	Leaves	Aeroponics	7 mg Se L^{-1} (as Na_2SeO_4)	391 (167–480)*	$n = 4$	Mazej *et al.* (2008)
Tomato	*Solanum lycopersicum* L.	Fruit	Five glasshouses, Almería, Spain		0·188 (0·015–0·363)*	n = 8	Guil-Guerrero and Rebolloso-Fuentes (2009)
Pepper	*Capsicum annuum* L.	Fruit	Five glasshouses, Almería, Spain		0·110 (0·047–0·200)*	$n = 10$	Guil-Guerrero *et al.* (2006)
Potato	*Solanum tuberosum* L.	Tubers	Field, CO, USA		1·551 (0·014–5·816)*	$n = 8$	Perla *et al.* (2012)

Data show the mean and, in parentheses, the minimum and maximum Se concentrations for *n* genotypes. Significant differences are indicated as $^{*}P < 0{\cdot}05$, $^{**}P < 0{\cdot}01$ and $^{***}P < 0{\cdot}001$.

2014). Pu *et al.* (2014) identified four QTLs affecting grain Se concentration on chromosomes 3D at 218 cM, 4A at 91 cM, 5B at 169 cM and 7D at 215 cM in a cross between a synthetic wheat (SHW-L1) and Chuanmei 32, and a single QTL on chromosome 4D at 100 cM in a cross between Chuanmai 42 and Chuannong 16. Yang *et al.* (2013) identified four QTLs affecting grain Se concentration in a genetic mapping population derived from a cross between wild emmer wheat (*Triticum dicoccoides* [Körn. ex Asch. and Graebn.] Schweinf.) and a tetraploid durum wheat. These occurred on chromosomes 5B, 6A and 6B. Chromosomal loci affecting Se concentrations of leaves and grain of paddy rice have also been reported in a genetc mapping population derived from an indica (Bala) and a japonica (Azucena) variety (Norton *et al.*, 2010, 2012). Several QTLs were found to affect grain Se concentration in this population, although the magnitude of their effects differed between environments. Chromosomal loci affecting grain Se concentration in rice were located on chromosome 1 (27·4 and 246·4 cM), chromosome 3 (80·6 cM), chromosome 6 (12·0, 20·3 and 103·5 cM), chromosome 7 (149·8 cM), chromosome 8 (16·9 cM), chromosome 9 (61·5 cM), chromosome 10 (66·1 cM) and chromosome 11 (105·9 cM). Two of these QTLs (on C3 and C7) also influenced leaf Se concentration, suggesting that Se accumulation in leaves, and its subsequent remobilization to developing grain, could be important in determining grain Se concentrations (Norton *et al.*, 2010). None of the causal genes underpinning QTLs affecting Se accumulation in gain of wheat or rice is currently known.

Genetic variation in seed Se concentration has been reported among genotypes of several legume species (Table 2), although data from field trials indicate that genetic effects on seed Se concentration are generally small when compared with environmental effects (Thavarajah *et al.*, 2010; Garrett *et al.*, 2013; Ray *et al.*, 2014). When grown at several sites in Saskatchewan (Canada), genetic effects on seed Se concentration of common bean (*Phaseolus vulgaris* L.) or field pea (*Pisum sativum* L.) were not significant ($P > 0{\cdot}1$), although genotype × environment interactions did affect seed Se concentrations in common bean (Thavarajah *et al.*, 2010; Garrett *et al.*, 2013; Ray *et al.*, 2014). This is consistent with studies performed in the glasshouse on common bean (Smrkolj *et al.*, 2007). Similarly, no single nucleotide polymorphism (SNP) markers could be associated with variation in seed Se concentration among 94 pea genotypes grown in the field in Saskatchewan (Diapari *et al.*, 2015). In contrast, genotypic variation was found to affect seed Se concentrations in both chickpea (*Cicer arietinum* L.) and lentil (*Lens culinaris* Medik.) grown in Saskatchewan (Thavarajah *et al.*, 2008; Thavarajah and Thavarajah, 2012; Ray *et al.*, 2014; Rahman *et al.*, 2015). Significant genetic variation in seed Se concentration of lentil has also been observed in field trials conducted in other countries including Morocco, Turkey, Syria, Nepal, Australia and the USA (Thavarajah *et al.*, 2011). Significant genetic variation in seed Se concentration has also been observed among genotypes of mung bean (*Vigna radiata* [L.] R.Wilczek; Nair *et al.*, 2015) and soybean (*Glycine max* [L.] Merr.; Yang *et al.*, 2003), and two QTLs have been identified, one on chromosome 8 and another on chromosome 18, that explain about 21 % of the variation in seed Se concentration in a recombinant inbred population of soybean derived from a cross between Williams82 and DSR-173 (Ramamurthy *et al*., 2014). Interestingly, the QTL on chromosome 8 includes *GmSULTR2;1* (Ramamurthy *et al*., 2014).

Despite large environmental effects, significant genetic effects on Se concentration have been observed for onion bulbs (*Allium cepa* L.; Kopsell and Randle, 1997), leaves of rapid-cycling *Brassica oleracea* (Kopsell and Randle, 2001), broccoli florets (*B. oleracea* L. Italica Group; Bañuelos *et al*., 2003; Farnham *et al*., 2007; Ramos *et al*., 2011*b*), sprouts of cauliflower (*B. oleracea* L. Botrytis Group), kale (*B. oleracea* L. Acephala Group) and Chinese cabbage (*Brassica rapa* L.; Ávila *et al*., 2014), shoots of Indian mustard (Bañuelos *et al*., 1997), leaves of chicory (*Cichorium intybus* L.; Mazej *et al*., 2007) and leaves of lettuce (*Lactuca sativa* L.; Ramos *et al*., 2011*a*). In lettuce, the ability of genotypes to accumulate Se supplied as selenate was positively correlated with the expression of *LsSULTR1;1*, *LsAPS1* and *LsAPR1* (Ramos *et al*., 2011*a*). Significant genetic variation has also been observed in tomato (*Solanum lycopersicum* L.) fruit (Guil-Guerrero and Rebolloso-Fuentes, 2009), pepper (*Capsicum annuum* L.) fruit (Guil-Guerrero *et al*., 2006) and potato tubers (Perla *et al*., 2012).

TRANSGENIC APPROACHES TO INCREASE SELENIUM ACCUMULATION

Transgenic plants have been generated with greater Se tolerance, Se accumulation or Se volatilization than their non-transgenic counterparts (Table 3; Terry *et al*., 2000; Pilon-Smits and LeDuc, 2009; Pilon-Smits, 2012). These have been created for a variety of purposes. They have been used to provide fundamental knowledge of the transport proteins involved in the uptake and movement of Se in plants and to gain insight into the biochemical pathways and, in particular, the rate-limiting steps and control of Se metabolism in plants. The manipulation of Se transport and biochemistry can benefit crop production either directly, by allowing the development of crops with greater Se tolerance that can grow on soils with high soil Se concentrations, or indirectly, through the remediation of agricultural land with high soil Se concentrations using plants that can remove more Se from soils either by accumulating more Se in harvested tissues or by volatilizing more Se to the atmosphere. It can also benefit crop quality through Se biofortification of produce, not only by enabling greater Se concentrations to be accumulated in edible produce but also by synthesizing the most beneficial Se compounds for human and animal health.

Much of the research using transgenic plants has been directed towards the remediation of land with high soil Se concentrations (Terry *et al*., 2000; Pilon-Smits and LeDuc, 2009; Zhu *et al*., 2009; Pilon-Smits, 2012). This research has focused on (*a*) increasing plant tolerance of high soil Se concentrations; (*b*) increasing Se transport to the shoot; (*c*) increasing Se accumulation in shoot tissues; and (*d*) increasing Se volatilization. Overexpressing genes encoding transporters for selenate, selenite or selenoamino acids in the plasma membrane of particular cells can increase the capacity for Se uptake and transport within the plant. However, unless this is accompanied by an ability to tolerate greater tissue Se concentrations or volatilize more Se, it is unlikely to allow greater tolerance of Se in the rhizosphere or phytoremediation potential.

