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REGULAR ARTICLE

Selenium fertilization strategies for bio-fortification of food: an agro-ecosystem approach

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Abstract
Aims Although the global importance of selenium (Se) deficiency to human and animal health has been recognized for decades, strategic Se fertilization interventions addressing agro-ecosystem specific conditions have not been developed. This research aims to identify such strategies based on an inventory of production-ecological factors controlling the potential impact of Se fertilizers on crop performance and nutritional content.
Methods The effect of agro-ecosystem properties on crop response to Se fertilization was assessed using a meta-analysis approach based on 243 experiments performed during 1960 to 2014.
Results The meta-analysis confirms the high impact of fertilization as an effective agronomic biofortification strategy. Site specific properties strongly affect crop responses to Se fertilization implying the need for tailor-made solutions. However, the minor influence of soil organic matter, total soil Se levels and acidity suggests that consideration of other agro-ecosystem properties like climate and bioavailable Se measurements is also required to optimize fertilizer strategies.
Conclusions Fertilization characteristics including formulation, dose and timing were found to be driving variables enhancing crop Se uptake. The highest uptake efficiencies are found for foliar and selenate based fertilizers. The current low recoveries and the scarce resource availability challenges the fertilizer approach to develop strategies that maximize the uptake efficiency of Se.

Keywords Agro-ecosystem approach · Biofortification · Fertilization · Meta-analysis · Micronutrients · Selenium

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Introduction

Selenium (Se) is an essential micronutrient for humans, animals and certain lower plants (algae, fungi, bacteria) but its supply through the food systems can vary widely. It has been postulated that a large part of the world's population (0.5–1 billion people) has suboptimal Se intake, and is hence at increased risk of several diseases (Combs 2001; Haug et al. 2007). The Se status of humans depends mainly on their Se uptake through their diet, while plant Se uptake is related to the geographical

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variation in soil's plant available Se level (Sillanpää and Jansson 1992) and the input via Se deposition (Wen and Carignan 2007). Natural deposition of Se varies depending on the vicinity to the coast, altitude and prevailing wind directions (Wen and Carignan 2007). For example, in the UK, Haygarth (1994) estimated a Se deposition ranging between 2 and 7 g ha^{-1}.

The distribution of Se levels in the world is very uneven, usually ranging from near zero up to 1200 mg kg^{-1} in seleniferous soils (Oldfield 2002). Selenium in the soil is ultimately derived from the parent material. Its content markedly depends on the origin and geological history of soil, and is controlled by mineralogy, weathering degree and prevailing soil formation processes (Hartikainen 2005). High Se soils largely come from sedimentary rocks (especially Cretaceous sediments) whereas low Se soils are typically derived from igneous rocks and found in regions with limited atmospheric deposition and high erosion rates (Christophersen et al. 2012). Se levels are often higher in the topsoil than in the local bedrock due to root uptake by plants and long term accumulation of atmospheric deposition. Se deficiency occurs when Se levels in soil are below 0.6 mg kg^{-1} (Gupta and Gupta 2000) or when prevailing soil conditions reduce plant availability of the Se present.

Although the global importance of Se deficiency has been recognized for decades, strategic micronutrient interventions to overcome this deficiency are still limited. Basically, there are two groups of fortification strategies to increase Se intake by humans. The first strategy entails the direct increase of Se intake by either supplementation of livestock, direct food fortification or supplementation with Se pills. In the second strategy agronomic activities like plant breeding and fertilization are used to increase Se levels in staple food crops. Which strategy works best depends on the natural, societal and economic properties of local agro-eco- and food systems (Miller and Welch 2013). An agronomic biofortification example is the Finnish government who have made it mandatory to add selenate to all multi-element fertilizers to overcome Se deficiency in Finland. Because of the worldwide relationship between available Se in soil and uptake by plants (Sillanpää and Jansson 1992), adapting the fortification strategy to local properties of agro-ecosystems may target specific Se deficient areas with least exhaustion of the world's scarce Se resources (Haug et al. 2007; Voortman 2012) and minimal adverse environmental side-effects (Mäkelä et al. 1995).

The entrance of Se into the terrestrial food chain is primarily dictated by the availability of Se in soil for plants. This bioavailability of the Se that is present in soil depends on the predominant chemical speciation as Se can exist in different oxidation states varying between plus six and minus two, including selenate, selenite, elemental Se and selenide, but also catenated species (Hartikainen 2005). Each of these compounds differ in bioavailability. The Se speciation in soil is basically controlled by three mechanisms: oxidation vs. reduction, mineralization vs. immobilization, and volatilization. The rate coefficients of these processes vary depending on Se species, microbial activity, pH and redox conditions, and soil properties (Chasteen 1998; Dungan and Frankenberger 1999; Stavridou et al. 2012). Plants acquire Se predominantly as selenate, but are also able to take up selenite and Se containing amino acids (Hopper and Parker 1999; Zhao et al. 2005).

An essential part of a resource efficient and sustainable agronomic fortification strategy includes proper use of Se fertilizers that takes the spatial soil variability, climatic conditions, and cropping systems into consideration. Inorganic fertilization is the most common practice to enhance Se levels in crops (e.g., Gissel-Nielsen and Bisbjerg 1970; Mikkelsen et al. 1989; Lyons et al. 2004a; b; Broadley et al. 2006). It is generally assumed that only a small portion (<5 %) of soil applied Se is utilized by plants (Haug et al. 2007). The effectiveness of Se fertilization depends on Se species, fertilizer dose, application technique, timing, and prevailing soil properties: the uptake efficiency can range from less than 1 to more than 50 % (Mikkelsen et al. 1988; Johnsson 1991; Yläranta 1985, 1990; Tveitnes et al. 1996; Sharma et al. 2009; Stroud et al. 2010a; Keskinen et al. 2010; Longchamp et al. 2012; Kikkert et al. 2013). Common agricultural practices as liming, irrigation, fertilization with nitrogen, phosphorus and sulfate also affect the Se uptake due to natural enrichment of fertilizers with Se, anion competition during uptake, and enhanced Se retention or dilution by increased yield potential (Williams and Thornton 1972; Mikkelsen and Wan 1990; Dhillon and Dhillon 2000; Zhao et al. 2007; Stroud et al. 2010b; Lee et al. 2011). Studies addressing the interaction between Se fertilization, soil properties, crop species and agronomic practices are however scant, hampering the development of a sustainable fertilizer strategy. In addition, experimental results differ due to methodological issues which should also be addressed (Bitterli et al. 2010). Fertilization strategies should be based on generic principles that are derived from systematic identification of relevant factors, in order for application practices to be effectively tuned to location specific characteristics.

