

1 **Hyperaccumulators of metal and metalloid trace**
2 **elements: facts and fiction**

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Abstract

BACKGROUND

Plants that accumulate metal and metalloid trace elements to extraordinarily high concentrations in their living biomass have inspired much research worldwide during the last decades. Hyperaccumulators have been recorded and experimentally confirmed for elements such as nickel, zinc, cadmium, manganese, arsenic and selenium. However, to date, hyperaccumulation of lead, copper, cobalt, chromium and thallium remain largely unconfirmed. Recent uses of the term in relation to rare-earth elements require critical evaluation.

SCOPE

Since the mid-1970s the term 'hyperaccumulator' has been used millions of times by thousands of people, with varying degrees of precision, aptness and understanding that have not always corresponded with the views of the originators of the terminology and of the present authors. There is therefore a need to clarify the circumstances in which the term 'hyperaccumulator' is appropriate and to set out the conditions that should be met when the terms are used. We outline here the main considerations for establishing metal or metalloid hyperaccumulation status of plants, (re)define some of the terminology and note potential pitfalls.

CONCLUSIONS

Unambiguous communication will require the international scientific community to adopt standard terminology and methods for confirming the reliability of analytical data.

Keywords: Hyperaccumulator, metallophyte, trace elements, metal, metalloid, hydroponic experiments. phytoextraction.

Introduction

The term 'hyperaccumulator' was devised by one of the present authors (Reeves) as part of the title of a paper reporting the extraordinary accumulation of nickel by the tree *Sebertia acuminata* (now *Pycnandra acuminata*) in New Caledonia (Jaffré et al. 1976; Swenson and Munzinger 2010). The term 'hyperaccumulation' can be found in Brooks et al. (1977) and in many subsequent publications, being used to describe accumulation of Ni to $>1,000 \mu\text{g/g}$ in dry leaf tissue. This level was chosen as being 100-1,000 times higher than that normally found in plants on soils not of ultramafic origin, and 10-100 times higher than that found for most other plants on Ni-rich ultramafic soils. Although there was some arbitrariness in the choice of this criterion, it was noted that in many ultramafic floras, Ni concentrations of 100-1,000 $\mu\text{g/g}$ are quite rare, and accumulation to

>1,000 µg/g seems to represent a distinct form of plant response, implying some characteristic and unusual metabolic functionalities.

An attempt to give greater precision to the definition of Ni hyperaccumulation was made by Reeves (1992) for Ni: “a hyperaccumulator of Ni is a plant in which a Ni concentration of at least 1,000 µg/g has been recorded in the dry matter of any above-ground tissue in at least one specimen growing in its natural habitat”. This indicates that the use of the term should not be based on analyses of whole plants or subterranean plant parts, (i) because of the difficulty of ensuring that the samples are free of soil contamination, and (ii) because plants that immobilize metals in the root system are relatively common, whereas active accumulation in above-ground tissues is more diagnostic of hyperaccumulation (Baker 1981; Baker et al. 1994b). To make the original definition even more precise, above-ground tissue should be regarded as plant leaves only for establishing hyperaccumulator status, and it is also important to note that the criterion for hyperaccumulation is thereby thus set at the organ level (leaves), and not at the level of specific tissues or organelles (e.g. epidermis) or the latex. Furthermore ‘accumulation’ should imply only active accumulation inside the plant leaf tissue, via the roots; passive accumulation via air-borne deposition on plant leaves is not to be considered when (hyper)accumulation is discussed.

This more detailed definition is also intended to clarify questions surrounding cases where (1) some specimens of a species may be found with >1,000 µg/g and others with <1,000 µg/g, or (2) a species has been found to take up high levels of a metal under artificial conditions, such as through substantial metal-salt amendments to an experimental soil or a nutrient solution. Plants would qualify as hyperaccumulators under case (1) but not under (2). Concentrations of metals can greatly differ between plant parts; in some plants metal concentrations in the xylem or latex are many times those in the leaf. Examples include *Sebertia acuminata* with 257,400 µg/g in latex and 11,700 µg/g in leaves (Jaffré et al. 1976) and *Phyllanthus balgooyi* with 90,000 µg/g in the phloem tissues and 16,000 µg/g in leaves (Hoffmann et al. 2003). It appears to be very unusual, however, for a plant to reach hyperaccumulator threshold concentrations in other organs or the latex/sap, but not in leaves. The implication of the phrase ‘growing in its natural habitat’ is that hyperaccumulators must achieve their high metal concentrations while remaining healthy enough to maintain a self-sustaining population.