In non-accumulator plants, the conversion of selenate to selenite within plastids appears to be the rate-limiting step in the assimilation of Se into organic compounds (Pilon-Smits *et al*., 2009). Overexpression of *AtATPS1*, *PaAPR* or both *AtATPS1* and *PaAPR* in arabidopsis results in greater concentrations of organic Se in leaves, but a decrease in total leaf Se concentration (Table 3; Sors *et al*., 2005*a*) and, although overexpression of *PaAPR* results in greater tolerance of selenate in the rhizosphere in arabidopsis, the overexpression of *AtATPS1* does not (Sors *et al*., 2005*a*). In contrast, the overexpression of *AtATPS1* in Indian mustard, a Se-indicator plant, results in greater concentrations of Se and organic Se in leaves and greater tolerance of selenate in the rhizosphere (Pilon-Smits *et al*., 1999*b*; Van Huysen *et al*., 2004; Bañuelos *et al*., 2005*b*). The overexpression of genes involved in glutathione synthesis, such as glutathione synthase and γ-glutamyl-cysteine synthase, also appears to increase Se concentrations in leaves and Se tolerance of Indian mustard grown on seleniferous soils (Bañuelos *et al*., 2005*b*), whereas overexpression of cystathione-γ-synthase results in greater tolerance of selenite in the rhizosphere, reduced leaf Se concentrations and greater Se volatilization (Van Huysen *et al*., 2003, 2004).

The ability to tolerate Se in plant tissues and, thereby, to accumulate greater Se concentrations can be increased by the overexpression of genes encoding SMT, particularly if combined with overexpressing *ATPS* (Table 3). The overexpression of *SMT*, with or without the overexpression of *ATPS*, results in greater tolerance of selenite, and sometimes also selenate, in the rhizosphere, greater total Se, SeMSeCys and γ-glutamyl-SeMSeCys concentrations in leaves, and greater Se volatilization in transgenic plants compared with untransformed controls (Ellis *et al*., 2004; LeDuc *et al*., 2004, 2006; Bañuelos *et al*., 2007; Kubachka *et al*., 2007; Matich *et al*., 2009; McKenzie *et al*., 2009). The overexpression of genes encoding SeCyslyases has had variable effects on the tolerance of transgenic plants to selenate and selenite in the rhizosphere, but has consistently resulted in greater leaf Se concentrations and less Se incorporation into proteins in transgenic plants exposed to selenite or selenite than in untransformed plants (Garifullina *et al*., 2003; Pilon *et al*., 2003; Van Hoewyk *et al*., 2005; Bañuelos *et al*., 2007). Finally, the overexpression of *AtSBP1* has been shown to increase selenite tolerance in transgenic arabidopsis (Agalou *et al*., 2005).

CONCLUSIONS AND PERSPECTIVES

Selenium is an essential mineral element for the well-being of animals and a beneficial element for plants. However, excess Se can be toxic to both animals and plants. There is considerable interest in understanding how plants acquire and accumulate Se, not only to facilitate appropriate dietary Se intakes for animal and humans, which often requires Se biofortification of edible crops, but also to remediate land contaminated anthropogenically by excess Se and to appreciate the ecology of native plants inhabiting seleniferous soils. Recently, researchers have begun to identify the genetic factors influencing Se acquisition and accumulation by plants. Initially, this work focused on elucidating the genes encoding enzymes involved in Se uptake, metabolism and distribution within the plant. Application of

TABLE 3. *Phenotypes of transgenic plants overexpressing genes involved in selenium uptake and metabolism*

Overexpressed gene	Enzyme	Plant	Tolerance of Se in the rhizosphere			Leaf Se concentration			Reference
			Field soil	Selenite	Selenate	Total	Organic	Volatilization	
ShST1	Sulphate transporter	Indian mustard			No effect	Increase, selenate supply			de Souza *et al*. (2000)
AtATPS1	ATP-sulphurylase	Arabidopsis			Decrease	Decrease	Increase		Sors *et al*. (2005*a*)
AtATPS1	ATP-sulphurylase	Indian mustard	No effect		Increase	Increase	increase	No effect	Pilon-Smits *et al*. (1999*b*); Van Huysen *et al*. (2004); Bañuelos *et al*. (2005*b*)
AtATPS1	ATP-sulphurylase	Tobacco			No effect	No effect, selenate supply			McKenzie *et al*. (2009)
PaAPR	Adenosine 5′-phosphosulphate reductase	Arabidopsis			Increase	Decrease	Increase		Sors *et al*. (2005*a*)
AtATPS1 + *PaAPR*	ATP-sulphurylase + adenosine 5′-phosphosulphate reductase	Arabidopsis				Decrease	Increase		Sors *et al*. (2005*a*)
Escherichia coli gshII	Glutathione synthetase	Indian mustard	Increase			Increase			Bañuelos *et al*. (2005*b*)
Escherichia coli gshI	γ-Glutamyl-cysteine synthetase	Indian mustard	No effect			Increase			Bañuelos *et al*. (2005*b*)
TgSAT (m)	Serine acetyltransferase	Arabidopsis			No effect	Decrease	Increase		Sors *et al*. (2005*a*)
SoCS (cp)	Cysteine synthase	Indian mustard			No effect	No effect			de Souza *et al*. (2000)
AtCGS1 (cp)	Cystathionine-γ-synthase	Indian mustard	No effect	Increase	No effect	Decrease, selenite supply No effect, selenate supply		Increase	Van Huysen *et al*. (2003, 2004)
AbSMT1	SeCys methyltransferase	Arabidopsis		Increase	Increase	Increase	Increase in SeMSeCys and GluMSeCys	Increase	LeDuc *et al*. (2004); Ellis *et al*. (2004)
AbSMT	SeCys methyltransferase	Indian mustard	No effect	Increase	Increase	Increase	Increase in SeMSeCys	Increase in laboratory, no effect in field	LeDuc *et al*. (2004); Bañuelos *et al*. (2007); Kubachka *et al*. (2007)
AbSMTA	SeCys methyltransferase	Tobacco			No effect	Increase	Increase in SeMSeCys and GluMSeCys	Increase	Matich *et al*. (2009); McKenzie *et al*. (2009)
AtATPS1 + *AbSMT*	ATP-sulphurylase + SeCys methyltransferase	Indian mustard		Increase	Increase	Increase	Increase in SeMSeCys and GluMSeCys		LeDuc *et al*. (2006)
BoATPS1 + *AbSMTA*	ATP-sulphurylase + SeCys methyltransferase	Tobacco			No effect	Increase	Increase in SeMSeCys and GluMSeCys	Increase	Kubachka *et al*. (2007) Matich *et al*. (2009); McKenzie *et al*. (2009)
AtCpNifS	Cysteine lyase	Arabidopsis		No effect	Increase	Increase	Decrease in protein		Van Hoewyk *et al*. (2005)
Mus musculus SL (cp)	Selenocysteine lyase	Indian mustard	Increase	Decrease	Decrease	Increase	Decrease in protein	No effect	Garifullina *et al*. (2003); Bañuelos *et al*. (2007)
Mus musculus SL (cyt)	Selenocysteine lyase	Arabidopsis		Increase	Increase	Increase	Decrease in protein		Pilon *et al*. (2003)
Mus musculus SL (cp)	Selenocysteine lyase	Arabidopsis		Decrease	Decrease	Increase	Decrease in protein		Pilon *et al*. (2003)
AtSBP1	Selenium-binding protein	Arabidopsis		Increase					Agalou *et al*. (2005)

The phenotypes listed are tolerance of Se in the soil under field conditions, tolerance of selenite and selenate in the rhizosphere determined in laboratory experiments, effects on total Se concentration and organic Se compounds in leaves, and Se volatilization.

this knowledge has allowed the genetic manipulation of Se metabolism to increase Se accumulation in harvested tissues and Se volatilization to the atmosphere, benefitting both biofortification and phytoremediation strategies. It has also informed our appreciation of the possible mechanisms driving the evolution of species that hyperaccumulate Se in their tissues. Appreciable variation in Se concentrations in analogous tissues has been attributed to genetic factors both between and within plant species. Considerable effort is currently being invested in identifying chromosomal loci (QTLs) underlying these differences, which will enable the selection and breeding of crops with greater ability to acquire and accumulate Se in appropriate chemical forms in their edible tissues. Although our knowledge of the genetics of Se accumulation in plants appears rudimentary at present, it will increase rapidly as the modern toolbox of molecular techniques are applied. It is laudable that this effort will be built on the solid foundations of plant physiology and biochemistry.