To guide strategic and effective Se fertilization, we aim to assess the impact of fertilizer strategies across agro-ecosystems in relation to soil and crop properties. Using a meta-analysis approach we quantify the mean influence of soil properties, crop species and agronomic practices (describing specific characteristics of agro-ecosystems) on the crop response to Se fertilization. Meta-analysis is a statistical technique that reckons with methodological differences between studies and integrates independent data quantitatively (Gurevitch and Hedges 1999, 2001). We hypothesize that site specific agro-ecosystem properties are dominant factors controlling crop responses to Se fertilization. More specifically, we address the following objectives: 1) to determine how much of the variation in crop Se response is related to fertilization characteristics versus soil and crop properties, and 2) to assess whether methodology, management and environment have a consistent impact on crop Se response to Se fertilizer species.

Material and methods

The average response of crops to Se fertilization was quantified across a large number of studies varying in cropping systems, climatic conditions, agro-ecosystem properties, and fertilizer strategies (Gurevitch and Hedges 2001; Ros et al. 2009, 2011). Scientific databases with English journals only were searched in January 2014 using keywords "selenium" in combination with "fertilizer", "fertilization", "uptake", "amendment", or "additive" over the period 1960 to 2014. Crop specific studies were additionally included by a search with the keyword "selenium" in combination with crop names "wheat", "cereal", "maize", "grass", or "rice". A total of 218 studies were collected, of which 94 studies included reliable data for a meta-analysis. Papers were excluded from analyses when missing quantitative information on: Se content or Se uptake, the number of replication and fertilizer dose. A full description of data collection, analysis procedure and the main data derived from each paper is available as Supporting Information.

Meta-analyses generally makes use of standardized metrics of an effect size and their associated sampling variances (Gurevitch and Hedges 2001). Effect size metrics that have been used in ecological and soil science meta-analyses include the standardized mean difference, Pearson's correlation coefficient, and the log response ratio (Hedges et al. 1999). We used the commonly used natural log of the response ratio as the effect size in this study, because it quantifies the proportionate change resulting from experimental manipulation (in our case, Se fertilization). For the remaining of this paper we abbreviate the 'natural log response ratio' as 'response ratio'. The response ratio is the relative change due to a treatment: it is calculated by dividing the mean crop response of a fertilized treatment by the mean of an unfertilized treatment. The advantage of using the response ratio has been demonstrated by Hedges et al. (1999). In this study the response variables are both Se content of the crop (mg Se/kg dry weight) and Se uptake (g Se/ha). Se uptake is the product of Se content and crop yield. Take note that this analysis focusses on the crop response to Se fertilization and that it does not answer how natural crop Se levels are controlled by agro-ecosystem properties. Mean crop responses of experimental and control groups with their standard deviations and replicates were collected from each study. Studies which did not report a statistical variance were also included by using an arbitrary SD value based on a coefficient of variation (CV) of 1.25 times the average CV in the other studies, taking into account crop specific differences for field and pot experiments. Unidentified Error bars were assumed to represent the standard error.

Data was subdivided into various groups related to factors that could affect Se content or uptake of crops. The factors included were: location, year, basic fertilization doses (with N, P_2O_5, K_2O or S), soil properties (Se, clay, pH and organic C), fertilization characteristics (Se species, application form, timing and dose), and crop properties (crop species, crop part analyzed). Response data were normally distributed.

Publication bias (under-reporting of experiments without significant results) can lead to an overestimation of the fertilizer induced crop response. Rank correlation tests of Kendall and Spearman (Rosenberg et al. 2000) were applied to test the presence of publication bias. Fail-safe numbers (Rosenthal 1979) were also calculated in order to know the number of non-significant, unpublished or missing studies that need to be added in order to change the outcomes of current meta-analysis. If this number is large relative to the number of observed studies (Gurevitch and Hedges

2001 gave a threshold of >5 x n + 10 with n the number of observed studies), there is confidence that the observed result, even with some publication bias, is a reliable estimate of the crop response to Se fertilization.

Meta-analytical models assume independence between observed effects among studies. In practice, dependencies arise due to multiple treatment studies (e.g., multiple fertilizer doses are compared with a common control group), multiple endpoint studies (e.g., multiple crop parameters are determined on the same sample) or other forms of clustering (e.g., observations derived from the same research group) (Gleser and Olkin 2009). We accounted for this non-independence by using multivariate meta-modelling with restricted maximum-likelihood estimation, as implemented in Metafor (Viechtbauer 2010). Paper number was used to specify the random-effects structure of the model. Crop responses among studies were assumed to be independent while effects within a paper receive correlated random effects assuming a symmetric compound structure. Pseudo R^2 values (McFadden's method) and Akaike's Information Criteria (AIC) were used to compare regression models. The best model is characterized by high R^2 and low AIC values.

Results

Dataset characteristics

We collected observations from 94 papers, 243 experiments and 3865 treatments where the effect of Se fertilization was quantified. The majority of observations (n = 2493) were taken from field-experiments while the remaining (n = 1299) were collected from pot experiments in greenhouses or from growth chamber trials using culture solutions. As this study is restricted to English journals most experiments were performed in the northern hemisphere. On a continental level, about 39 % of the experiments were performed in Europe, 28 % in North America, 17 % in Australia (particularly New Zealand) and 5 to 6 % in each of Asia, South America and Africa. The most common crops were grassland and cereals: together they comprised 64 % of the collected data. The remaining crops included herbage crops (14 %), maize (5 %), and soybean and rice (4 %). Most observations were done on grains and shoots; only 20 % included analysis of crop roots and straw. Crop yield was usually not given. This is corroborated by the fact that the majority of the observations (81 %) determined Se content in the crop rather than Se uptake (Fig. 2) as Se uptake is the product of concentration and yield. The most common fertilizers were selenate salts (56 % of the observations) followed by selenite (35 %). The remaining 9 % of the observations used mixtures of selenate and selenite (4 %), organic products, selenide or elemental Se (5 %). Fertilizer dose ranged from 0.5 to 13,500 g ha^{-1} with a median dose of 34 g ha^{-1} (assuming a soil density of 1350 kg m^{-3} and a soil layer of 10 cm when data were given in mass units). There is an uneven distribution in the amount of Se fertilizer applied in the analyzed studies; the majority supplied either less than 10 (32 %) or more than 80 g Se ha^{-1} (39 %, Fig. 3). This unevenness in the distribution may partly be due to the difference in application rate between the two most common types of Se-fertilizer. Fertilizer doses for selenate (median dose 14 g ha^{-1}) is substantially lower compared to selenite (median dose 280 g ha^{-1}, Fig. 3). Applied selenate has a higher efficiency, compared to selenite. In addition, fertilizer doses in pot experiments are usually higher than those in field experiments.