Subsequent to its original publication, the terminology of hyperaccumulation has been expanded to elements other than Ni. A comprehensive discussion of the early reports on unusual accumulation of Zn, Cd, Pb, Co, Cu, Mn, Cr and Se is given in the review by Reeves and Baker (2000) and records of unusual accumulation of As have been noted by Reeves (2005). As the interest in plants accumulating these elements developed, the

concepts and definitions of hyperaccumulation have been extended. Malaisse et al. (1978) used the 1,000 µg/g criterion for Cu accumulation, and Brooks et al. (1980) argued for this to be applied also to Co. Reeves and Brooks (1983b) used the same criterion in discussing Pb, but for Mn and Zn, which are normally present at higher and more widely varying concentrations (about 20-400 µg/g), a 10,000-µg/g threshold was suggested by Baker and Brooks (1989), following the use of the term 'hypermanganèsofiphore' for plants with this level of Mn accumulation (Jaffré 1980). Normal Cd levels are so low (0.03-5.0 µg/g in most plant species) that those plants capable of concentrating this element to >100 µg/g should be regarded as Cd hyperaccumulators (Baker et al. 1994a), having significant phytoremediation potential.

We consider accumulation of major soil elements (Fe, Ca, Mg, Na and Al) to constitute a different phenomenon to hyperaccumulation of trace elements, and do not discuss these further here (for a discussion of Al accumulation see Metali et al. 2012).

The basis for hyperaccumulation threshold criteria

The metal supply to a plant ranges from deficiency to optimum and eventual toxicity, and differs greatly between elements, being particularly narrow for transition metals such as Zn, Cu and Ni (Clemens et al. 2002). When a species establishes on a soil with either a too low or a too high metal supply, adjustments will take place within the limits of phenotypic plasticity followed by adaptation and evolution of efficiency or tolerance in populations over time (Schat 1999; Pollard et al. 2002; Ernst 2006,). The uptake and metabolism of non-essential metals and metalloids (e.g. Cd, As, Pb) is not regulated as tightly as for essential metals (e.g. Zn, Cu) because of interference or lack of specificity of the ecophysiology of plants (Ernst 2006). There have been efforts to define typical concentrations of metals and metalloids in plants, and the worldwide 'standard reference plant' has elemental concentrations (µg/g) of Ni (1.5), Zn (50), Cd (0.05), Pb (1), Cu (10), Co (0.2), Cr (1.5), Mn (200), Tl (0.02), As (0.1) and Se (0.02) (Markert 1994; Dunn 2007).

The hyperaccumulation threshold criterion for Ni was not only chosen because it is 10-1,000-fold higher than the average concentration of that element in plant leaves but also because 1,000 µg/g seemed to separate two modes of a bimodal frequency curve (Brooks and Radford 1978; Brooks et al. 1979). These frequency curves showed more or less lognormally distributed concentrations up to about 1,000 µg/g and an outlying cluster at exceptionally high concentrations. This bimodal pattern is particularly apparent in phylogenetically restricted data sets, such as in the genus *Alyssum* in the Brassicaceae (Brooks 1987, 1998; Pollard et al. 2002). Such bimodality has also been found in some edaphically limited datasets of plants growing on ultramafic soils, such as a dataset from

temperate ultramafic plants which showed a sharp discontinuity, but not in a dataset with tropical ultramafic plants which showed an approximate lognormal distribution (Reeves 1992; Reeves et al. 2007).

Further (meta)analysis for a range of metals (Broadley et al. 2001; Watanabe et al. 2007) has dealt with accumulation of elements in plants, but do not clarify whether hyperaccumulators form a qualitatively distinct group (a bimodal pattern), which would indicate a different physiology, or whether hyperaccumulators are merely the tail of a positively skewed continuous (lognormal) distribution. Such datasets are not suitable for defining hyperaccumulation criteria because of the relative rarity of hyperaccumulators, making it statistically difficult to distinguish between bimodality and skewness. This is exemplified by the approximately 23,000 species within the Asterales, of which only 38 are hyperaccumulators under the current criteria (Broadley et al. 2001). Only datasets limited phylogenetically or edaphically (e.g. from metalliferous soils) could be of use in this respect. For phylogenetically limited datasets, there are however few candidates other than the genus *Alyssum*. On a global scale the genera *Phyllanthus* and *Psychotria* are some of the largest for Ni hyperaccumulators, but compared to the overall size of these huge genera the hyperaccumulators will still be a minority. On the other hand, the genus *Buxus* in Cuba has 17 Ni hyperaccumulators and 17 non-accumulators (Reeves et al. 1996), showing distinct bimodality. Much will thus depend on the selection of the genera and the geographical delimitation. Edaphically limited datasets may be inappropriate for statistical recognition of hyperaccumulators because of various forms of sampling bias, e.g. a specific search for new hyperaccumulators. This means that providing statistical evidence for a qualitatively distinct group and basing thresholds on the genus delimitation is extremely difficult.