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LITERATURE CITED

Agalou A, Roussis A, Spaink HP. 2005. The *Arabidopsis* selenium-binding protein confers tolerance to toxic levels of selenium. *Functional Plant Biology* **32**: 881–890.

Alford ÉR, Lindblom SD, Pittarello M, *et al.* 2014. Roles of rhizobial symbionts in selenium hyperaccumulation in *Astragalus* (Fabaceae). *American Journal of Botany* **101**: 1895–1905.

Alfthan G, Eurola M, Ekholm P, *et al.* 2015. Effects of nationwide addition of selenium to fertilizers on foods, and animal and human health in Finland: from deficiency to optimal selenium status of the population. *Journal of Trace Elements in Medicine and Biology* **31**: 142–147.

Angiosperm Phylogeny Group. 2009**.** An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* **161**: 105–121.

Aureli F, Ouerdane L, Bierla K, Szpunar J, Prakash NT, Cubadda F. 2012. Identification of selenosugars and other low-molecular weight selenium metabolites in high-selenium cereal crops. *Metallomics* **4**: 968–978

Ávila FW, Yang Y, Faquin V, *et al.* 2014. Impact of selenium supply on Se-methylselenocysteine and glucosinolate accumulation in selenium-biofortified Brassica sprouts. *Food Chemistry* **165**: 578–586.

Baker AJM. 1981. Accumulators and excluders – strategies in the response of plants to heavy metals. *Journal of Plant Nutrition* **3**: 643–654.

Bañuelos GS, Ajwa HA, Wu L, Guo X, Akohoue S, Zambrzuski S. 1997. Selenium-induced growth reduction in Brassica land races considered for phytoremediation. *Ecotoxicology and Environmental Safety* **36**: 282–287.

Bañuelos GS, Pasakdee S, Finley JW. 2003. Growth response and selenium and boron distribution in broccoli varieties irrigated with poor quality water. *Journal of Plant Nutrition* **26**: 2537–2549.

Bañuelos GS, Lin ZQ, Arroyo I, Terry N. 2005*a*. Selenium volatilization in vegetated agricultural drainage sediment from the San Luis Drain, Central California. *Chemosphere* **60**: 1203–1213.

Bañuelos G, Terry N, LeDuc DL, Pilon-Smits EAH, Mackey B. 2005*b*. Field trial of transgenic Indian mustard plants shows enhanced phytoremediation of selenium-contaminated sediment. *Environmental Science and Technology* **39**: 1771–1777.

Bañuelos G, LeDuc DL, Pilon-Smits EAH, Tagmount A, Terry N. 2007. Transgenic Indian mustard overexpressing selenocysteine lyase or selenocysteine methyltransferase exhibit enhanced potential for selenium phytoremediation under field conditions. *Environmental Science and Technology* **41**: 599–605.

Bañuelos GS, Fakra SC, Walse SS, *et al.* 2011. Selenium accumulation, distribution, and speciation in spineless prickly pear cactus: a drought- and salt-tolerant, selenium-enriched nutraceutical fruit crop for biofortified foods. *Plant Physiology* **155**: 315–327.

Barberon M, Berthomieu P, Clairotte M, Shibagaki N, Davidian J-C, Gosti F. 2008. Unequal functional redundancy between the two *Arabidopsis thaliana* high-affinity sulphate transporters *SULTR1;1* and SULTR1;2. *New Phytologist* **180**: 608–619

Barneby RC. 1964. *Atlas of North American Astragalus*. Volumes I and II. New York: The New York Botanical Garden.

Beath OA. 1943. Toxic vegetation growing on the salt wash sandstone member of the Morrison formation. *American Journal of Botany* **30**: 698–706.

Beath OA, Eppson HF, Gilbert CS. 1937. Selenium distribution in and seasonal variation of type vegetation occurring on seleniferous soils. *Journal of the American Pharmaceutical Association* **26**: 394–405.

Beath OA, Gilbert CS, Eppson HF. 1939*a*. The use of indicator plants in locating seleniferous areas in the Western United States. I. General. *American Journal of Botany* **26**: 257–269.

Beath OA, Gilbert CS, Eppson HF. 1939*b*. The use of indicator plants in locating seleniferous areas in the Western United States. II. Correlation studies by states. *American Journal of Botany* **26**: 296–315.

Beath OA, Gilbert CS, Eppson HF. 1940. The use of indicator plants in locating seleniferous areas in western United States. III. Further studies. *American Journal of Botany* **27**: 564–573.

Beath OA, Gilbert CS, Eppson HF. 1941. The use of indicator plants in locating seleniferous areas in western United States. IV. Progress report. *American Journal of Botany* **28**: 887–900.

Bell PF, Parker DR, Page AL. 1992. Contrasting selenate–sulfate interactions in selenium-accumulating and nonaccumulating plant species. *Soil Science Society of America Journal* **56**: 1818–1824.

Birringer M, Pilawa S, Flohé L. 2002. Trends in selenium biochemistry. *Natural Product Reports* **19**: 693–718.

Bitterli C, Bañuelos GS, Schulin R. 2010. Use of transfer factors to characterize uptake of selenium by plants. *Journal of Geochemical Exploration* **107**: 206–216.

Broadley MR, White PJ, Bryson RJ, *et al.* 2006. Biofortification of UK food crops with selenium. *Proceedings of the Nutrition Society* **65**: 169–181.

Brown TA, Shrift A. 1982. Selenium: toxicity and tolerance in higher plants. *Biological Reviews* **57**: 59–84

Buchner P, Stuiver CEE, Westermann S, *et al.* 2004. Regulation of sulfate uptake and expression of sulfate transporter genes in *Brassica oleracea* L. as affected by atmospheric H_2S and pedospheric sulphate nutrition. *Plant Physiology* **136**: 3396–3408.

Buchner P, Parmar S, Kriegel A, Carpentier M, Hawkesford MJ. 2010. The sulfate transporter family in wheat: tissue-specific gene expression in relation to nutrition. *Molecular Plant* **3**: 374–389.

Byers HG. 1935. *Selenium occurrence in certain soils in the United States with a discussion of related topics. United States Department of Agriculture Technical Bulletin 482*. Washington, DC: US Department of Agriculture.

Byers HB, Miller TJ, Williams KT, Lakin HW. 1938. *Selenium occurrence in certain soils in the United States with a discussion of related topics, third report. United States Department of Agriculture Technical Bulletin 601*. Washington, DC: US Department of Agriculture.

Byrne SL, Durandeau K, Nagy I, Barth S. 2010. Identification of ABC transporters from *Lolium perenne* L. that are regulated by toxic levels of selenium. *Planta* **231**: 901–911.

Cabannes E, Buchner P, Broadley MR, Hawkesford MJ. 2011. A comparison of sulfate and selenium accumulation in relation to the expression of sulfate transporter genes in *Astragalus* species. *Plant Physiology* **157**: 2227–2239.

Cai XJ, Block E, Uden PC, Zhang Z, Quimbly BD, Sullivan JJ. 1995. *Allium* chemistry: identification of selenoamino acids in ordinary and selenium-enriched garlic, onion, and broccoli using gas chromatography with atomic emission detection. *Journal of Agricultural and Food Chemistry* **43**: 1754–1757.

Cao MJ, Wang Z, Wirtz M, Hell R, Oliver DJ, Xiang CB. 2013. SULTR3;1 is a chloroplast-localized sulphate transporter in *Arabidopsis thaliana*. *The Plant Journal* **73**: 607–616.

Cappa JJ, Pilon-Smits EAH. 2014. Evolutionary aspects of elemental hyperaccumulation. *Planta* **239**: 267–275.

Cappa JJ, Cappa PJ, El Mehdawi AF, McAleer JM, Simmons MP, Pilon-Smits EAH. 2014. Characterization of selenium and sulfur accumulation across the genus *Stanleya* (Brassicaceae): a field survey and common-garden experiment. *American Journal of Botany* **101**: 830–839.

Cappa JJ, Yetter C, Fakra S, *et al.* 2015. Evolution of selenium hyperaccumulation in *Stanleya* (Brassicaceae) as inferred from phylogeny, physiology and X-ray microprobe analysis. *New Phytologist* **205**: 583–595.

Carey A-M, Scheckel KG, Lombi E, *et al.* 2012. Grain accumulation of selenium species in rice (*Oryza sativa* L.). *Environmental Science and Technology* **46**: 5557–5564.

