Biofortification of UK food crops with selenium

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Se is an essential element for animals. In man low dietary Se intakes are associated with health disorders including oxidative stress-related conditions, reduced fertility and immune functions and an increased risk of cancers. Although the reference nutrient intakes for adult females and males in the UK are 60 and 75 μg Se/d respectively, dietary Se intakes in the UK have declined from >60 μg Se/d in the 1970s to 35 μg Se/d in the 1990s, with a concomitant decline in human Se status. This decline in Se intake and status has been attributed primarily to the replacement of milling wheat having high levels of grain Se and grown on high-Se soils in North America with UK-sourced wheat having low levels of grain Se and grown on low-Se soils. An immediate solution to low dietary Se intake and status is to enrich UK-grown food crops using Se fertilisers (agronomic biofortification). Such a strategy has been adopted with success in Finland. It may also be possible to enrich food crops in the longer term by selecting or breeding crop varieties with enhanced Se-accumulation characteristics (genetic biofortification). The present paper will review the potential for biofortification of UK food crops with Se.

Agronomy: Diet: Fertilisers: Genetics: Plants: Selenium

Physical, chemical and biological properties of selenium

Se is a naturally-occurring oxygen-group (group VIA) element (for review, see Fordyce, 2005). Se has an atomic mass of approximately 79 and six natural isotopes exist, 77Se, 76Se, 75Se, 77Se, 78Se, 80Se and 82Se. It is a chalcophile (‘S-loving’) element, replacing S in common sulfide minerals such as pyrite, chalcopyrite, pyrrhotite and sphalerite. It also forms several rare minerals including crookinite ((Cu, Tl, Ag)2Se), berzelianite (Cu2Se) and tiemannite (HgSe). Se exists in four main oxidation states, −2 (selenide), 0 (elemental Se), +4 (selenite) and +6 (selenate), and is highly mobile under oxidising conditions, although its mobility decreases with decreasing pH (Gondi et al. 1992). Se is immobile under reducing conditions; elemental Se or metal selenides will form in conditions of low H+ (pH) and electron (pe/Eh; a measure of the tendency of a chemical system to undergo redox reactions) activity. The solution chemistry of Se is principally (oxy)anionic, with selenite (SeO3 2−) and selenate (SeO4 2−) corresponding to sulfite and sulfate, although elemental Se is also stable over a wide pH range under reducing conditions (Brookins, 1987). Selenate is the major species in soil solution at high redox (pe + pH > 15). In the medium redox range (pe + pH 7.5–15) selenite species predominate. Selenide species are stable only at low redox (pe + pH < 7.5; Elrashidy et al. 1987, 1989). In contrast with S species, the lower redox state (+4; selenite) is more stable than the higher redox state (+6; selenate). Mobile selenate entering a drainage system is readily reduced to selenium if pe/Eh falls, whilst at lower pH levels selenium is likely to be strongly absorbed by hydrous secondary iron oxides and, to a lesser extent, by clays and organic matter.

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Abbreviations: HAST, high-affinity sulfate transporter; Sec, selenocysteine.
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Se is a biologically-active element that can form direct Se–C bonds, which occur in a range of organic compounds including selenoamino acids and selenoproteins. Selenoproteins have essential functional roles in a wide array of prokaryotes, archaeabacteria and eukaryotes (Driscoll & Copeland, 2003; Castellano et al. 2004). Se is incorporated into selenoproteins as the twenty-first amino acid selenocysteine (Sec), which is encoded by an UGA codon in the selenoprotein mRNA. Since UGA is normally read as a stop codon, the translation of selenoproteins requires several factors including a cis-acting Sec insertion sequence (frequently located in the 3′ untranslated region of selenoprotein genes), a novel Sec-charged tRNA that contains the anticodon UCA on which Sec is universally synthesised and additional trans-acting factors that allow delivery of Sec-tRNA\(^{Sec}\) to the ribosome (Driscoll & Copeland, 2003). About twenty-five to thirty Sec-containing proteins have been identified in eukaryotes, although these proteins are not distributed evenly amongst taxa; for example, selenoproteins have not yet been found in yeast and land plants. In organisms whose genomes lack Sec-containing genes selenoprotein homologues occur in which Sec is replaced by cysteine (Castellano et al. 2004).