Relatively little is known regarding the soil properties involved (Fig. 4). The initial Se content of the soils was unknown in more than 50 % of the observations. Soil Se levels were usually determined by Aqua Regia extraction methods approximating the total Se levels in soils. Most of the soils had Se levels of less than 0.3 mg kg^{-1} but levels up to 4.5 mg kg^{-1} were also present. The majority of soils had clay contents between 5 and 15 % indicative for texture classes ranging from loamy sand to silty loam. About 15 % of the soils were classified as soils with clay contents between 15 and 35 % and only 7 % had more than 35 % clay. Soil pH ranged from 4 to 8.5 of which 12 % had pH values below 5.5, 34 % with pH values between 5.5 and 6.0 and about 36 % with pH values above 6. Soil organic matter ranged from 1.0 g C kg^{-1} in a sandy soil up to 551 g C kg^{-1} in a peat soil (assuming 58 % of organic matter to be C). The majority was classified as mineral soils.

Overall crop response

Application of Se fertilizers had an overall positive effect on Se uptake of crops ($P < 0.05$). Selenium uptake by crops increased on average by more than 900 % (across all observations), indicating that significant amounts of Se can be taken up by plants irrespective of specific agro-ecosystem properties. This effect may be overestimated due to a strong bias in our dataset ($P < 0.001$) towards a positive crop response to Se fertilization. This is not surprising knowing the ability of crops to take up selenate and selenite and the fact that most studies are done on Se deficient soils. Nevertheless, the fail-safe number of around 0.4 billion indicates that crops positively respond to Se fertilization.

When distinguishing between field, pot and growth chamber experiments (Fig. 1) crop response to Se fertilization is significantly positive when the response ratio and its confidence interval are greater than zero (dotted black line). Across all observations, Se fertilization increased Se uptake by 543 % in field experiments, by 1140 % in pot experiments and by >5000 % for solution cultures performed in growth chambers. This strong increase in solution cultures is not surprising since the control treatment in these experiments is usually characterized by extremely low Se concentrations. Possibly this positive effect may be even larger as volatilization and transfer from high Se-treatments to control and low Se-treatments may occur in growth chambers, and when poorly ventilated, also in greenhouses (Terry et al. 2000). These differences emphasize that laboratory results are not simply applicable to a field situation. The observations of aquatic solution cultures are therefore removed from further analysis and discussion.

Crop responses almost doubled when experiments were performed under optimum and controlled environmental conditions in greenhouses compared to field trials (Figs. 1 and 2a). This was partly due to substantially higher fertilizer doses used in the greenhouse experiments. Both crop Se uptake and Se contents showed a similar response to fertilization. Differences between crop parts were also small: the average crop response ranged from 800 to 1000 % with the smallest response observed in roots and the highest response in grains. Differences between continents were not significant suggesting that observations derived from temperate regions are applicable to the tropics as well (data not shown). Possibly due to the fact that this study is restricted to English journals, the number of experiments performed in the tropics is relatively small, and additional data is necessary to prove this suggestion.

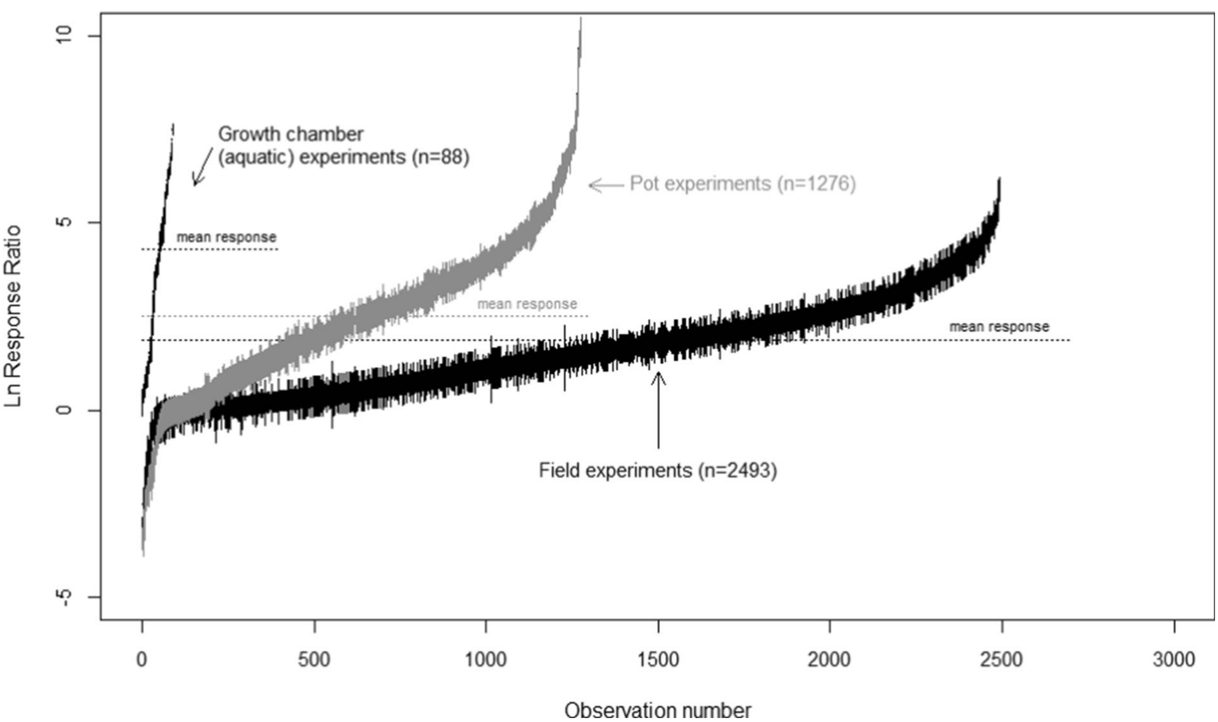

Fig. 1 Cumulative meta-analysis: response to Se fertilization for field, pot and growth chamber experiments. A response of zero means no effect (lnRR = ln(MeanFertilized/MeanUnfertilized)). Vertical lines represent 95 %-confidence intervals for individual experimental units. Observations are in ascending order