Chang JC, Gutenmann WH, Reid CM, Lisk DJ. 1995. Selenium content of Brazil nuts from two geographic locations in Brazil. *Chemosphere* **30**: 801–802.

Chao D-Y, Baraniecka P, Danku J, *et al.* 2014. Variation in sulfur and selenium accumulation is controlled by naturally occurring isoforms of the key sulfur assimilation enzyme ADENOSINE 5'-PHOSPHOSULFATE REDUCTASE2 across the Arabidopsis species range. *Plant Physiology* **166**: 1593–1608.

Chilimba ADC, Young SD, Black CR, *et al.* 2011. Maize grain and soil surveys reveal suboptimal dietary selenium intake is widespread in Malawi. *Scientific Reports* **1**: 72.

Chilimba ADC, Young SD, Black CR, Meacham MC, Lammel J, Broadley MR. 2012. Agronomic biofortification of maize with selenium (Se) in Malawi. *Field Crops Research* **125**: 118–128.

Combs GF. 2001. Selenium in global food systems. *British Journal of Nutrition* **85**: 517–547.

Dernovics M, García-Barrera T, Bierła K, Preud'homme H, Lobiński R. 2007. Standardless identification of selenocystathionine and its gamma-glutamyl derivatives in monkeypot nuts by 3D liquid chromatography with ICP-MS detection followed by nanoHPLCQ-TOF-MS/MS. *Analyst* **132**: 439–449.

DeTar RA, Alford ÉR, Pilon-Smits EAH. 2015. Molybdenum accumulation, tolerance and molybdenum–selenium–sulfur interactions in *Astragalus* selenium hyperaccumulator and nonaccumulator species. *Journal of Plant Physiology* **183**: 32–40.

Dhillon KS, Dhillon SK. 2003. Distribution and management of seleniferous soils. *Advances in Agronomy* **79**: 119–184.

Dhillon KS, Dhillon SK. 2009. Accumulation and distribution of selenium in some vegetable crops grown in selenate-Se treated clay loam soil. *Frontiers of Agriculture in China* **3**: 366–373.

Diapari M, Sindhu A, Warkentin TD, Bett K, Tar'an B. 2015. Population structure and marker-trait association studies of iron, zinc and selenium concentrations in seed of field pea (*Pisum sativum* L.). *Molecular Breeding* **35**: 30.

Doehlert DC, Simsek S, Thavarajah D, Thavarajah P, Ohm J-B. 2013. Detailed composition analyses of diverse oat genotype kernels grown in different environments in North Dakota. *Cereal Chemistry* **90**: 572–578.

Dumont E, De Pauw L, Vanhaecke F, Cornelis R. 2006. Speciation of Se in *Bertholletia excelsa* (Brazil nut): a hard nut to crack? *Food Chemistry* **95**: 684–692.

Dutilleul C, Jourdain A, Bourguignon J, Hugouvieux V. 2008. The Arabidopsis putative selenium-binding protein family: expression study and characterization of SBP1 as a potential new player in cadmium detoxification processes. *Plant Physiology* **147**: 239–251.

El Kassis E, Cathala N, Rouached H, *et al.* 2007. Characterization of a selenate-resistant Arabidopsis mutant. Root growth as a potential target for selenate toxicity. *Plant Physiology* **143**: 1231–1241.

El Mehdawi AF, Pilon-Smits EAH. 2012. Ecological aspects of plant selenium hyperaccumulation. *Plant Biology* **14**: 1–10.

El Mehdawi AF, Quinn CF, Pilon-Smits EAH. 2011. Effects of selenium hyperaccumulation on plant–plant interactions: evidence for elemental allelopathy? *New Phytologist* **191**: 120–131.

El Mehdawi AF, Paschke MW, Pilon-Smits EAH. 2015. *Symphyotrichum ericoides* populations from seleniferous and nonseleniferous soil display striking variation in selenium accumulation. *New Phytologist* **206**: 231–242.

Ellis DR, Sors TG, Brunk DG, *et al.* 2004. Production of Se-methylselenocysteine in transgenic plants expressing selenocysteine methyltransferase. *BMC Plant Biology* **4**: 1.

van der Ent A, Baker AJM, Reeves RD, Pollard AJ, Schat H. 2013. Hyperaccumulators of metal and metalloid trace elements: facts and fiction. *Plant and Soil* **362**: 319–334.

Eurola M, Hietaniemi V, Kontturi M, *et al.* 2004. Selenium content of Finnish oats in 1997–1999: effect of cultivars and cultivation techniques. *Agricultural and Food Science* **13**: 46–53.

Fairweather-Tait SJ, Bao Y, Broadley MR, *et al.* 2011. Selenium in human health and disease. *Antioxidants and Redox Signaling* **14**: 1337–1383.

Fan M-S, Zhao F-J, Poulton PR, McGrath SP. 2008. Historical changes in the concentrations of selenium in soil and wheat grain from the Broadbalk experiment over the last 160 years. *Science of the Total Environment* **389**: 532–538.

Fang WX, Wu PW. 2004. Elevated selenium and other mineral element concentrations in soil and plant tissues in bone coal sites in Haoping area, Ziyang County, China. *Plant and Soil* **261**: 135–146.

Farnham MW, Hale AJ, Grusak MA, Finley JW. 2007. Genotypic and environmental effects on selenium concentration of broccoli heads grown without supplemental selenium fertilizer. *Plant Breeding* **126**: 195–200.

Feist LJ, Parker DR. 2001. Ecotypic variation in selenium accumulation among populations of *Stanleya pinnata*. *New Phytologist* **149**: 61–69.

Feng R, Wei C, Tud S. 2013. The roles of selenium in protecting plants against abiotic stresses. *Environmental and Experimental Botany* **87**: 58–68.

Ferri T, Coccioli F, De Luca C, Callegari CV, Morabito R. 2004. Distribution and speciation of selenium in *Lecythis ollaria* plant. *Microchemical Journal* **78**: 195–203.

Fordyce FM. 2013. Selenium deficiency and toxicity in the environment. In: O, Selinus B Alloway, JA Centeno, *et al*, eds. *Essentials of medical geology*, revised edn. Dordrecht: Springer, 375–416.

Freeman JL, Zhang L, Marcus MA, Fakra S, McGrath SP, Pilon-Smits EAH. 2006. Spatial imaging, speciation and quantification of Se in the hyperaccumulator plants *Astragalus bisulcatus* and *Stanleya pinnata*. *Plant Physiology* **142**: 124–134.

Freeman JL, Tamaoki M, Stushnoff C, *et al.* 2010. Molecular mechanisms of selenium tolerance and hyperaccumulation in *Stanleya pinnata*. *Plant Physiology* **153**: 1630–1652.

Galeas ML, Zhang LH, Freeman JL, Wegner M, Pilon-Smits EAH. 2007. Seasonal fluctuations of selenium and sulfur accumulation in selenium hyperaccumulators and related nonaccumulators. *New Phytologist* **173**: 517–525.

Garifullina GF, Owen JD, Lindblom SD, Tufan H, Pilon M, Pilon-Smits EAH. 2003. Expression of a mouse selenocysteine lyase in *Brassica juncea* chloroplasts affects selenium tolerance and accumulation. *Physiologia Plantarum* **118**: 538–544

Garrett RG, Gawalko E, Wang N, Richter A, Warkentin TD. 2013. Macro-relationships between regional-scale field pea (*Pisum sativum*) selenium chemistry and environmental factors in western Canada. *Canadian Journal of Plant Science* **93**: 1059–1071.

Garvin DF, Welch RM, Finley JW. 2006. Historical shifts in the seed mineral micronutrient concentration of US hard red winter wheat germplasm. *Journal of the Science of Food and Agriculture* **86**: 2213–2220.

Gigolashvili T, Kopriva S. 2014. Transporters in plant sulphur metabolism. *Frontiers in Plant Science* **5**: 422.

Gionfriddo E, Naccarato A, Sindona G, Tagarelli A. 2012. A reliable solid phase microextraction-gas chromatography–triple quadrupole mass spectrometry method for the assay of selenomethionine and selenomethylselenocysteine in aqueous extracts: difference between selenized and not-enriched selenium potatoes. *Analytica Chimica Acta* **747**: 58–66.

Grant TD, Montes-Bayón M, LeDuc D, Fricke MW, Terry N, Caruso JA. 2004. Identification and characterization of Se-methyl selenomethionine in *Brassica juncea* roots. *Journal of Chromatography A* **1026**: 159–166.