Other criteria, not based upon nominal threshold values, could be considered to define hyperaccumulation. In particular, hyperaccumulators have a very high bioconcentration factor (shoot:soil ratio) as a result of their physiological make-up enabling active metal sequestration and concentration, and it has been suggested that this should be a critical factor in recognition of hyperaccumulators (Hobbs and Streit 1986). However, the bioconcentration factor in isolation cannot serve as a definition of hyperaccumulation when based on field-collected material, because it is manifested as a genotype \times environment interaction and is controlled by both the genetically-determined physiology of the plants and the local edaphic conditions (Pollard et al. 2002). Hyperaccumulators can sequester metals even from soils with low metal concentrations; for example, some populations of *Thlaspi caerulescens* and *Arabidopsis halleri* growing on normal soils still exhibit hyperaccumulation (Reeves et al. 2001; Bert et al. 2002; Assunção et al. 2003). As such there is no unequivocal relationship between leaf metal content and the total metal concentration in the soil or its bioavailability, which is a characteristic feature of

hyperaccumulators (Baker 1981). A complicating factor is that no chemical extraction method (including CaCl_2 , DTPA, EDTA, ammonium acetate) universally and accurately replicates the bioavailable soil metal fraction for hyperaccumulators, although advances are made with more realistic approaches e.g. carboxylic acid extraction (Feng et al. 2005) and in better replicating the soil-rhizosphere interface e.g. Diffusive Gradients in Thin films; DGT (Zhang et al. 2004; Tandy et al. 2011; Watanabe et al. 2011). Even if an ideal soil extraction method could be formulated, the logic of the shoot:soil ratio is questionable. Metal concentrations in plants are measured on a dry-weight basis and are thus, to a good approximation, a ratio of metal mass to cellulose mass. Soil measurements, however, are a ratio of metal mass to the solid fraction of the soil. As the denominators of these ratios are totally different, it is not apparent why they should be directly comparable. Moreover, high soil metal concentrations could result in a bioconcentration factor < 1 , for example in ultramafic soils with 3,000 $\mu\text{g/g}$ Ni in the soil and 2,000 $\mu\text{g/g}$ in a plant (while such a plant would clearly have an abnormal physiology), or conversely plants growing on soils deficient in essential trace elements (e.g. Zn) might be extremely efficient in sequestration and hence have very high bioconcentration factors yet low absolute concentrations. The bioconcentration factor however might have use in a comparative way, when growing plants in homogenized soil or in hydroponic culture but this has little advantage over simple comparisons of foliar metal concentrations.

Another criterion sometimes proposed for defining hyperaccumulation is the shoot-to-root quotient of metal concentrations (or translocation ratio), which typically is >1 in hyperaccumulators (Macnair 2003). While a useful property in supporting other evidence of hyperaccumulation, this ratio cannot be used alone to define hyperaccumulation for several reasons: (i) the difficulty of sampling roots from many plants, especially trees; (ii) the difficulty in analysis of ensuring that roots are free of all soil contamination and externally sorbed metal ions; (iii) the fact that the relative concentrations on a dry weight basis of a metal in various plant organs (leaves, roots, stems, fruits, seeds, etc.) may depend as much on the proportion of structural material in those tissues as on the detailed solution transport processes; (iv) a plant with, for example, 10 $\mu\text{g/g}$ metal in the root and 20 $\mu\text{g/g}$ in the leaves, while having a translocation ratio >1 , is of no special importance in the context of hyperaccumulation; (v) metal partitioning into shoots relative to the roots may depend on external metal supply (Talke et al. 2006) and the higher root-to-shoot biomass ratio of some hyperaccumulators can also contribute to relatively high shoot-to-root metal quotients (Krämer et al. 1997).

In contrast to these attempts to define hyperaccumulation on statistical grounds, the 'Holy Grail' (Baker and Whiting 2002) would be an over-arching, 'physiological definition' of hyperaccumulation, based on structural, functional, or metabolic characters unique to

hyperaccumulators. Knowledge of the physiology and genetics of hyperaccumulation has been greatly advanced in recent years (Pence et al. 2000; Talke et al. 2006; Courbot et al. 2007; Willems et al. 2007; Hanikenne et al. 2008; Richau et al. 2009). However, the inherent complexities of the phenomenon, such as the specificity for different metals (Zhao et al. 2002; Assunção et al. 2003) and the array of different physiologies enabling hyperaccumulation (Van de Mortel et al. 2006; Richau et al. 2009) make a workable physiological definition still far away.