### Selenium inputs to soils

The Se concentrations of most soils in the world are low (normal range 0.01–2.0 mg Se/kg; mean 0.4 mg Se/kg), although concentrations ≤1200 mg Se/kg can occur in seleniferous soils (Fordyce, 2005). The Se content of most soils is primarily under geological control, and high-Se soils are associated with particular shales, sandstones, limestones and slate and coal series, including those formed in Cretaceous, Jurassic, Triassic, Carboniferous, Ordovician and Permian periods (Fordyce, 2005). Seleniferous soils are widespread in the Great Plains of the USA, Canada, South America, China and Russia. Other notable inputs of Se to soils include atmospheric deposition of Se originating from volcanic activity, weathering of rocks, sea spray and volatilisation-recycling from biota. All these factors contribute to global Se cycling. In the UK atmospheric Se deposition is approximately 2.2–6.5 g Se/ha per year (Fordyce, 2005). Anthropogenic sources of Se to soils arise from fossil fuel combustion, metal processing, applications of fertilisers, lime and manure, and disposal of sewage sludge (Fordyce, 2005). Se from fossil fuel combustion and metal processing is deposited to soils predominantly in rainwater, which contains 0.00001–0.001 mg Se/l (De Gregori et al. 2002). A correlation between the intensity of coal combustion and Se deposition has been observed in the Se content of historical plant samples (Haygarth et al. 1993). The use of fertilisers and irrigation water containing Se will also contribute to soil Se inputs in certain areas. For example, (NH\(_4\))\(_2\)SO\(_4\) fertilisers contain ≤36 mg Se/kg, whilst phosphate rocks and single superphosphate can contain ≤55 mg Se/kg and ≤25 mg Se/kg respectively (White et al. 2004). Since single superphosphate has generally been replaced by triple superphosphate, which typically contains <4 mg Se/kg, fertiliser inputs of Se to soils have fallen in recent years in many parts of the world.

### Selenium concentration of UK soils and stream sediments

The British Geological Survey has been surveying the baseline geochemistry of UK drainage sediments in streams, water samples and soils since the late 1960s (Geochemical Baseline Survey of the Environment; Johnson & Breward, 2004). For Se, soils and/or stream sediments in Wales and in the Midlands of England have been sampled at a density of one to two samples per km\(^2\). Samples of stream sediments and surface waters have been analysed for Se in Wales and the west Midlands, whilst in the Humber–Trent drainage basin and in the east Midlands soils, stream sediments and surface waters have been analysed for Se (Fig. 1). From these data it can be observed that total Se in soils and stream sediments in the UK range from 0.1 mg Se/kg to 4.0 mg Se/kg, with >95% of the UK soils containing <1 mg Se/kg. Despite the low abundances of this strongly chalcophile element there is a good resolution of Se-enriched features in restricted areas.