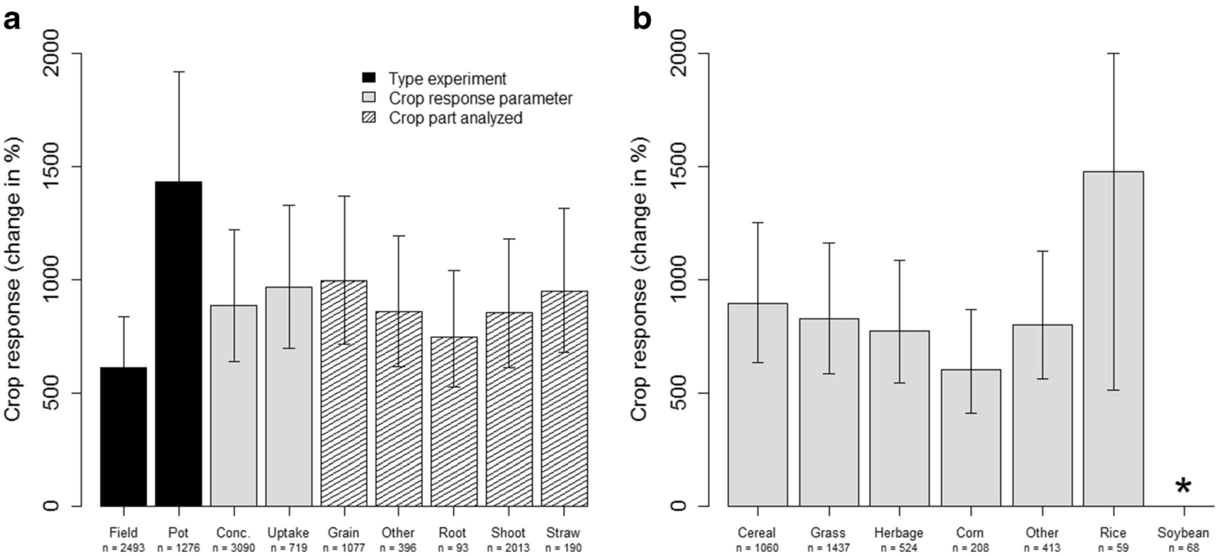

Fig. 2 Averaged effect of methodology (part **a**) and crop species (part **b**) on crop response (change in %) to Se fertilization. *Error bars* are 95 %-confidence intervals. *Asterisk* denotes data removal due to unrealistic crop response

Crop responses to Se fertilization strongly varied between studies: about 58 % of the total variance could be explained by variation between studies (the random-effect component), indicating that site specific properties or methodological aspects create substantial variation in crop responses. While accounting for this between study variation, the most important factors controlling the crop response were identified as fertilization characteristics (Se species, dose, application and timing; see Appendix). Fertilization characteristics increased the pseudo R^2 value of the null model, consisting of the random effects only, by 7 to 13 %. Soil and crop properties seem less relevant: pseudo R^2 value increased with less than 5 %. Hence, Se fertilization is always effective to increase crop Se uptake while the effectiveness can be increased by proper fertilizer management.

Fertilization factors

The most important factors controlling crop response to Se fertilizers were application time, chemical speciation, and fertilizer dose. Crop Se uptake increased with 400 % at low Se doses (< 10 g ha^{-1}) whereas it increased up to 1500 % when more than 40 g Se ha^{-1} was applied (Fig. 3a). Application of elemental Se or organic Se fertilizers had almost no effect on Se uptake whereas selenate application resulted in the highest crop response. Selenate seemed far more effective than selenite: the average crop response was +743 % for selenite and +1243 % for selenate despite the fact that the median application rate was higher for selenite (280 g ha^{-1}) than for selenate (14 g ha^{-1}). Thus selenate was on average over all treatments and experimental conditions 33 times more effective than selenite (% crop response per gram applied Se). Soil application via granules or seed enrichment (via coating or soaking of the seeds) could result in similar responses to soil applied fertilizer. Foliar application seemed to be most effective: the average crop response almost doubled the response of soil applied fertilizers (Fig. 3a). Most foliar and liquid fertilizers were applied during the vegetative stage of crops, enabling and stimulating quick uptake of applied Se. As foliar fertilizer is applied before extensive leaf cover, it is in fact a combination of foliar and soil-applied Se. Crop responses decreased with time between fertilizer application and crop harvest. Fertilizers applied before the growing season (usually in spring) increased Se uptake by almost 900 % whereas in season application increased Se uptake by 2000 %. Residual effects were observed of up to 4 years after fertilizer application where the effects of soil applied Se lasted longer than foliar applied Se.

Agro-ecosystem properties

Crop response differed between different crop species with slightly higher responses for cereals than for grasses and corn (Fig. 2b). The crop response for soybean is removed for realistic scaling of the graph; the