As a workable approach, we propose to set hyperaccumulation threshold criteria at a level that is (i) 2-3 orders of magnitude higher than in plant leaves on normal soils, and (ii) at least one order of magnitude greater than the usual range in plant leaves on metalliferous soils. However, nominal thresholds should be applied sensibly and not regarded as a 'magical' or absolute cut-off, e.g. a plant that consistently accumulates 900 µg/g Ni still exhibits extreme physiological behaviour, and should therefore be regarded as a hyperaccumulator of that metal. As such, nominal threshold criteria are part of an operational framework, complemented with a suite of characteristics which include (a) a bioconcentration factor >1 (but often >50); (b) a shoot-to-root metal concentration quotient >1 and (c) extreme metal tolerance ('hypertolerance') due to effective biochemical detoxification (Baker and Whiting 2002).

Patterns of hyperaccumulation in natural populations

Hyperaccumulators can be further categorized according to the consistency of their metal accumulation behaviour. We distinguish here between 'obligate' (also called 'strict') and 'facultative' hyperaccumulators. The obligate hyperaccumulator species are endemic to some type of metalliferous soil and always exhibit metal uptake at the level defined for hyperaccumulation. Facultative hyperaccumulators, on the other hand, are species with populations of which (some) individuals are hyperaccumulators and other individuals of the same species are not (Pollard et al. 2002). Facultative hyperaccumulation can result from (i) genetic differences between different (separated) populations of a species; or (ii) soil-based differences, i.e. differences in metal ion availability and uptake. The latter can result from variations in (1) the total concentration in the soil of the element of interest; (2) the presence of the metal in different phases or chemical forms; (3) differences in soil pH; (4) the concentrations of major elements in the soil; (5) physical factors, such as the local rainfall, soil porosity and evaporation characteristics. Facultative hyperaccumulation applies when the species or at least a local population possesses the inherent propensity for metal accumulation *and* the local soil factors provide sufficient metal availability. The frequency of occurrence of different facultative hyperaccumulators on metalliferous vs. normal soils varies: some species occur predominantly on metalliferous soils, while others occur predominantly on normal soils.

The facultative hyperaccumulator category covers a variety of situations. It includes particularly those species that occur on both metalliferous and non-metalliferous (normal) soils, showing hyperaccumulation from only the metalliferous ones. On normal soils, such plants do not hyperaccumulate, either because they cannot do so because of a genetic difference, or (more generally) because of the low availability of the metal in question.

Leaf analysis of the widespread *Rinorea bengalensis*, for example, includes 23 specimens showing Ni concentrations of 1,000-17,750 µg/g from ultramafic soils, and another 77 specimens with 1-300 µg/g from other soils (Brooks and Wither 1977; Reeves unpublished) and is hence a typical facultative hyperaccumulator. There are more complex cases however, for example the Australian *Pimelea leptospermoides* that is apparently restricted to Ni-rich ultramafic soils, but shows a wide range of Ni concentrations (15-2,800 µg/g) from those soils (Reeves unpublished). Some species are able to hyperaccumulate from soils with low metal content, for example *Thlaspi* (*Noccaea*) *caerulescens* that has been found on various localities (e.g. sites in Luxembourg, France, Spain, Scotland and Sweden) with very high Zn concentrations on soil with low Zn status (Reeves et al. 2001; Assunção et al. 2003).

Critical evaluation of hyperaccumulation reports

The hyperaccumulator plants reported to date fall broadly into eight groups: (i) plants from ultramafic soils showing Ni (and rarely Co) hyperaccumulation; (ii) plants of soils enriched in chalcophile elements such as Zn, Pb, Cd and Tl, which may show hyperaccumulation of any of these elements; (iii) plants from soils rich in Cu and Co, showing hyperaccumulation of either or both of these elements; (iv) plants showing Mn hyperaccumulation, which can occur from some ultramafic soils and from some other substrates; (v) plants with unusually high Se concentrations from soils with elevated concentrations of this element; (vi) plants that have been identified as hyperaccumulators based on uptake of elements from industrially polluted soils, which include many of the elements listed above, along with reports of Cr and As hyperaccumulation; (vii) plants reported to hyperaccumulate light rare earth elements such as Ce and La; and (viii) plants reported to hyperaccumulate major soil elements (i.e. those above trace-element concentration) such as Fe or Al, a category which we will not discuss further. Although the term hyperaccumulation has been applied in all these cases, the amount of experimental support and scientific understanding varies widely.

Nickel

As indicated in the introduction to this paper, nickel was the first element designated as being hyperaccumulated by plants. Nickel hyperaccumulators comprise the great

majority of the current reports of hyperaccumulation, and there is broad agreement that 1,000 µg/g represents a useful criterion for their recognition. Various additional terms have been used to indicate other levels of Ni accumulation. Brooks et al. (1977) described the small number of plants in their study that showed 100-1,000 µg/g Ni as 'strong accumulators', and at the highest end of the scale, Jaffré and Schmid (1974) used the term 'hypernickelophores' for plants with >10,000 µg/g (1%) in the dry matter. It is doubtful whether these additional categories are required. Certainly those species regularly showing more than 1% Ni are good candidates for applications such as phytoremediation and phytomining, but they seem to form part of a continuum that begins around 1,000 µg/g.