In Wales stream-sediment Se concentrations are primarily under geological control, including sulfide mineralisation in Snowdonia, with secondary mixed iron-manganese oxide enrichment in mid-Wales and industrial contamination in the south Wales coalfield and in the industrial west Midlands (Fig. 1(a)). Strong sulfate-selenate associations occur in the Triassic terrain of the Worcester and Stafford basins related to the evaporitic component of the Mercia Mudstone group. In Humber–Trent stream sediments and soils (Fig. 1(b,c)) Se concentrations are high over the basal Visean deposits and lower parts of the Namurian deposits in the south-west of the region where there is a well-developed Black Shale sequence within the Widmerpool Formation. Se concentrations are also high over the area of the Trent Valley between Newark and Gainsborough, where the Quaternary alluvial sediments may contain material derived from the former area. One isolated Se anomaly is attributable to coal waste adjacent to a power station. Relatively high values also follow the Permian and Jurassic limestone outcrops. Very low Se concentrations are present over the marine alluvium of the coastal strip and the Fens, although natural stream coverage is poor in the latter area. In stream sediments and soils of the east Midlands (Fig. 1(d,e)) high Se levels are prominent at sites over river alluvium in the Dove, Derwent and Trent valleys. These high levels are almost certainly a result of material derived from the Black Shale lithology of the Widmerpool Formation and the hydrothermal sulfide mineralisation of the Peak District. Low Se concentrations occur over Triassic terrain generally, especially to the south of Birmingham and Coventry, with higher concentrations over the lower and middle Jurassic terrain. Elsewhere, high Se concentrations around Birmingham are likely to be industrial in origin, whilst a prominent high-Se feature extending from the north of Grantham to the south of Peterborough may be associated with peat deposits. High Se concentrations in the
Fig. 1. (Cont.)
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south-east of the map may be associated with the Bedfordshire brick industry, but this association is not yet certain (Fig. 1(e)).

Uptake, assimilation and accumulation of selenium by plants

Se has no proven function in plant nutrition. However, plants take up Se from the soil solution primarily as selenate, and to a much lesser extent as selenite. Selenate enters root cells through sulfate transporters in their plasma membranes (Terry et al. 2000; White et al. 2004). Sulfate transporters are encoded by a small family of genes in most plant species; these transporters are hydrophobic membrane proteins with twelve predicted membrane-spanning domains and few large extramembrane loops but, generally, with long N and C termini (Hawkesford, 2003, 2005). There are fourteen genes encoding sulfate transporters in the genome of Arabidopsis thaliana (L.) Heynh. and a similar number in groups of other plant species (Hawkesford, 2005). All sulfate transporters characterised to date can be placed into one of five groups based on their protein sequences (Hawkesford, 2003, 2005), with each group having distinct functional characteristics. Group 1 transporters, such as AtSultr1:1, AtSultr1:2 and AtSultr1:3, are high-affinity sulfate transporters (HAST) that are thought to catalyse most selenate influx to plant cells. Sulfate uptake is regulated by gene transcription (Hawkesford, 2005); AtSultr1:1 and AtSultr1:2 catalyse sulfate influx to Arabidopsis roots and their expression is induced by S starvation (Takahashi et al. 2000; Yoshimoto et al. 2002; Maruyama-Nakashita et al. 2003). The expression of these HAST also appears to correlate well with plant Se uptake. For example, plants lacking group 1 HAST have reduced selenate uptake (Shibagaki et al. 2002), whilst the overexpression of genes encoding group 1 HAST in transgenic plants increases Se uptake (Terry et al. 2000). Interestingly, although the expression of genes encoding HAST is generally reduced when a plant has sufficient S, increasing the selenate concentration in the rhizosphere of S-replete plants can increase shoot S concentrations (Bell et al. 1992; White et al. 2004). This phenomenon has been interpreted as the consequence of either selenate or Se metabolites de-repressing the expression of genes encoding HAST (Takahashi et al. 2000;
White et al. (2004). Although several of the HAST will transport selenite, the molecular structure responsible for their anionic selectivity is not known.