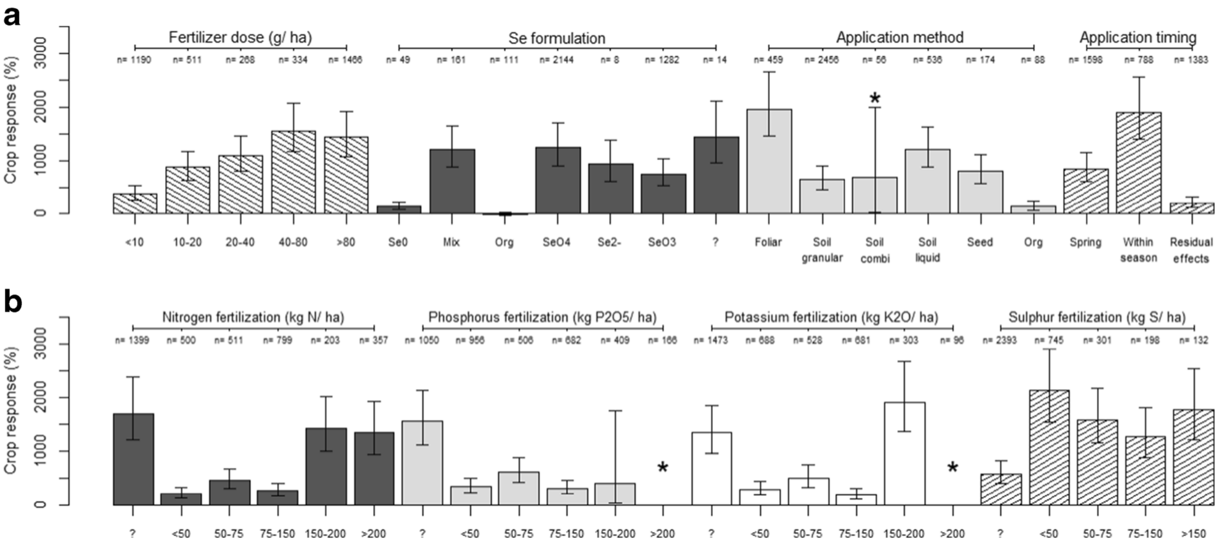

Fig. 3 Averaged effect of fertilizers issues (part **a**) and NPKS fertilization (part **b**) on relative crop response (change in %) to Se fertilization. *Error bars* are 95 %-confidence intervals. *Asterisk* denotes data removal due to unrealistic crop responses

observed response was unusually high (compared to all other crops) and likely related to the limited number of studies involved (n = 2). Nitrogen fertilization resulted in substantially higher crop responses to Se fertilization, in particular when more than 150 kg N ha^{-1} was applied (Fig. 3b). Phosphorus and potassium fertilization had minor effects on Se uptake within the common range of P or K doses. In contrast, crop responses tend to decrease with sulfur doses except for doses above 150 kg S ha^{-1}. Experiments missing the information on NPK fertilizers had significantly higher crop responses. The reason for this finding remains unknown. The soil properties pH, organic carbon and Se content had only a minor (although significant) effect on the variation in crop responses. Crop responses were highest in soils with Se levels below 0.2 mg kg^{-1} and decreased down to 900 % for all other soils. Soil acidity had no clear effect on the fertilizer induced crop response with one exception for high responses in alkaline soils (> 3300 % when pH > 8). Soil organic matter had no effect for these cases where the soil organic carbon content was determined. Crop responses linearly decreased with clay content Fig. 4.

Estimating crop response to Se fertilizers

We combined the most relevant factors in one multilevel predictive model to estimate the crop response to Se fertilization (see Appendix for details). Considering all factors, fertilizer type and dose explained about 69 % of the variation within studies. Crop species, experimental type, and soil properties such as pH, organic matter, initial Se levels and NPKS fertilization had a significant impact on the predicted crop response, but the model improvement (derived from pseudo R^2 values and AIC criteria) was small. The best estimate of the crop response to Se fertilizers within studies, could be derived from a combination of fertilizer dose, fertilizer type, application strategy and the clay content of the soil. To illustrate the impact of fertilizer dose and timing, crop responses were estimated for a sandy soil fertilized with selenate (soil or foliar applied) and selenite (Fig. 5a). In this situation, selenate fertilizers had higher uptake efficiencies than selenite fertilizers: applying both fertilizers at a dose of 14 g ha^{-1} (the median dose for selenate fertilizers) resulted in a crop response of +590 % for selenate and +260 % for selenite (Fig. 5a). When both fertilizers are applied at similar and low doses it appears that selenate fertilizers are almost twice as effective as selenite fertilizers. Note that this difference in effectiveness is dose dependent; in several experiments selenate has often been found to be 10–20 times more effective than selenite, likely due to a combined effect of effectiveness and dose. The residual effect of both fertilizers decreased over time with the highest decrease for selenate fertilizers (Fig. 5b). The decrease over succeeding years was relatively smaller for selenite than that for selenate indicting that relatively more Se became unavailable for plant uptake presumably due to (irreversible) sorption to soil particles.

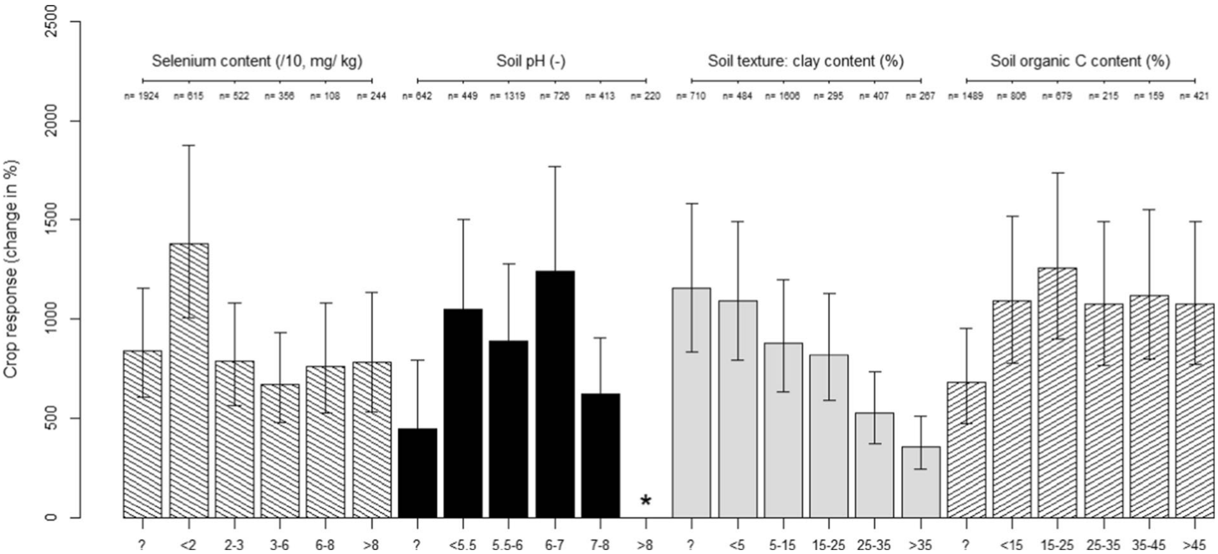

Fig. 4 Averaged effect of soil properties as selenium content, pH, clay and organic C content on crop response (change in %) to Se fertilization. *Error bars* are 95 %-confidence intervals. *Asterisk* denotes data removal due to unrealistic high crop responses. Classes denoted by "?" include all trials where soil properties are unknown