Zinc

Zinc hyperaccumulation is also well-established as occurring in natural populations (Reeves and Brooks 1983a; Reeves 1988; Escarré et al. 2000) and well-studied in experimental systems (Shen et al. 1997). Reeves and Baker (2000) suggested that the 10,000 µg/g criterion of Baker and Brooks (1989) might in some cases be regarded as unduly restrictive. In particular, for Zn, present in most plants on zinc-rich soils at 50-500 µg/g, it might be more appropriate to regard Zn levels above 3,000 µg/g as remarkable, and deserving of being described as hyperaccumulation. An example is *Gomphrena canescens* from Australia with 9,000 µg/g Zn (Cole et al. 1968). Furthermore, some very strongly Zn-accumulating species might then not be described as non-accumulators, a term used by Shen et al. (1997) for *Thlaspi ochroleucum*, which can be found with up to 6,300 µg/g Zn and 5-100 µg/g Cd on zinc-rich soils (Reeves 1988 and unpublished), as well as 5,200 µg/g Ni on ultramafic soils (Reeves 1988). The lower criterion for Zn was also proposed by Broadley et al. (2007) and Krämer (2010). For phytoremediation potential, and also for biological reasons (3,000 µg/g Zn is more than enough to suggest 'abnormal physiology'), there is likely to be interest in any species that consistently shows such Zn levels, particularly if Cd levels are also abnormally high.

Cadmium

Work in several laboratories from about 1994 onwards has revealed the Cd-hyperaccumulating ability of *Thlaspi (Noccaea) caerulescens* (Robinson et al. 1998; Escarré et al. 2000; Lombi et al. 2000, 2001b; Reeves et al. 2001) and *Arabidopsis halleri* (Bert et al. 2002, 2003). The genetic propensity for Cd hyperaccumulation varies strongly between populations (Lombi et al. 2001b; Assunção et al. 2003; Bert et al. 2003; Roosens et al. 2003). More recently, several Cd hyperaccumulators have been described from China, notably *Rorippa globulosa* (Sun et al. 2007), *Solanum nigrum* (Wei et al. 2006; Gao et al. 2010), *Sedum alfredii* (Deng et al. 2008) and *Viola baoshanensis* (Liu et al. 2004; Li et al. 2010). We note that much of the research with Cd hyperaccumulators from this region, and some reports of 'new hyperaccumulators' are based on hydroponic

experiments with artificial exposure to Cd. However, some of these cases of Cd hyperaccumulation do exist under natural conditions (Wang et al. 2009; Wu et al. 2010). Almost all natural Cd-rich soils (e.g. calamine soils mineralised with Zn-Pb-Cd) are also extremely enriched in Zn. Cadmium hyperaccumulators must therefore also be very Zn-tolerant in their natural habitats, and hence Zn-toxicity in effect limits Cd-hyperaccumulation. For example, *Arabis paniculata* from China can accumulate 20,800 µg/g Zn as well as 2,300 µg/g Pb, and 434 µg/g Cd (Tang et al. 2009). Caution should however be exercised when putative Cd-hyperaccumulators are grown in soils amended only with Cd. This stresses again that hyperaccumulators have to be recorded from the natural habitats and exemplifies the importance of using natural soils in experiments.

Lead

There are several reports of Pb concentrations above 1,000 µg/g in plant material, using material collected directly from the field (Johnston and Proctor 1977; Williams et al. 1977; Barry and Clark 1978; Deram and Petit 1997; Rotkittikhun et al. 2006) or supplied by herbaria (Reeves and Brooks 1983b). It is certainly true that some species such as *Thlaspi (Noccaea) caerulescens* can accumulate Pb in shoots to levels of the order of 300 µg/g from Pb-amended nutrient solution, whilst immobilizing Pb in the roots at levels close to 30,000 µg/g (Baker et al. 1994b). Recent experiments have shown that some populations of *T. caerulescens* from southern France can accumulate Pb at >1,000 µg/g in leaf dry matter in nature, as well as from nutrient solution amended with low molar concentrations of Pb (Mohtadi et al. 2012). Similar reports have been made from Thailand where 26 taxa collected from a lead mine area were shown to accumulate foliar lead to these levels (Rotkittikhun et al. 2006).