Following uptake selenite is likely to be transported to the plastids, or may remain in the cytoplasm where it is assimilated via the S assimilation pathway (for reviews of Se assimilation in plants, see Terry et al. 2000; Ellis & Salt, 2003; for a review of S assimilation see Hawkesford, 2005). Briefly, selenite is activated by ATP sulphurylase (as high as 22 g/kg DM) has been reported in the fruit of some species within the Lecythidaceae family. This neotropical family of trees comprises 325 species within ten genera (Morton et al., 2003). Extreme Se accumulation has been suggested, since increased Se concentration protects B. juncea against infection with Fusarium and Alternaria and against herbivory by aphids and caterpillars but not snails (Hanson et al., 2003, 2004). Examples of Se hyperaccumulators include members of the Fabaceae (Astragalus bisulcatus, A. racemosus Pursh), Asteraceae (Aster occidentalis (Nutt.) Torr. & A. Gray, Machaeranthera ramosa A. Nelson), and Brassicaceae (Stanleya pinnata (Pursh) Britton). In Se accumulators Se predominantly occurs as non-protein-amino acid forms, Se-methylSec, and in a conjugated form as γ-glutamyl-methylSec, but also as selenocystathione, selenohomocysteine, γ-glutamyl-selenocystathione, methyl selenol and selenate (Pickering et al., 2000, 2003). Extreme Se accumulation has been reported in the fruit of some species within the Lecythidaceae family. This neotropical family of trees comprises 325 species within ten genera (Morton et al., 1998), including the familiar edible Brazil nut (Bertholletia excelsa Humb. & Bonpl.) and less-familiar edible nuts such as the Paradise nut (Lecythis zubucaya Aubl.). However, the ingestion of certain other Lecythis species, including Coco de Mono (L. ollaria Loefl.) and Sapucaia nut (L. elliptica Kunth), can induce acute selenosis in human subjects (Kerdel-Vegas, 1966; Dickson, 1969), characterised by symptoms of hair and nail loss, alongside other dermatological, neurological and gastric disorders (Fordyce 2005). In B. excelsa the dominant form of Se is selenomethionine (Vonderheide et al. 2002; Kannamkumarath et al. 2005).

Selenium is an essential element for man

Se was identified as an essential element for mammals in the 1950s (Schwarz & Foltz, 1957). There are approximately thirty mammalian selenoproteins, about half of which have been characterised (Rayman, 2002). These proteins include those with functional roles as antioxidants (e.g. glutathione peroxidase) and those that contribute to protein stability, transcription of mRNA and other biochemical functions. Given these functions it is not surprising that Se is important for human health, and Se deficiency in human subjects has been linked to a plethora of physiological disorders (Rayman, 2000, 2002; Jackson et al. 2004). For example, low Se status causes Keshan disease (a cardiomyopathy) and Kashin-Beck disease (an osteoarthritdis disorder) in parts of China where dietary Se intakes are extremely low (Fordyce, 2005). As a result of its role as an antioxidant, low Se status has also been linked to CVD, pancreatitis, asthma and inflammatory response syndrome (Rayman, 2000, 2002). Further, there is evidence that low Se status impacts on immune system functioning, response to viral infection, female (e.g. reduced rates of miscarriage) and male (e.g. sperm development and function) fertility and thyroid functioning if Se and I status are both deficient (Rayman, 2002).

There is substantial evidence that Se is a potent anticarcinogen when it is present at levels above those required for the maximal expression of selenoproteins, i.e. well above those levels associated with incipient Se deficiency.
(Combs, 2005). Indeed, both organic and inorganic forms of Se consistently inhibit cell growth and stimulate programmed cell death in vitro, whilst there is supporting (albeit inconclusive) epidemiological evidence of inverse relationships between Se status and the incidence of cancer (Combs, 2005). For example, in a randomised clinical trial 200 μg Se/d has been shown to reduce total cancer incidences by a factor of 0.63 and to reduce incidences of carcinomas of the prostate and colon-rectum by 0.51 and 0.46 respectively (Clark et al. 1996, 1998; Combs, 2005).