Guil-Guerrero JL, Rebolloso-Fuentes MM. 2009. Nutrient composition and antioxidant activity of eight tomato (*Lycopersicon esculentum*) varieties. *Journal of Food Composition and Analysis* **22**: 123–129.

Guil-Guerrero JL, Martínez-Guirado C, del Mar Rebolloso-Fuentes M, Carrique-Pérez A. 2006. Nutrient composition and antioxidant activity of 10 pepper (*Capsicum annuum*) varieties. *European Food Research and Technology* **224**: 1–9.

Hammel C, Kyriakopoulos A, Behne D, Gawlik D, Brätter P. 1996. Protein-bound selenium in the seeds of coco de mono (*Lecythis ollaria*). *Journal of Trace Elements in Medicine and Biology* **10**: 96–102.

Harris J, Schneberg KA, Pilon-Smits EAH. 2014. Sulfur–selenium–molybdenum interactions distinguish selenium hyperaccumulator *Stanleya pinnata* from non-hyperaccumulator *Brassica juncea* (Brassicaceae). *Planta* **239**: 479–491.

Hart DJ, Fairweather-Tait SJ, Broadley MR, *et al.* 2011. Selenium concentration and speciation in biofortified flour and bread: retention of selenium during grain biofortification, processing and production of Se-enriched food. *Food Chemistry* **126**: 1771–1778.

Hsu F-C, Wirtz M, Heppel SC, *et al.* 2011. Generation of Se-fortified broccoli as functional food: impact of Se fertilization on S metabolism. *Plant, Cell and Environment* **34**: 192–207.

Hugouvieux V, Dutilleul C, Jourdain A, Reynaud F, Lopez V, Bourguignon J. 2009. Arabidopsis putative Selenium-Binding Protein1 expression is tightly linked to cellular sulfur demand and can reduce sensitivity to stresses requiring glutathione for tolerance. *Plant Physiology* **151**: 768–781.

Ihnat M. 1989. Plants and agricultural materials. In: M Ihnat, ed. *Occurrence and distribution of selenium*. Boca Raton, FL: CRC Press, 33–105.

Ilbas AI, Yılmaz S, Akbulut M, Bogdevich O. 2012. Uptake and distribution of selenium, nitrogen and sulfur in three barley cultivars subjected to selenium applications. *Journal of Plant Nutrition* **35**: 442–452.

Inostroza-Blancheteau C, Reyes-Díaz M, Alberdi M, *et al.* 2013. Influence of selenite on selenium uptake, differential antioxidant performance and gene expression of sulfate transporters in wheat genotypes. *Plant and Soil* **369**: 47–59.

Institute of Medicine. 2000. *Dietary reference intakes for vitamin C, vitamin E, selenium, and carotenoids*. Washington DC: National Academies Press.

Joy EJM, Ander EL, Young SD, *et al.* 2014. Dietary mineral supplies in Africa. *Physiologia Plantarum* **151**: 208–229.

Joy EJM, Broadley MR, Young SD, *et al.* 2015. Soil type influences crop mineral composition in Malawi. *Science of the Total Environment* **505**: 587–595.

Kápolna E, Gergely V, Dernovics M, Illés A, Fodor P. 2007. Fate of selenium species in sesame seeds during simulated bakery process. *Journal of Food Engineering* **79**: 494–501.

Kápolna E, Laursen KH, Husted S, Larsen EH. 2012. Bio-fortification and isotopic labelling of Se metabolites in onions and carrots following foliar application of Se and ^{77}Se. *Food Chemistry* **133**: 650–657.

Kataoka T, Hayashi N, Yamaya T, Takahashi H. 2004*a*. Root-to-shoot transport of sulfate in Arabidopsis. Evidence for the role of SULTR3;5 as a component of low-affinity sulfate transport system in the root vasculature. *Plant Physiology* **136**: 4198–4204.

Kataoka T, Watanabe-Takahashi A, Hayashi N, *et al.* 2004*b*. Vacuolar sulfate transporters are essential determinants controlling internal distribution of sulfate in Arabidopsis. *The Plant Cell* **16**: 2693–2704.

Knight SH, Beath OA. 1937. *The occurrence of selenium and seleniferous vegetation in Wyoming. University of Wyoming Agricultural Experiment Station Bulletin 221*. Laramie: University of Wyoming.

Knott SG, McCray CWR. 1959. Two naturally occurring outbreaks of selenosis in Queensland. *Australian Vetinary Journal* **35**: 161–165

Kopsell DA, Randle WM. 1997. Short-day onion cultivars differ in bulb selenium and sulphur accumulation which can affect bulb pungency. *Euphytica* **96**: 385–390.

Kopsell DA, Randle WM. 2001. Genetic variances and selection potential for selenium accumulation in a rapid-cycling *Brassica oleracea* population. *Journal of the American Society for Horticultural Science* **126**: 329–335.

Kubachka KM, Meija J, LeDuc DL, Terry N, Caruso JA. 2007. Selenium volatiles as proxy to the metabolic pathways of selenium in genetically modified *Brassica juncea*. *Environmental Science and Technology* **41**: 1863–1869.

Lakin HW, Byers HG. 1941. *Selenium occurrence in certain soils in the United States with a discussion of related topics, sixth report. United States Department of Agriculture Technical Bulletin 530*. Washington, DC: US Department of Agriculture.

Lakin HW, Byers HG. 1948. *Selenium occurrence in certain soils in the United States with a discussion of related topics, seventh report. United States Department of Aghriculture Technical Bulletin 530*. Washington, DC: US Department of Agriculture.

LeDuc DL, Tarun AS, Montes-Bayon M, *et al.* 2004. Overexpression of selenocysteine methyltransferase in Arabidopsis and Indian mustard increases selenium tolerance and accumulation. *Plant Physiology* **135**: 377–383.

LeDuc DL, AbdelSamie M, Montes-Bayón M, Wu CP, Reisinger SJ, Terry N. 2006. Overexpressing both ATP sulfurylase and selenocysteine methyltransferase enhances selenium phytoremediation traits in Indian mustard. *Environmental Pollution* **144**: 70–76.

Lee S, Woodward HJ, Doolittle JJ. 2011. Selenium uptake response among selected wheat (*Triticum aestivum*) varieties and relationship with soil selenium fractions. *Soil Science and Plant Nutrition* **57**: 823–832.

Li H-F, McGrath SP, Zhao F-J. 2008. Selenium uptake, translocation and speciation in wheat supplied with selenate or selenite. *New Phytologist* **178**: 92–102.

Lindblom SD, Valdez-Barillas JR, Fakra SC, Marcus MA, Wangeline AL, Pilon-Smits EAH. 2013. Influence of microbial associations on selenium localization and speciation in roots of *Astragalus* and *Stanleya* hyperaccumulators. *Environmental and Experimental Botany* **88**: 33–42.

Lyi SM, Heller LI, Rutzke M, Welch RM, Kochian LV, Li L. 2005. Molecular and biochemical characterization of the selenocysteine *Se*-methyltransferase gene and *Se*-methylselenocysteine synthesis in broccoli. *Plant Physiology* **138**: 409–420.

Lyons G, Ortiz-Monasterio I, Stangoulis J, Graham R. 2005*a*. Selenium concentration in wheat grain: is there sufficient genotypic variation to use in breeding? *Plant and Soil* **269**: 269–380.

Lyons GH, Genc Y, Stangoulis JCR, Palmer LT, Graham RD. 2005*b*. Selenium distribution in wheat grain, and the effect of postharvest processing on wheat selenium content. *Biological Trace Element Research* **103**: 155–168.

Mangan B-u-N, Hui L, Lashari MS, Shah AN, Licao C, Weining S. 2015. Nutritional characteristics and starch properties of Tibetan barley. *International Journal of Agricultural Policy and Research* **3**: 293–299.

Matich AJ, McKenzie MJ, Brummell DA, Rowan DD. 2009. Organoselenides from *Nicotiana tabacum* genetically modified to accumulate selenium. *Phytochemistry* **70**: 1098–1106.

Matich AJ, McKenzie MJ, Lill RE, *et al.* 2012. Selenoglucosinolates and their metabolites produced in *Brassica* spp. fertilised with sodium selenate. *Phytochemistry* **75**: 140–152.