Much higher foliar concentrations can be achieved with the use of Pb-complexing and mobilizing agents such as EDTA and EDDS ('induced phytoextraction' *sensu* Salt et al. 1998), as shown in work on *Brassica juncea* and *B. carinata* grown in hydroponic solution or in EDTA-treated soil (Kumar et al. 1995; Vassil et al. 1998). As noted above, we do not regard extreme accumulation achieved through hydroponics or chemically-amended soils as hyperaccumulation. *Brassica juncea* has no specific uptake mechanisms for Pb and part of the enhanced uptake results from damage to the root membrane by EDTA (Vassil et al. 1998). Moreover, such in situ chelate-induced phytoextraction introduces serious environmental problems and is cost prohibitive for large-scale application (Chaney et al. 2007). The chelating agents used to induce in situ phytoextraction cause Pb to become mobile and leach out and contaminate groundwater and surrounding soils, a pollution scenario that is nearly impossible to control. At the optimal concentration in the soil solution these chelating agents (EDTA) are also very expensive (Chaney et al. 2002). Although much recent scientific inquiry has focused on reducing the risks of the technology, by searching for chelating agents that are more

biodegradable (e.g. EDDS, NTA which are more expensive than EDTA), unavoidable contamination issues largely remain (Romkens et al. 2001; Wu et al 2004; Nowack et al. 2006).

The high values recorded in material grown naturally have always been from the vicinity of Zn/Pb mine sites or smelters. Here, there has invariably been a local long-term exposure to metals from the surface expression of underlying geological sources. Under these conditions there is abundant opportunity for contamination by wind-blown or rain-splashed dusts and soil, or even (in the case of smelters) from vapour-phase deposition. We regard the existing records as doubtful, and requiring further confirmation through the use of samples that have been treated to remove surface contamination. Rigorous washing with de-ionized water or a detergent solution are effective methods to clean the surface of roots and leaves from particulates (McLaughlin et al. 1985; Azcue 1996). Such washing may not remove metals that are fully enclosed by wax, however, which requires intensive washings with non-polar solvents in order to remove all cuticular metals, but this may in turn damage the underlying tissue and release metals from the internal structure. Where intensive treatment with non-polar wax-dissolving agents (e.g. hexane) in an ultrasonic bath does not significantly decrease the foliar metal concentration, then hyperaccumulator status can be affirmed, but when such washings decrease foliar metal concentrations it is still unknown whether the metal arrived in the cuticle via the air or via the roots. In *Thlaspi caerulescens* metal accumulation in the cuticle can also occur in metal-free air (Schat unpublished), which makes hexane washing problematic.

Accurate mass calculations comparing the leaf Pb with the total soil Pb can give an estimate of potential Pb contamination, but an option to exclude surface contamination with Pb and other metals from the analysis is to grow the plants from seed in their natural soil in the glasshouse or a climate room, where aerial deposition can be entirely precluded. Such controlled experiments are necessary in any instance where surface contamination is suspected, except when foliar metal concentrations are far in excess of the total soil concentrations (which is often not the case for mine tailings and smelter sites). In addition, an experiment to distinguish between Pb entering the plant via the root system and that deposited externally, using two soils of very different Pb isotopic composition, has been devised by Reeves et al. (2005); the experiment itself has not yet been conducted.

Copper and cobalt

Copper hyperaccumulators have been recorded from the DR Congo (with at least 32 species; Reeves and Baker 2000; Reeves 2005) and also from China, with species such as *Elsholtzia splendens* (*E. haichowensis*) (Jiang et al. 2004) and *Commelina communis* (Wang et al. 2004). There are also five records >1,000 µg/g Cu from Sri Lanka, which

includes *Geniosporum tenuiflorum* with 2,299 µg/g (Rajakaruna and Baker 2006) and from Salajar Island (Indonesia) with seven records >300 µg/g Cu, up to 600 µg/g in *Laportea ruderalis* (Brooks et al. 1978). The evidence for copper hyperaccumulation is, however, limited and most of the copper hyperaccumulators that have been described from the DR Congo (Malaisse et al. 1978; Brooks et al. 1982; Leteinturier 2002) could not be verified in a recent study which employed intensive washing of the plant leaf material (Faucon et al. 2007). The authors of this study found that 12 species that were studied and which were previously recorded as copper hyperaccumulators did indeed have high copper concentrations, but rarely exceeded the limit for hyperaccumulation. They concluded that the large variation of plant concentrations within a single site, significant linear soil/plant correlation (pointing to 'bioindicator' behaviour) and relatively low concentrations in many specimens are uncharacteristic for hyperaccumulators. It seems that most of the earlier analytical results were contaminated by dust. For example, 0.2 mg of malachite included as a dust with 100 mg of plant leaf genuinely containing 10 µg/g Cu is enough to raise the apparent Cu concentration to more than 1,150 µg/g (Reeves and Baker 2000).