Selenium intake and status have declined in the UK
Individual Se intakes range from 3 to 7000 μg Se/d worldwide, although most intakes are at the lower end of this distribution (Fordyce, 2005). Se intake in the UK has declined from >60 μg Se/d in 1974 to 29–39 μg Se/d (for reviews, see Rayman, 1997, 2000, 2002, 2004). In several other EU countries Se intakes are less than half the UK reference nutrient intakes of 60 and 75 μg Se/d for females and males respectively (Rayman, 2004). A concomitant decline in Se status based on analysis of blood and serum has been reported, and thus the UK population may be at risk from an increased prevalence of certain health disorders (Rayman, 1997, 2000, 2002, 2004). Cereals represent a major source of Se in most UK diets, and the decline in Se intake and status in the UK has been attributed to changes in the sourcing of the wheat used for flour production from grains that are high in Se concentration and grown on high-Se soils in North America to UK-sourced wheat that has been grown on low-Se soils and has a low grain Se content. The use of UK wheat in grits has risen from 15% in the 1950s to >80% in 2005 (Lea, 2005).

The baseline Se concentration of wheat grain used in UK bread has been analysed in samples taken in 1982, 1992 and 1998 (Adams et al., 2002), and a minimal difference in mean grain Se concentration between these samples has been found (0.025, 0.033 and 0.025 mg Se/kg respectively, with interquartile ranges varying from 0.015 to 0.019 mg Se/kg). By comparison, mean values of 0.370 and 0.457 mg Se/kg have been reported for US wheat grain and 0.760 mg Se/kg for Canadian grain (Adams et al. 2002). Worldwide, the Se content of wheat grain ranges from 0.001 to 30 mg/kg, being predominantly within the range 0.020–0.600 mg Se/kg (Lyons et al. 2005a). It is important to emphasise that the primary reason for higher concentrations of Se in US and Canadian wheat grain than in wheat grain from the UK is a result of differences in the underlying geology and consequent higher Se concentrations in the North American soils. It is less related to differences in historical or current agronomic practices or to soil nutrient depletion. Consistent with the hypothesis of a link between Se content of wheat and dietary Se intake and status is the observation that in New Zealand Se intake and status increased when Australian wheat containing higher levels of Se were imported (Watkinson, 1981; Thomson & Robinson, 1996). In addition to changes in the sourcing of wheat grain, levels of Se in UK diets may also have declined in recent years because of changes in fertiliser practices (e.g. replacing single superphosphate with triple superphosphate; White et al. 2004), or dilution in the crop as a result of improved yields (Adams et al. 2002). Further, since Se and pyritic S concentrations are correlated in coal (Spears et al. 1999), declines in Se inputs may also be related to a decline in the intensity of coal combustion following the Clean Air Act of 1956 (Ministry of Housing and Local Government, 1956; Haygarth et al. 1993) and/or the use of low-S coal or desulphurisation combustion technologies.

Biofortifying crops in the UK
The decline in Se intake and status in the UK can be rectified by dietary diversification, mineral supplementation of human subjects or livestock, food fortification during processing or through crop biofortification (Rayman, 2002, 2004). Since foods such as Brazil nuts, offal and crab meat, which naturally contain high levels of Se, are not eaten in great quantities, the potential for dietary diversification to increase Se delivery in the UK is limited (Rayman, 2002). The use of high-Se-containing supplements, including yeast-based formulations, appears to be an effective and a safe option for human subjects (Rayman, 2004). However, supplements are relatively expensive and only a small proportion of the population are likely to take such personal intervention measures, particularly since recent EU legislation restricts the sale of such supplements. During flour processing in the UK statutory nutrients are currently added to flour using a pre-blend that contains CaCO₃, Fe, thiamin and nicotinamide. Although Se could be fortified through this route, alterations to this blend would require a change in legislation. There is also a food safety issue associated with storing concentrated Se compounds in a mill or a baking environment. The present review will therefore focus on the strategy of biofortification, defined as increasing the bioavailable concentrations of essential elements in edible portions of crop plants through the use of fertilisers (agronomic biofortification) or through crop selection or breeding (genetic biofortification; Graham et al. 2001; Bouis, 2003; Bouis et al. 2003; Lyons et al. 2003).