Matich AJ, McKenzie MJ, Lill RE, McGhie TK, Chen RKY, Rowan DD. 2015. Distribution of selenoglucosinolates and their metabolites in *Brassica* treated with sodium selenate. *Journal of Agricultural and Food Chemistry* **63**: 1896–1905.

Mazej D, Osvald J, Stibilj V. 2008. Selenium species in leaves of chicory, dandelion, lamb's lettuce and parsley. *Food Chemistry* **107**: 75–83.

McCray CWR, Hurwood IS. 1963. Selenosis in North-Western Queensland associated with a marine Cretaceous formation. *Queensland Journal of Agricultural Science* **20**: 475–498.

McKenzie MJ, Hunter DA, Pathirana R, *et al.* 2009. Accumulation of an organic anticancer selenium compound in a transgenic Solanaceous species shows wider applicability of the selenocysteine methyltransferase transgene from selenium hyperaccumulators. *Transgenic Research* **18**: 407–424.

McQuinn SD, Sleper DA, Mayland HF, Krause GF. 1991. Genetic variation for selenium content in tall fescue. *Crop Science* **31**: 617–620.

Mikkelsen RL, Page AL, Bingham FT. 1989. Factors affecting selenium accumulation by agricultural crops. In: LW Jacobs, AC Chang, RH Dowdy, RC Severson, LE Sommers, VV Volk, eds. *Selenium in agriculture and the environment*. Soil Science Society of America, Special Publication **23**: 65–94.

Moreno Rodriguez MJ, Cala Rivero V, Jiménez Ballesta R. 2005. Selenium distribution in topsoils and plants of a semi-arid Mediterranean environment. *Environmental Geochemistry and Health* **27**: 513–519.

Moxton AL, Olson OE, Searight WV. 1939. *Selenium in rocks, soils and plants. South Dakota Agricultural Experimental Station Technical Bulletin 2*. Brookings, SD: South Dakota Agricultural Experimental Station.

Murphy KM, Reeves PG, Jones SS. 2008. Relationship between yield and mineral nutrient concentrations in historical and modern spring wheat cultivars. *Euphytica* **163**: 381–390.

Nair RM, Thavarajah P, Giri RR, *et al.* 2015. Mineral and phenolic concentrations of mungbean [*Vigna radiata* (L.) R. Wilczek var. *radiata*] grown in semi-arid tropical India. *Journal of Food Composition and Analysis* **39**: 23–32.

Nelson AG, Quideau SA, Frick B, *et al.* 2011. The soil microbial community and grain micronutrient concentration of historical and modern hard red spring wheat cultivars grown organically and conventionally in the black soil zone of the Canadian prairies. *Sustainability* **3**: 500–517.

Németh A, Reyes JFG, Kosáry J, Dernovics M. 2013. The relationship of selenium tolerance and speciation in Lecythidaceae species. *Metallomics* **5**: 1663–1673.

Norton GJ, Deacon CM, Xiong L, Huang S, Meharg AA, Price AH. 2010. Genetic mapping of the rice ionome in leaves and grain: identification of

QTLs for 17 elements including arsenic, cadmium, iron and selenium. *Plant and Soil* **329**: 139–153.

Norton GJ, Duan GL, Lei M, Zhu YG, Meharg AA, Price, AH. 2012. Identification of quantitative trait loci for rice grain element composition on an arsenic impacted soil: influence of flowering time on genetic loci. *Annals of Applied Biology* **161**: 46–56.

Ogra Y, Anan Y. 2012. Selenometabolomics explored by speciation. *Biological and Pharmaceutical Bulletin* **35**: 1863–1869.

Ogra Y, Ishiwata K, Iwashita Y, Suzuki KT. 2005. Simultaneous speciation of selenium and sulfur species in selenized odorless garlic (*Allium sativum* L. Shiro) and shallot (*Allium ascalonicum*) by HPLC-inductively coupled plasma-(octopole reaction system)-mass spectrometry and electrospray ionization-tandem mass spectrometry. *Journal of Chromatography A* **1093**: 118–125.

Ogra Y, Kitaguchi T, Ishiwata K, Suzuki N, Iwashita Y, Suzuki KT. 2007. Identification of selenohomolanthionine in selenium-enriched Japanese pungent radish. *Journal of Analytical Atomic Spectrometry* **22**: 1390–1396.

Ouerdane L, Aureli F, Flis P, *et al.* 2013. Comprehensive speciation of low-molecular weight selenium metabolites in mustard seeds using HPLC–electrospray linear trap/orbitrap tandem mass spectrometry. *Metallomics* **5**: 1294–1304.

Paul S, Datta SK, Datta K. 2015. miRNA regulation of nutrient homeostasis in plants. *Frontiers in Plant Science* **6**: 232.

Perla V, Holm DG, Jayanty SS. 2012. Selenium and sulfur content and activity of associated enzymes in selected potato germplasm. *American Journal of Potato Research* **89**: 111–120.

Pfister JA, Davis TZ, Hall JO. 2013. Effect of selenium concentration on feed preferences by cattle and sheep. *Journal of Animal Science* **91**: 5970–5980.

Pickering IJ, Wright C, Bubner B, *et al.* 2003. Chemical form and distribution of selenium and sulfur in the selenium hyperaccumulator *Astragalus bisulcatus*. *Plant Physiology* **131**: 1460–1467.

Piergiovanni AR, Rizzi R, Pannacciulli E, Gatta CD. 1997. Mineral composition in hulled wheat grains: a comparison between emmer (*Triticum dicoccon* Schrank) and spelt (*T. spelta* L.) accessions. *International Journal of Food Sciences and Nutrition* **48**: 381–386.

Pilbeam DJ, Greathead HMR, Drihem K. 2015. Selenium. In: AV Barker, DJ Pilbeam, eds. *A handbook of plant nutrition*, 2nd edn. Boca Raton, FL: CRC Press, 165–198.

Pilon M, Owen JD, Garifullina GF, *et al.* 2003. Enhanced selenium tolerance and accumulation in transgenic Arabidopsis expressing a mouse selenocysteine lyase. *Plant Physiology* **131**: 1250–1257.

Pilon-Smits EAH. 2012. Plant selenium metabolism – genetic manipulation, phytotechnological applications, and ecological implications. In: MH Womg, ed. *Environmental contamination: health risks and ecological restoration*. Boca Raton, FL: CRC Press, 293–311.

Pilon-Smits EAH, LeDuc DL. 2009. Phytoremediation of selenium using transgenic plants. *Current Opinion in Biotechnology* **20**: 207–212.

Pilon-Smits EAH, de Souza MP, Hong G, *et al.* 1999*a*. Selenium volatalization and accumulation by twenty aquatic plant species. *Journal of Environmental Quality* **28**: 1011–1018.

Pilon-Smits EAH, Hwang SB, Lytle CM, *et al.* 1999*b*. Overexpression of ATPsulphurylase in *Brassica juncea* leads to increased selenite uptake, reduction and tolerance. *Plant Physiology* **119**: 123–132.

Pilon-Smits EAH, Quinn CF, Tapken W, Malagoli M, Schiavon M. 2009. Physiological functions of beneficial elements. *Current Opinion in Plant Biology* **12**: 267–274.

Pommerrenig B, Diehn TA, Bienert GP. 2015. Metalloido-porins: essentiality of Nodulin 26-like intrinsic proteins in metalloid transport. *Plant Science* **238**: 212–227.

Pu ZE, Yu M, He QY, *et al.* 2014. Quantitative trait loci associated with micronutrient concentrations in two recombinant inbred wheat lines. *Journal of Integrative Agriculture* **13**: 2322–2329.

Quinn CF, Galeas ML, Freeman JL, Pilon-Smits EAH. 2007. Selenium: deterrence, toxicity, and adaptation. *Integrated Environmental Assessment and Management* **3**: 460–462.

Rahman MM, Erskine W, Materne MA, McMurray LM, Thavarajah P, Thavarajah D, Siddique KHM. 2015. Enhancing selenium concentration in lentil (*Lens culinaris* subsp. *culinaris*) through foliar application. *Journal of Agricultural Science* **153**: 656–665.

Ramamurthy RK, Jedlicka J, Graef GL, Waters BM. 2014. Identification of new QTLs for seed mineral, cysteine, and methionine concentrations in soybean [*Glycine max* (L.) Merr.]. *Molecular Breeding* **34**: 431–445.