Discussion

Agricultural crops can be Se deficient either because of low Se levels in soil or because of poor plant availability of the Se present in the soil or a combination of both. Our analysis confirms the potential of fertilization as agronomic biofortification strategy by the overwhelming evidence that almost any fertilizer application is able

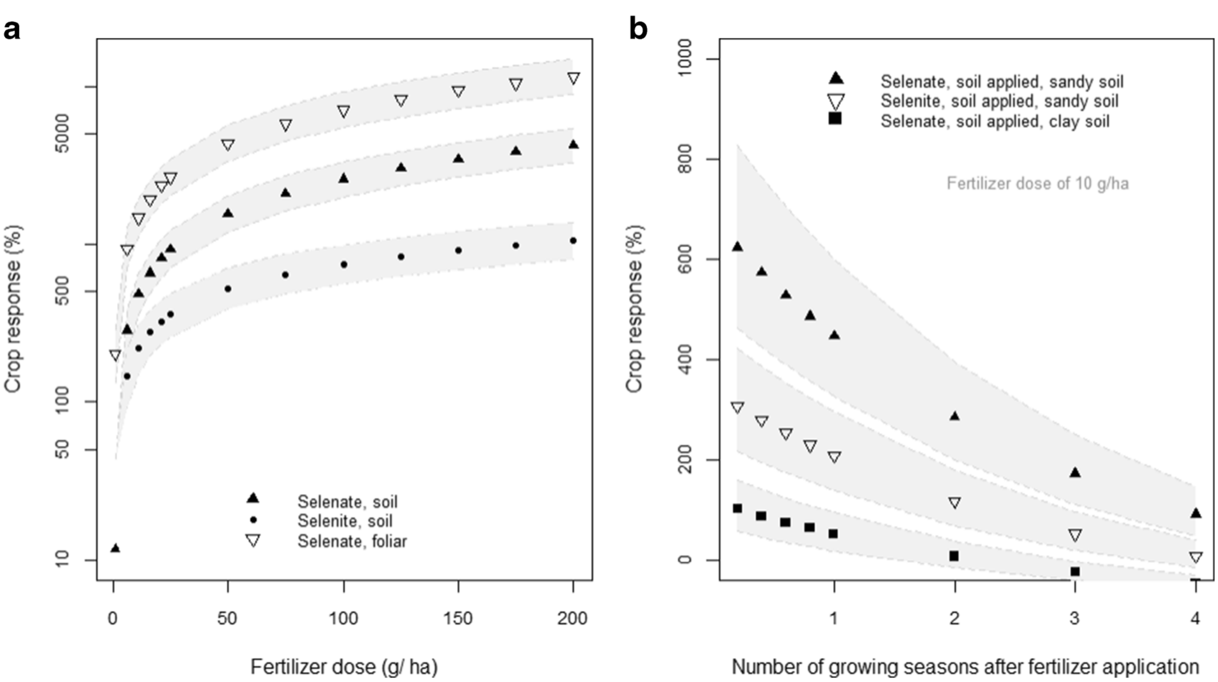

Fig. 5 Predicted crop response (%) to fertilizer dose for soil and foliar applied selenate, soil applied selenite on a sandy soil (part **a**) and residual effects over time for soil applied selenate in a clay and sandy soil and soil applied selenite in a sandy soil, applied with a dose of 10 g Se ha^{-1} for all fertilizers (part **b**)

to increase crop Se levels. The average increase in Se uptake due to fertilization is +543 % across all studies. The most illustrative example is the agronomic biofortification approach of the Finnish government who obliged to add selenate to all multi-element fertilizers. The effect of adding Se to fertilizers has been marked: Se levels have increased in 125 indigenous food items including wheat, meat and dairy products (Eurola et al. 1991) whereas the human intake increased from 25 μg day^{-1} in 1975 to 124 μg day^{-1} in 1989. The strong variation between studies (crop responses range from <65 % up to >3500 %) suggests that site specific agro-ecosystem properties are likely to control the crop uptake of applied Se. This suggests that any desired increase in crop Se levels can be achieved by choosing a proper site specific Se fertilizer strategy. In addition, large variability in crop responses clearly shows that a sound understanding of the soil-plant system is necessary to make realistic use of such data in decision support systems. Some therefore argue that currently available data is unsuitable to account for spatial and temporal variation in Se response to fertilization, limiting the use of mathematical models to optimize fertilizer doses locally (Bitterli et al. 2010), an argument confirmed by our meta-analysis. Others are more optimistic on the potential of GIS modelling tools (Spadoni et al. 2007; Winkel et al. 2012) or suggest alternative strategies by combining highly enriched crop products (from highly fertilized fields) with common products grown on unfertilized soils for example (Haug et al. 2007). In any case, agronomic biofortification strategies need to address site specific properties in order to develop sustainable and resource efficient solutions to overcome Se deficiencies.

Feasible fertilizer and application technologies for Se have been studied since the 1960's (Gissel-Nielsen et al. 1984; Gissel-Nielsen 1998). Most of these experiments focused on various selenate and selenite salts, being applied as soil fertilizers or in combination with basic nitrogen or phosphorus fertilizers. We show that application technology and fertilizer strategy are highly important: crop responses increase with fertilizer dose and vary with Se speciation, application methodology and timing. The higher crop response to selenate fertilizers compared to selenite fertilizers is mainly due to the higher solubility and plant availability of selenate compared to selenite. When compared for a sandy soil and an equal dose for both fertilizer sources ranging from 5 to 200 g Se ha^{-1}, the uptake of selenate can be 2 to 4 times higher. We showed for example that selenate is almost twice as effective as selenite at a given dose of 10 g Se ha^{-1} for a sandy soil (Fig. 5). Comparing the uptake at different application rates for selenate and selenite increases the difference between both fertilizers. Crop Se levels rapidly increase after fertilization, but diminish after Se levels in soil solution decrease. Its half-life time has been estimated at 21 to 80 days in grassland ecosystems (Watkinson 1983; Shand et al. 1992; Rimmer et al. 1990; Bahners 1987), where others observed a positive crop response even after 3 years (Kiely and Crosse 1984; Culleton et al. 1997). Our analysis shows that the residual effect varies between soil texture classes and Se speciation (Fig. 5): crop responses diminish more rapidly when selenate based fertilizers are used, in particular in clayey soils. In addition, foliar applications are almost twice as effective as soil applied granular fertilizers or seed enrichment treatments. Knowing the impact of fertilizer type, application strategy and timing allows one to develop sustainable fertilization strategies targeting site specific causes for Se deficiency.