Agronomic biofortification
The potential for using Se-containing fertilisers to increase crop Se concentrations, and thus dietary Se intakes, in the UK has been proposed previously (Adams et al. 2002; Rayman, 2002; Arthur, 2003). Possible strategies for Se fertilisation in the UK based on data obtained from other parts of the world will be reviewed. Strategies based on fertilising both pasture or forage crops for consumption by livestock and crops intended for direct human consumption will be considered.

Biofortification of pastures or forages using Se fertilisers has been widely demonstrated (for reviews, see Gissel-Nielsen, 1998; Gupta & Gupta, 2002). The primary driver for supplying pastures or forages with increased Se has been to prevent disorders amongst grazing livestock. For example, the muscular dystrophy disorder, white muscle disease, is associated with low-Se-status soils, notably in
In Ireland Se uptake by ryegrass (Lolium perenne L.) has been shown to increase, as has that of fescue (Festuca spp.) top-dressed at the same rate (Valle et al. 1996; Eurola et al. 1989, 1991, 2004; Aro et al. 1997; Venäjänemä et al. 1996). Notably, the Se concentration of wheat bran has increased in 125 indigenous food items (Eurola et al. 1989, 1991, 2004; Aro et al. 1997; Venäjänemä et al. 1996). The primary aim of the Finnish policy was a 10-fold increase in the Se content of all fruit and vegetables was reported in the years following initial Se applications, a...
before Se supplementation (except lettuce (Lactuca sativa L.) and spinach (Spinacia oleracea L.), for which Se contents were 0.01 and 0.02 mg/kg DM respectively; Eurola et al. 1989). After Se fertilisation ≥10-fold (and ≤100-fold) increases in the Se concentration of vegetable and fruit crops were reported (Eurola et al. 1989). Although the Se concentration of all crops has increased, more subtle effects have also been noted. For example, Se fertilisation has increased the Se concentration of oats (Avena sativa L.; Eurola et al. 2004). Not surprisingly, the grain Se concentration is greater in crops supplied with fertilisers incorporating Se at 10 mg/kg than at 6 mg/kg, and it is lower in grain from organic production systems in which no fertilisers have been added. The Se concentration of oat grain is higher in seasons of low precipitation, and cultivar differences have been detected in variety trials. The Se concentrations of meat, meat products, fish, dairy products and processed foods have all increased following the introduction of Se fertilisation (Eurola et al. 1991); for example, for pig muscle meat and liver the Se concentrations were found to have increased from 0.08 and 0.49 mg/kg respectively in 1985 to a peak of 0.30 and 0.73 mg/kg respectively in 1989 (Venäläinen et al. 1997).

Similarly, the Se concentrations for cattle muscle and liver increased from 0.07 and 0.28 mg/kg respectively in 1985 to 0.21 and 0.51 mg/kg respectively in 1989. Based on average Finnish diets, it has been reported (Eurola et al. 1991) that there was an increase in Se intake from 25 μg/d per capita in 1975–6 to 124 μg/d per capita in 1989, and an increase in the consumption of Se from all foodstuffs. Notably, for cereals the increase in Se consumption was from 9 to 30 μg/d per capita between 1975–6 and 1989. Over the same period the increase in the Se consumption (μg/d per capita) was from 0 to 4 for vegetables and fruit, from 7.7 to 45 for meat, from 7.9 to 12 for fish and from 5.4 to 32 for dairy products and eggs (Eurola et al. 1991). Furthermore, a concomitant increase in blood (Varo et al. 1988) and serum (Wang et al. 1998) Se concentrations has been reported. For example, for Finnish children aged <15 years of age, the increase in mean serum Se was from 0.87 (range 0.54–1.44) μmol/l in 1985 to 1.26 (range 0.96–1.57) μmol/l in 1986 (Wang et al. 1998). Similarly, in adults, serum Se increased from 1.04 (range 0.62–1.35) μmol/l in 1985 to 1.30 (range 0.87–1.72) μmol/l in 1986. These increases have been subsequently maintained. Increases in the Se status of Finnish human milk between 1987 and 1995 have also been noted (Kantola & Vartiainen, 2001). Thus, the use of Se fertilisers in Finland has increased the crop Se content, increased dietary Se intakes and increased the Se status of the Finnish population (Rayman, 2002).