Ramos SJ, Rutzke MA, Hayes RJ, Faquin V, Guilherme LRG, Li L. 2011*a*. Selenium accumulation in lettuce germplasm. *Planta* **233**: 649–660.

Ramos SJ, Yuan Y, Faquin V, Guilherme LRG, Li L. 2011*b*. Evaluation of genotypic variation of broccoli (*Brassica oleracea* var. *italic*) in response to selenium treatment. *Journal of Agricultural and Food Chemistry* **59**: 3657–3665.

Ray H, Bett K, Tar'an B, Vandenberg A, Thavarajah D, Warkentin T. 2014. Mineral micronutrient content of cultivars of field pea, chickpea, common bean, and lentil grown in Saskatchewan, Canada. *Crop Science* **54**: 1698–1708.

Rayman MP. 2012. Selenium and human health. *Lancet* **379**: 1256–1268.

Rayman MP, Infante HG, Sargent M. 2008. Food-chain selenium and human health: spotlight on speciation. *British Journal of Nutrition* **100**: 238–253.

Reeves RD, Baker AJM. 2000. Metal-accumulating plants. In: I Raskin, BD Ensley, eds. *Phytoremediation of toxic metals: using plants to clean up the environment*. New York: Wiley, 193–229.

Rodríguez LH, Morales DA, Rodríguez ER, Romero CD. 2011. Minerals and trace elements in a collection of wheat landraces from the Canary Islands. *Journal of Food Composition and Analysis* **24**: 1081–1090

Rosenfeld I, Beath OA. 1964. *Selenium: geobotany, biochemistry, toxicity, and nutrition*. New York: Academic Press.

Rouached H, Wirtz M, Alary R, *et al.* 2008. Differential regulation of the expression of two high-affinity sulfate transporters, SULTR1.1 and SULTR1.2, in Arabidopsis. *Plant Physiology* **147**: 897–911.

Schiavon M, Pilon M, Malagoli M, Pilon-Smits EAH. 2015. Exploring the importance of sulphate transporters and ATPsulphurylases for selenium hyperaccumulation – comparison of *Stanleya pinnata* and *Brassica juncea* (Brassicaceae). *Frontiers in Plant Science* **6**: 2.

Seppänen MM, Kontturi J, Heras IL, Madrid Y, Cámara C, Hartikainen H. 2010. Agronomic biofortification of *Brassica* with selenium – enrichment of SeMet and its identification in *Brassica* seeds and meal. *Plant and Soil* **337**: 273–283.

Shao SX, Mi XB, Ouerdane L, *et al.* 2014. Quantification of Se-methylselenocysteine and its γ-glutamyl derivative from naturally Se-enriched green bean (*Phaseolus vulgaris vulgaris*) after HPLC-ESI-TOF-MS and orbitrap MS^n-based identification. *Food Analytical Methods* **7**: 1147–1157.

Shibagaki N, Rose A, McDermott JP, *et al.* 2002. Selenate-resistant mutants of *Arabidopsis thaliana* identify *Sultr1;2*, a sulfate transporter required for efficient transport of sulfate into roots. *The Plant Journal* **29**: 475–486.

Shinmachi F, Buchner P, Stroud JL, *et al.* 2010. Influence of sulfur deficiency on the expression of specific sulfate transporters and the distribution of sulfur, selenium, and molybdenum in wheat. *Plant Physiology* **153**: 327–336.

da Silva EG, Mataveli LR, Arruda MA. 2013. Speciation analysis of selenium in plankton, Brazil nut and human urine samples by HPLC-ICP-MS. *Talanta* **110**: 53–57.

Smrkolj P, Stibilj V, Kreft I, Kapolna E. 2005. Selenium species determination in selenium enriched pumpkin (*Cucurbita pepo* L.) seeds by HPLC–UV–HG-AFS. *Analytical Sciences* **21**: 1501–1504.

Smrkolj P, Stibilj V, Kreft I, Germ M. 2006. Selenium species in buckwheat cultivated with foliar addition of Se(VI) and various levels of UV-B radiation. *Food Chemistry* **96**: 675–681.

Smrkolj P, Osvald M, Osvald J, Stibilj V. 2007. Selenium uptake and species distribution in selenium-enriched bean (*Phasolus vulgaris* L.) seeds obtained by two different cultivations. *European Food Research and Technology* **225**: 233–237.

Sors TG, Ellis DR, Na GN, *et al.* 2005*a*. Analysis of sulfur and selenium assimilation in *Astragalus* plants with varying capacities to accumulate selenium. *The Plant Journal* **42**: 785–797.

Sors TG, Ellis DR, Salt DE. 2005*b*. Selenium uptake, translocation, assimilation and metabolic fate in plants. *Photosynthesis Research* **86**: 373–389.

Sors TG, Martin CP, Salt DE. 2009. Characterization of selenocysteine methyltransferases from *Astragalus* species with contrasting selenium accumulation capacity. *The Plant Journal* **59**: 110–122.

Souza GA, Hart JJ, Carvalho JG, *et al.* 2014. Genotypic variation of zinc and selenium concentration in grains of Brazilian wheat lines. *Plant Science* **224**: 27–35.

de Souza MP, Pilon-Smits EAH, Terry N. 2000. The physiology and biochemistry of selenium volatilization by plants. In: I Raskin, BD Ensley, eds. *Phytoremediation of toxic metals: using plants to clean-up the environment*. New York: John Wiley and Sons, 171–190.

Stoffaneller R, Morse NL. 2015. A review of dietary selenium intake and selenium status in Europe and the Middle East. *Nutrients* **7**: 1494–1537.

Sugihara S, Kondo M, Chihara Y, Yuji M, Hattori H, Yoshida M. 2004. Preparation of selenium-enriched sprouts and identification of their selenium species by high-performance liquid chromatography-inductively coupled plasma mass spectrometry. *Bioscience, Biotechnology, and Biochemistry* **68**: 193–199.

Sura-de Jong M, Reynolds RJB, Richterova K, *et al.* 2015. Selenium hyperaccumulators harbor a diverse endophytic bacterial community characterized by high selenium resistance and plant growth promoting properties. *Frontiers in Plant Science* **6**: 113.

Tagmount A, Berken A, Terry N. 2002. An essential role of *S*-adenosyl-L-methionine:L-methionine *S*-methyltransferase in selenium volatilization by plants. Methylation of selenomethionine to selenium-methyl-L-selenium-methionine, the precursor of volatile selenium. *Plant Physiology* **130**: 847–56.

Takahashi H, Watanabe-Takahashi A, Smith FW, Blake-Kalff M, Hawkesford MJ, Saito K. 2000. The roles of three functional sulphate transporters involved in uptake and translocation of sulphate in *Arabidopsis thaliana*. *Plant Journal* **23**: 171–182.

Takahashi H, Buchner P, Yoshimoto N, Hawkesford MJ, Shiu S-H. 2012. Evolutionary relationships and functional diversity of plant sulfate transporters. *Frontiers in Plant Science* **2**: 119.

Tamaoki M, Freeman JL, Pilon-Smits EAH. 2008. Cooperative ethylene and jasmonic acid signaling regulates selenite resistance in Arabidopsis. *Plant Physiology* **146**: 1219–1230.

Tegeder M. 2012. Transporters for amino acids in plant cells: some functions and many unknowns. *Current Opinion in Plant Biology* **15**: 315–321.

Terry N, Carlson C, Raab TK, Zayed AM. 1992. Rates of selenium volatilization among crop species. *Journal of Environmental Quality* **21**: 341–344.

Terry N, Zayed AM, de Souza MP, Tarun AS. 2000. Selenium in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **51**: 401–432.

Thosaikham W, Jitmanee K, Sittipout R, Maneetong S, Chantiratikul A, Chantiratikul P. 2014. Evaluation of selenium species in selenium-enriched pakchoi (*Brassica chinensis* Jusl var *parachinensis* (Bailey) Tsen & Lee) using mixed ion-pair reversed phase HPLC–ICP-MS. *Food Chemistry* **145**: 736–742.

Thavarajah D, Thavarajah P. 2012. Evaluation of chickpea (*Cicer arietinum* L.) micronutrient composition: biofortification opportunities to combat global micronutrient malnutrition. *Food Research International* **49**: 99–104.

Thavarajah D, Ruszkowski J, Vandenberg A. 2008. High potential for selenium biofortification of lentils (*Lens culinaris* L.). *Journal of Agriculture and Food Chemistry* **57**: 10747–10753.