Knowing that mean Se levels in wheat vary from 7 to 22 μg kg^{-1} for UK and Scandinavian countries (Broadley et al. 2010), and a nutritional value of about 50 to 100 μg kg^{-1} required to ensure animal and human health (Hawkesford and Zhao 2007), a fertilizer induced increase in crop Se levels of about 500 % is sufficient to prevent Se deficiency in humans and feedstock. Assuming fertilizer recoveries of 10 % (Haug et al. 2007), wheat production of 7 tons ha^{-1} and that 50 % of the added Se ends up in the grains, about 4 to 13 g Se ha^{-1} should be applied to reach the required nutritional value. This estimated fertilizer dose falls within common fertilizer doses recommended according to Finnish and Canadian guidelines (Eurola et al. 1991; Hartikainen 2005; Gupta 1995; Broadley et al. 2006). Others have found slightly higher recoveries of 14 to 18 % in grains (Lyons et al. 2004a; b; Lyons 2010), 8 to 32 % in wheat (Eich-Greatorex et al. 2007), and <5 to 25 % in grains (Tveitnes et al. 1996) whereas results of Yläranta (1990) and Ekholm et al. (1995) suggest that more than 90 % of applied Se is unavailable for crop uptake. The low recovery of applied Se is confirmed by our meta-analysis in spite of the high crop responses observed. The use of the response ratio in meta-analysis limits accurate estimates of crop uptake efficiencies, but using the predictive model with fertilizer dose, Se species and application strategy as explanatory variables, we estimated that 30 to 60 g soil applied selenate, 190 to 600 g soil applied selenite and 4.5 to 10 g foliar applied selenate per hectare are needed to increase the Se uptake of wheat from 7 up to 100 μg kg^{-1}. Consequently, the average Se recovery remains below 30 % even for the foliar applied Se. This low recovery for foliar applied Se may be partly ascribed to the fact that is generally applied during the vegetative stage of crops before extensive leaf cover, a result of which it is in fact a combination of foliar and soil-applied Se. Nevertheless, the efficiency of foliar applied Se is on average 8 times more efficient than soil applied fertilizers suggesting that foliar is preferred over soil application.

Fertilization with macronutrients might affect the Se content of crops (Stroud et al. 2010a, b; Lee et al. 2011) since SO_4^{2-} and PO_4^{3-} compete with Se for crop uptake (Gupta and Gupta 2000; Severson and Gough 1992) and macronutrients generally alter root growth (resulting in a larger volume soil to explore) and aboveground biomass development (resulting in decreasing Se concentrations). Our meta-analysis showed only a minor effect of macronutrient fertilization on crop responses to Se fertilization even when the different Se fertilizer species are taken into account. However, in particular for selenate fertilizers we observed a strong tendency for decreasing crop responses to Se fertilization with increasing S and P doses (not shown). Crop responses decreased almost linearly (2.5 times on average) with P and S dose. Use of selenite fertilizers weakens the observed tendency: differences due to S and P fertilizers became smaller. The reduced Se uptake at high P levels is not only due to ion competition during uptake but also due to co-precipitation. When phosphate fertilizers have been applied and precipitation of phosphate minerals occurs, Se remains fixed in the precipitate (Christophersen et al. 2012). Conversely, phosphate may also cause desorption of selenite ions bound to soil minerals, as phosphate is bound more strongly than selenite (Nakamaru et al. 2006). The observed decrease in Se uptake due to sulphate (Fig 3) has been explained by ion competition for transporters in plant roots (Terry et al. 2000; Christophersen et al. 2012). The reducing effect of sulphate (in particular for selenite) has been found in previous studies (Dhillon and Dhillon 2000; Lyons et al. 2004a, b; Mikkelsen et al. 1989; Gissel-Nielsen 1973).

Nevertheless, our analysis suggests that Se fertilization characteristics such as Se chemical speciation, dose, timing and application method counteract any negative effects of macronutrient fertilizers. The most important macronutrient effect is likely caused by increased crop production since high fertilized fields have substantial higher Se yields than low fertilized fields. Similar findings might be true for agronomic practices such as liming, manuring or irrigation, practices that are known to affect Se availability in soils (Gissel-Nielsen 1971; Gupta and Winter 1981; Bisbjerg and Gissel-Nielsen 1969; Davies and Watkinson 1966; Johnsson 1991). A more detailed analysis of liming and irrigation experiments is necessary to quantify their influence on crop Se uptake and to develop tailor-made Se fertilizer strategies reckoning with site specific agronomic activities or farm strategies.

To guide strategic fertilizer interventions it is important to understand both the fate of Se in soil and causes for its deficiency related to specific ecological circumstances (Eurola and Hietaniemi 2004). Because chemical, biological and physical soil properties vary among agro-ecosystems, it is not surprising that the capacity of soils to supply Se has a high spatial variability. Soil conditions such as pH, redox potential, soil texture and the contents of iron (hydr)oxides and organic matter strongly influence the Se speciation and subsequently its bioavailability to plants (Gissel-Nielsen et al. 1984; Mikkelsen et al. 1989; Hawkesford and Zhao 2007; Christophersen et al. 2012). Although soil properties influence Se levels in soil, the fertilizer induced crop response seems remarkably constant over different soil groupings varying in total Se levels, soil acidity and organic matter content. These findings suggest that the effectiveness of Se fertilization is partly affected by soil texture and likely controlled more strongly by other agro-ecological factors like climate related variables (unaccounted for in this study).