Cu concentrations in plant leaves are controlled within a narrow range (≈ 10 µg/g) even on metalliferous soils, and regardless of the difficulties in obtaining contamination-free plant leaves, the current hyperaccumulator criterion for copper is probably too high (Faucon et al. 2007). This relates also to the current situation with cobalt hyperaccumulators. Cobalt concentrations are normally very low in plant leaves (0.03-2 µg/g) and even on metalliferous soils seldom reach 20 µg/g. Cobalt hyperaccumulators are predominantly known from the DR Congo. In addition, Co reaches 530-845 µg/g in *Nyssa sylvatica* on non-metalliferous soils in the US (Kubota et al. 1960; Brooks et al. 1977; Robinson et al. 1999). There are two records of *Phyllanthus* species from Cuba and New Guinea respectively (with Co values of 200-1,100 µg/g) (Reeves 2003; 2005), both from ultramafic soils. It is important to note that in ultramafic soils Ni might limit Co-hyperaccumulation, because Ni is usually present in concentrations 10-fold greater than those of Co (Malik et al. 2000). Krämer (2010) proposed to lower the hyperaccumulation criteria for Co and Cu to 300 µg/g, and we affirm this.

Chromium

Chromium hyperaccumulation is another phenomenon for which evidence is mostly lacking. In soils chromium generally has very low plant availability, and thus low potential uptake (Han et al. 2004), although in New Caledonia (Becquer et al. 2003) and Brazil (Garnier et al. 2006) relatively high available chromium (VI) has been reported, which could cause phytotoxicity. Examples where chromium hyperaccumulation has been described include *Leersia hexandra* (Zhang et al. 2007) and *Spartina argentinensis* (Redondo-Gómez et al. 2010). However, chromium values differed greatly between sites

and plants; this might indicate surface contamination and/or the inability to remove surface contamination during analysis, which, as with copper, might cause spurious results. Given the very low chromium concentrations in plants, both on normal (< 1 µg/g) and metalliferous (ultramafic) soils (<50 µg/g), it is proposed to set the criterion at 300 µg/g for hyperaccumulator status.

Thallium

Currently only a small number of thallium hyperaccumulators have been reported, all from Southern France: *Biscutella laevigata* with up to 15,200 µg/g Tl (Anderson et al. 1999), *Iberis intermedia* with up to 2,810 µg/g Tl (LaCoste et al. 1999, Leblanc et al. 1999) and *Silene latifolia* with up to 1,489 µg/g (Escarré et al. 2011). Various authors have proposed threshold hyperaccumulation concentrations of either 500 µg/g (Leblanc et al. 1999) or 1,000 µg/g (McGrath 1998; Krämer 2010), without discussion or justification of why these values were selected. Further study is required to validate these reports and designate appropriate criteria, but given that Tl concentrations are generally < 0.02 µg/g in plant leaves, we propose a tentative threshold value of 100 µg/g.

Manganese

Manganese hyperaccumulation has been described in approximately 10 species (Baker and Brooks 1989; Fernando et al. 2009; Pollard et al. 2009). As mentioned above, the criterion for Mn hyperaccumulation is 10,000 µg/g, reflecting the general abundance of this element in soils and biological materials (Baker and Brooks 1989). The majority of Mn hyperaccumulators are from ultramafic soils, such as in several species in the genus *Gossia* (Myrtaceae) from Australia with up to 21,500 µg/g Mn (Fernando et al. 2009) and a number of Mn hyperaccumulators from New Caledonia including *Macadamia neurophylla* with up to 51,800 µg/g Mn (Jaffré 1979) and *Maytenus* spp. with up to 32,000 µg/g Mn (Jaffré 1977; Fernando et al. 2008). Hyperaccumulation of Mn has also been reported in *Phytolacca* spp. from industrially-polluted soils (Xue et al. 2004), and it appears that the phenomenon also occurs on naturally-occurring soils derived from manganiferous schist (Pollard unpublished).

Metalloids

The Se content of soils is usually 0.01-2 µg/g, but can greatly exceed this range, reaching concentrations of several hundred µg/g in soils derived from certain Cretaceous shales (Reeves 2005). Recognition that some plants contain exceptionally high concentrations of selenium has a long history, pre-dating the origin of hyperaccumulator terminology (Rosenfeld and Beath 1964; Terry et al. 2000). The recent literature is particularly rich in reports on the ecological significance of selenium hyperaccumulation in natural populations (Barillas et al. 2011). Most authors regard 1000 µg/g as a criterion for Se hyperaccumulation. However, because normal Se levels in plants are below 2 µg/g, a

case could be made for considering any plant with more than 100 µg/g as a hyperaccumulator of this element. Selenium hyperaccumulators are widespread in the US and Australia where they occur on Se-rich shale with about 10 µg/g Se (Reeves and Baker 2000). Most Se hyperaccumulators are in the families of Fabaceae such as the genus *Astragalus*, including *Astragalus bisulcatus* and the Brassicaceae including *Stanleya pinnata*, both these species hyperaccumulate up to 10,000 µg/g Se (Freeman et al. 2006).