Thavarajah D, Warkentin T, Vandenberg A. 2010. Natural enrichment of selenium in Saskachewan field peas (*Pisum sativum* L.). *Canadian Journal of Plant Science* **90**: 383–389.

Thavarajah D, Thavarajah P, Sarker A, *et al.* 2011. A global survey of effects of genotype and environment on selenium concentration in lentils (*Lens culinaris* L.): implications for nutritional fortification strategies. *Food Chemistry* **125**: 72–76.

Turakainen M, Hartikainen H, Seppänen MM. 2004. Effects of selenium treatments on potato (*Solanum tuberosum* L.) growth and concentrations of soluble sugars and starch. *Journal of Agricultural and Food Chemistry* **52**: 5378–5382.

Valdez Barillas JR, Quinn CF, Freeman JL, *et al.* 2012. Selenium distribution and speciation in the hyperaccumulator *Astragalus bisulcatus* and associated ecological partners. *Plant Physiology* **159**: 1834–1844.

Van Hoewyk D. 2013. A tale of two toxicities: malformed selenoproteins and oxidative stress both contribute to selenium stress in plants. *Annals of Botany* **112**: 965–972.

Van Hoewyk D, Garifullina GF, Ackley AR, *et al.* 2005. Overexpression of AtCpNifS enhances selenium tolerance and accumulation in Arabidopsis. *Plant Physiology* **139**: 1518–1528

Van Hoewyk D, Pilon M, Pilon-Smits EAH. 2008*a*. The functions of NifS-like proteins in plant sulfur and selenium metabolism. *Plant Science* **174**: 117–123.

Van Hoewyk D, Takahashi H, Hess A, Tamaoki M, Pilon-Smits EAH. 2008*b*. Transcriptome and biochemical analyses give insights into selenium-stress responses and selenium tolerance mechanisms in Arabidopsis. *Physiologia Plantarum* **132**: 236–253.

Van Huysen T, Abdel-Ghany S, Hale KL, LeDuc D, Terry N, Pilon-Smits EAH. 2003. Overexpression of cystathionine-γ-synthase enhances selenium volatilisation in *Brassica juncea*. *Planta* **218**: 71–78.

Van Huysen T, Terry N, Pilon-Smits EAH. 2004. Exploring the selenium phytoremediation potential of transgenic *Brassica juncea* overexpressing ATP sulfurylase or cystathionine-γ-synthase. *International Journal of Phytoremediation* **6**: 111–118

Vonderheide AP, Wrobel K, Kannamkumarath SS, *et al.* 2002. Characterization of selenium species in Brazil nuts by HPLC-ICP-MS and ES-MS. *Journal of Agricultural and Food Chemistry* **50**: 5722–5728.

Watanabe T, Broadley MR, Jansen S, *et al.* 2007. Evolutionary control of leaf element composition in plants. *New Phytologist* **174**: 516–523.

White PJ, Broadley MR. 2009. Biofortification of crops with seven mineral elements often lacking in human diets – iron, zinc, copper, calcium, magnesium, selenium and iodine. *New Phytologist* **182**: 49–84.

White PJ, Brown PH. 2010. Plant nutrition for sustainable development and global health. *Annals of Botany* **105**: 1073–1080.

White PJ, Bowen HC, Parmaguru P, *et al.* 2004. Interactions between selenium and sulphur nutrition in *Arabidopsis thaliana*. *Journal of Experimental Botany* **55**: 1927–1937.

White PJ, Bowen HC, Marshall B, Broadley MR. 2007*a*. Extraordinarily high leaf selenium to sulphur ratios define 'Se-accumulator' plants. *Annals of Botany* **100**: 111–118.

White PJ, Broadley MR, Bowen HC, Johnson SE. 2007*b*. Selenium and its relationship with sufur. In: MJ Hawkesford, LJ de Kok, eds. *Sulfur in plants – an ecological perspective*. Dordrecht: Springer, 225–252.

Williams KT, Lakin HW, Byers HG. 1940. *Selenium occurrence in certain soils in the United States, with a discussion of related topics: fourth report. United States Department of Agriculture Technical Bulletin 702*. Washington, DC: United States Department of Agriculture.

Williams PN, Lombi E, Sun GX, *et al.* 2009. Selenium characterization in the global rice supply chain. *Environmental Science and Technology* **43**: 6024–6030.

Wu L. 2004. Review of 15 years of research on ecotoxicology and remediation of land contaminated by agricultural drainage sediment rich in selenium. *Ecotoxicology and Environmental Safety* **57**: 257–269.

Ximénez-Embún P, Alonso I, Madrid-Albarrán Y, Cámara C. 2004. Establishment of selenium uptake and species distribution in lupine, Indian mustard, and sunflower plants. *Journal of Agricultural and Food Chemistry* **52**: 832–838.

Yan J, Wang F, Qin H, *et al.* 2011. Natural variation in grain selenium concentration of wild barley, *Hordeum spontaneum*, populations from Israel. *Biological Trace Element Research* **142**: 773–786.

Yang F, Chen L, Hu Q, Pan G. 2003. Effect of the application of selenium on selenium content of soybean and its products. *Biological Trace Element Research* **93**: 249–256.

Yang R, Wang R, Xue W, *et al.* 2013. QTL location and analysis of selenium content in tetraploid wheat grain. *Guizhou Agricultural Sciences* **10**: 1–4. [In Chinese]

Yoshimoto N, Inoue E, Saito K, Yamaya T, Takahashi H. 2003. Phloem-localizing sulfate transporter, Sultr1;3, mediates re-distribution of sulfur from source to sink organs in Arabidopsis. *Plant Physiology* **131**: 1511–1517.

Yuan LX, Zhu YY, Lin ZQ, Banuelos G, Li W, Yin XB. 2013. A novel selenocystine-accumulating plant in selenium-mine drainage area in Enshi, China. *PLoS Ine* **8**: e65615.

Zhang L-H, Abdel-Ghany SE, Freeman JL, Ackley AR, Schiavon M, Pilon-Smits EAH. 2006*a*. Investigation of selenium tolerance mechanisms in *Arabidopsis thaliana*. *Physiologia Plantarum* **128**: 212–223.

Zhang L, Byrne PF, Pilon-Smits EAH. 2006*b*. Mapping quantitative trait loci associated with selenate tolerance in *Arabidopsis thaliana*. *New Phytologist* **170**: 33–42.

Zhang L, Shi W, Wang X, Zhou X. 2006*c*. Genotypic differences in selenium accumulation in rice seedlings at early growth stage and analysis of dominant factors influencing selenium content in rice seeds. *Journal of Plant Nutrition* **29**: 1601–1618.

Zhang L, Ackley AR, Pilon-Smits EAH. 2007. Variation in selenium tolerance and accumulation among 19 *Arabidopsis thaliana* accessions. *Journal of Plant Physiology* **164**: 327–336.

Zhang L, Hu B, Li W, *et al.* 2014. OsPT2, a phosphate transporter, is involved in the active uptake of selenite in rice. *New Phytologist* **201**: 1183–119.

Zhao D-Y, Sun F-L, Zhang B, Zhang Z-Q, Yin LQ. 2015. Systematic comparisons of orthologous selenocysteine methyltransferase and homocysteine methyltransferase genes from seven monocots species. *Notulae Scientia Biologicae* **7**: 210–216.

Zhao F-J, Lopez-Bellido FJ, Gray CW, Whalley WR, Clark LJ, McGrath SP. 2007. Effects of soil compaction and irrigation on the concentrations of selenium and arsenic in wheat grains. *Science of the Total Environment* **372**: 433–439.

Zhao FJ, Su YH, Dunham SJ, *et al.* 2009. Variation in mineral micronutrient concentrations in grain of wheat lines of diverse origin. *Journal of Cereal Science* **49**: 290–295.

Zhao XQ, Mitani N, Yamaji N, Shen RF, Ma JF. 2010. Involvement of silicon influx transporter OsNIP2;1 in selenite uptake in rice. *Plant Physiology* **153**: 1871–1877.

Zhu Y-G, Pilon-Smits EAH, Zhao F-J, Williams PN, Meharg AA. 2009. Selenium in higher plants: understanding mechanisms for biofortification and phytoremediation. *Trends in Plant Science* **14**: 436–442.