Soil texture might affect the fate of Se in soil due to the presence of clay minerals and texture induced water retention properties. An increase in clay content will enhance the sorption capacity of soils and likely decreases the plant availability of applied Se (Christophersen et al. 2012). This study indeed shows a decreasing trend in crop response with increasing clay content (Fig. 4). The capacity of soils to supply or retain Se also differ between Se deficient and Se rich soils, where the plant uptake of added Se varies irrespective of the total Se levels in non-deficient soils. The absence of this relationship in our dataset can be explained by the fact that Se levels were determined by Aqua regia extraction methods, a measure for total rather than bioavailable Se levels in soil. Low total Se levels in soil are associated with low plant availability, but high levels are not necessarily indicative for high bioavailability. Distinct differences in solubility of Se species in soil have led to the development of numerous single and sequential extraction procedures to extract a plant available Se fraction (Keskinen 2012), but none of these procedures is broadly applicable across agro-ecosystems. This might be the result of the fact that most Se in soil extractions is organically bound being less available for crop uptake. Weng et al. (2011) showed for example that the correlation with crop uptake increases when the extraction procedure differentiate between organic and inorganic Se. Up to now, the use of regionally calibrated soil test procedures is still the best option to optimize fertilizer doses while matching crop demand with Se availability in soil. Another option might be to predict bioavailable soil Se based on the combination of total Se levels with other agro-ecosystem properties like soil type and climatic data (e.g., Spadoni et al. 2007; Winkel et al. 2012). The most accurate indication is to measure the actual Se level in the crop. Although it is accurate, it is relatively expensive and impractical as laboratory results will be too late to be able to adequately amend Se levels if necessary.

Though Se is an essential element for humans and livestock, it has no essential function in plant nutrition. Numerous studies indeed show no gains or losses in crop yields or harvest indexes upon addition of Se fertilizers (Broadley et al. 2010). A few studies showed Se induced growth stimulation for ryegrass, lettuce and potato due to antioxidant production or upregulation of sulfate transport and assimilation (Hartikainen and Xue 1999; Xue and Hartikainen 2000; Turakainen et al. 2004; Van Hoewyk et al. 2008). In most cases however, growth stimulation plays only a minor role: both Se uptake and Se content showed similar responses to fertilization, suggesting that crop yield is rarely affected by Se fertilization (Fig. 2a). This might complicate the use of agronomic biofortification approaches since farmers are unlikely to fertilize Se without incentives or government regulations that would make doing so profitable or mandatory (Miller and Welch 2013).

The meta-analysis shows a strong crop response to Se fertilization, particularly in the first years after fertilization. Most of the applied Se however is immobilized in the soil. Frequent addition of phosphorus fertilizers and high manure inputs in arable fields might reduce the plant availability of selenium by co-precipitation and ion competition. It has been speculated that the long-term history of application of Se-poor commercial fertilizers in Western and Central Europe could explain the lower Se availability usually found in these areas (Christophersen et al. 2012). In the USA and Canada, by contrast, large areas of unfertilized prairie land are characterized by excellent bioavailability of Se resulting in Se-enriched cereals (Haug et al. 2007). A meta-analysis focusing on the crop response in unfertilized situations would be valuable to clarify the impact of human activities and related agro-ecosystem properties on natural Se uptake. This might also underpin the request for commercial fertilizers with high Se-P concentration ratios (Christophersen et al. 2000).

A possible drawback of agronomic biofortification via fertilization is the frequent need for regular applications, which makes this approach costly, difficult in logistic terms and potentially negative for the environment (Carvalho and Vasconcelos 2013). Food fortification has been identified as a resource-efficient way to increase human Se intake making it also possible to design integrated strategies in which Se is combined with other micronutrients such as cobalamin, zinc, iodine and bromine (Haug et al. 2007). Nevertheless, plant breeding (for enhanced Se uptake by eg modifications to rooting system) and fertilization are recognized as desirable and promising methods to increase the Se status for whole populations in a way that is safe, effective and in a suitable chemical form (Lyons et al. 2003; Lyons et al. 2005a; b; Lyons 2010). Se fertilization is also easy to combine with other fortification approaches whereas environmental concerns appear to be unfounded (Vuori et al. 1994; Oldfield 2002; Mäkelä et al. 1995; Wang et al. 1995).

The scarce resource availability of Se however might limit widespread application of Se fertilizers. Almost all of the Se produced worldwide is recovered during copper, nickel and zinc electrolysis. The US Geolocical Survey reports a global reserve base of 172 kton Se (USGS 2013). When one third of the world's arable land is fertilized at 10 g Se ha^{-1}, selenium reserves are expected to be exhausted in less than 40 years (White and Broadley 2009; de Haes et al. 2012) whereas plant uptake recoveries usually remain below 35 %. Although the USGA reserve assumptions are conservative and other Se sources are also abundant (e.g. coal), current industrial production is entirely insufficient to meet a possible demand from the food chain (de Haes et al., 2012). We agree with White and Broadley (2009) and Haug et al. (2007) that Se should be stockpiled for the nutritional security of future generations. These findings challenge the fertilizer approach to come with strategies that maximize the uptake efficiency of Se. Indeed, our meta-analysis shows that fertilizer strategies can be used to increase the uptake efficiency by matching fertilizer type, dose and application to the local demand including any residual effects of former fertilizations. Accurate soil tests predicting the soil Se supply will further improve the sustainability of fertilizer strategies.

Outlook

Using a meta-analysis approach we showed that Se fertilization has high potential to boost Se uptake by crops, and subsequently the Se intake of animals and humans. The wide variation in application and uptake suggests that agro-ecosystem properties strongly affect crop responses to Se fertilization, revealing that agronomic biofortification strategies need to search for tailor-made solutions that account for site specific properties. The minor influence of soil organic matter, total Se levels in soil, soil acidity and crop species suggests that other agro-ecosystem properties like climate related variables (unaccounted for in this study) might be stronger drivers for uptake. Moreover, accurate estimation of bioavailable Se pools in soil might improve the uptake efficiency of applied Se fertilizers. The current low recoveries and the scarce resource availability challenges the fertilizer approach to come with strategies that maximize the uptake efficiency of Se. In most arable crops, selenate foliar fertilization seems the most effective fertilizer strategy to enhance crop Se uptake.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

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