**Genetic biofortification**

Although it may be possible to increase the consumption of crop species that are genetically predisposed to accumulate more Se, dietary diversification is not always feasible (Rayman, 2002). However, within-species genetic variation could be used to increase the delivery of Se to human diets, i.e. through genetic biofortification (Lyons et al. 2004). In the first instance, it may be possible to simply select existing varieties of crops that accumulate more Se. In the longer term, it may be possible to breed crops for increased Se concentration.

There are few data on varietal differences in Se accumulation for most crop species. However, in the most detailed study reported to date Lyons et al. (2005a) have surveyed grain Se concentrations in commercial and advanced breeding lines of wheat, in ancestral diploid (Aegilops tauschii (Coss.) Schmal.) and durum wheats (Triticum dicoccum (Schrank) Schub.) and their progeny, in wheat landrace accessions, in wheat recombinant inbred and doubled haploid mapping populations and in other cereal grains from barley (Hordeum vulgare L.), triticale (X Triticosecale Wittmack ex A. Camus.) and rye (Secale cereale L.). Grain Se concentrations vary from 0.005 to 0.720 mg Se/kg, although most of the variation in grain Se from these species is attributed to soil factors. However, A. tauschii accumulates most Se in the grain and there is therefore the potential to breed for increased grain Se concentration in wheat (Lyons et al. 2005a).

In other crops, 4-fold differences in shoot Se accumulation between four Lycopersicon cultivars (tomatoes and relatives) grown at low sulfate levels have been reported (Pezzarossa et al. 1999). Differences in short-term net Se uptake and shoot Se concentration have also been noted amongst eight Lycopersicon esculentum L. cultivars and six other Lycopersicon species, with greater variation in shoot Se concentration between wild Lycopersicon taxa than between cultivated Lycopersicon taxa (Shennan et al. 1990). Variation in Se accumulation has also been reported for soyabean (Glycine max (L.) Merr.; Yang et al. 2003; Zhang et al. 2003) and onion (Allium cepa L.; Kopsell & Randle, 1997), whilst Se accumulation in rapid-cycling Brassica oleracea L. has been shown to be moderately heritable, with expected gains of 5% per cycle of recurrent selection (Kopsell & Randle, 2001).

In non-crop species shoot Se concentrations have been found to vary amongst sixteen populations of Stanleya pinnata by 1.4-fold–3.6-fold and shoot Se concentrations correlate with the Se concentration of the soil from which the populations were originally collected (Feist & Parker, 2001).

For a given crop species, if sufficient genetic variation exists in Se accumulation, and if this variation is heritable, traditional breeding programmes could be developed that would provide an alternative to agronomic biofortification and thus minimise the need to use Se fertilisers except at the lowest soil Se concentrations (Lyons et al. 2004, 2005a).

In addition to identifying suitable germplasm for breeding, accelerated breeding strategies to increase Se concentration in crops may also be possible. For example, Se accumulation can be quantified in different accessions of model crop or non-crop plant species for which genetic maps are available. Inbred progeny from crosses between these two accessions can then be used to map Se accumulation to specific chromosomal loci, i.e. quantitative trait loci analyses (Vreugdenhil et al. 2003; Wissuwa, 2005). Following the identification of quantitative trait loci impacting on shoot Se accumulation, for example, candidate
genes or loci could be resolved through fine mapping, and sequence information could be used directly, for gene-based selection or marker-assisted breeding. An advantage of this strategy is that knowledge of the genes and/or chromosomal loci controlling Se accumulation in one plant species could be used in a different target crop species. It is also possible to devise breeding or selection strategies (conventional or through genetic modification) for increasing shoot Se concentration based on existing knowledge of Se (and S) uptake and assimilation. For example, overexpressing ATP sulphurylase and/or genes involved in glutathione synthesis increases shoot Se accumulation in transgenic *B. juncea* (Pilon-Smits *et al.* 1999; Bañuelos *et al.* 2005), whilst overexpressing a Sec methyltransferase gene that methylates Sec to methylSec in *A. bisulcatus* increases Se accumulation in transgenic *A. thaliana* and *B. juncea* (LeDuc *et al.* 2004).

**Perspective**

Se intake and status in the UK population can be increased in the short term through agronomic biofortification. The pasture and forage sector already uses commercial Se fertilisers and an increased usage in this sector could increase dietary Se intakes through meat and dairy products. However, in order to provide adequate quantities and forms of Se for the widest possible number in the population Se fertilisation of crops for direct human consumption is likely to be needed. Such a strategy has been adopted in Finland, and there is substantial evidence to demonstrate that this strategy is biologically safe and environmentally acceptable (Wang *et al.* 1994; 1995; Mäkelä *et al.* 1995). From a crop perspective, antagonistic and synergistic interactions between Se and S will occur during plant uptake that may affect crop quality (White *et al.* 2004). These interactions will depend on the prevailing relative concentration of each of the elements in the soil. However, at low external S, and under low rainfall conditions, Se fertiliser application rates of $\leq 200 \text{ g Se/ha}$ have not been found to induce toxic effects or to retard growth in a low-yielding wheat crop (Lyons *et al.* 2005b).

In cereals selenomethionine is the dominant organic form of Se. Wheat is the most efficient accumulator of Se within the common cereal crops (*wheat* $>$ *rice* $>$ *maize* $>$ *barley* $>$ *oats*) and it is one of the most important Se sources for human subjects in the UK (Lyons *et al.* 2003). Thus, wheat is an obvious target crop for agronomic biofortification to increase the dietary Se intake, and thus the Se status, of the UK population. Currently, the average Se level in the grain of UK wheat is 25–33 μg Se/kg (Adams *et al.* 2002). Since the application of 10 g Se/ha applied as Na$_2$SeO$_4$ to the soil or as a foliar feed is likely to increase grain concentrations by 10-fold, a Se-fertilisation strategy to rectify dietary Se deficiency for large sections of the population would require only a small addition of Se through fertilisation. In contrast, vegetables and fruit deliver small proportions of minerals to the diet (White & Broadley, 2005). Thus, altering Se concentrations of these crops will have a minimal effect on dietary Se intakes. However, some vegetables contain organic forms of Se that make them attractive complimentary targets for biofortification. For example, Se-methylSec occurring in *Allium* and *Brassica* crops can be converted directly into methyl selenol, a bioactive substance that may protect against cancer (Lu *et al.* 1995; Ip *et al.* 2002; Whanger, 2004).

In addition to providing adequate quantities and forms of Se, an effective fertilisation strategy must be demonstrably safe to the environment. Although $>$95% UK soils for which geochemical data are available contain $<1$ μg Se/g, elevated soil Se levels are associated with restricted geological, alluvial and industrial features (Fig. 1) and thus Se-fertilisation strategies must be devised and monitored appropriately. In the UK the quality and quantity of baseline geochemical data for soils, stream sediments and surface waters will enable such monitoring to be undertaken with confidence. However, total Se concentration in soil does not necessarily indicate its bioavailability, and thus factors influencing Se bioavailability must also be considered. In the longer term, it may be possible to exploit genotypic variation in Se accumulation in crops to select or breed varieties with increased Se concentration (Lyons *et al.* 2004, 2005a), thereby minimising the need to use Se fertilisers in all but the lowest soil Se situations. This strategy may have economic advantages over a strategy based entirely on fertilisation.

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Enhancing the nutritional value of plant foods