Hyperaccumulation of As, defined as a concentration above 1,000 µg/g, has been reported in ferns growing on industrially polluted soils, with further reports from laboratory screening (reviewed in Reeves 2005). Arsenic hyperaccumulation has been described for a number of *Pteris* spp., most notably *Pteris vittata* with up to 22,630 µg/g As (Ma et al. 2001; Wang et al. 2007) and other ferns such as *Pityrogramma calomelanos* with up to 8,350 µg/g As (Visoottiviseth et al. 2002). Because of the toxicity of As, this phenomenon has been intensively studied for its potential in phytoremediation. Arsenic also occurs in some aquatic species exposed to naturally elevated As concentrations in the water. The relatively frequent occurrence of As hyperaccumulation among hydrophytes (as opposed to terrestrial plants) is largely due to precipitation of water-borne As on or in the peripheral cell walls of the leaf, rather than ‘active uptake’ across the plasma membrane (Robinson et al. 2006). This is comparable with terrestrial plants trapping airborne contamination (see issues with supposed Pb, Co, Cu, Cr hyperaccumulation), especially those species growing in environments polluted by human activities.

Rare earth elements

Reports have appeared recently on the accumulation of light rare earth elements (LREEs) such as cerium (Ce) and lanthanum (La), predominantly from China (Shan et al. 2003; Wei et al. 2005; Lai et al. 2006; Wang et al. 2006). An example is *Dicroptheris dichotoma*, which accumulates up to 7,000 µg/g LREEs in its dry leaf biomass (Shan et al. 2003) and *Pronephrium simplex* with up to 3,000 µg/g LREEs (Lai et al. 2006). Little is known about the ecophysiological functions of LREEs or appropriate criteria for defining their hyperaccumulation. The reported hyperaccumulators have been described from industrial smelter sites, available for plant colonization only recently, and more information is needed to establish the routes of uptake of the elements into the plants. Again airborne contamination might be a factor here. Until more is known about the behaviour of LREEs in plants, hyperaccumulator criteria cannot be set.

Numbers of hyperaccumulators

As explained above, we propose to set hyperaccumulation threshold criteria at a minimum of 2-3 orders of magnitude higher than foliar concentrations on normal soils, and at least one order of magnitude greater than the range in foliar concentrations on metalliferous soils. On this basis, we recommend the following concentration criteria for different metals and metalloids in dried foliage: 100 µg/g for Cd, Se and Tl; 300 µg/g for Co, Cu and Cr; 1,000 µg/g for Ni, Pb and As; 3,000 µg/g for Zn; and 10,000 µg/g for Mn, with plants growing in their natural habitats. If these criteria are adopted more than 500 plant taxa have been cited in the literature to date as hyperaccumulators of one or more elements (As, Cd, Co, Cu, Mn, Ni, Pb, Se, Tl, Zn). This still represents a very small proportion of the (approximately) 300,000 recognized vascular plant species (The Plant List 2011). Approximate numbers for various elements are as follows: Ni (450), Cu (32), Co (30), Se (20), Pb (14), Zn (12), Mn (12), As (5), Cd (2), Tl (2). These numbers are subject to change, and may increase with further exploration and analysis. Some of the tentatively identified hyperaccumulators, particularly those of Cu, Co, or Pb, might also be removed from the list after further testing (for example in glasshouse experiments in which airborne contamination can be eliminated). It has been suggested that the preponderance of Ni plants is the result of a greater effort made into seeking these, but there is a more fundamental reason: the total area of Ni-rich ultramafic soils exposed worldwide is much greater than that presented by exposures of the other metals listed.

Experiments using hydroponic cultures and metal-amended soils

Baker and Whiting (2002) warn that “In their enthusiasm to report new hyperaccumulator plants, many authors have regularly assumed that if a normally non-accumulating plant can take up >10,000 µg/g Zn from hydroponic culture it can be assigned hyperaccumulator status.” It must be recognized that almost any plant can do this, but the ‘forced’ or ‘induced’ metal uptake often leads ultimately to plant mortality, and may have no relevance to the continuing life cycle of naturally occurring metallophyte populations, even though it may be of interest for some phytoremediation strategies. Many pieces of published experimental work have used metal-amended nutrient solutions containing amendments far in excess of the metal concentrations found in natural soil solution. Such experiments can be useful in demonstrating the tolerance of a species to a particular element, and in showing the fate within the plant of such massive exposure (*e.g.* how much becomes immobilized within the root system and how much is translocated to the shoots), but have very limited relevance to the natural environment in which the species evolved: the experiments are almost never taken so far as to demonstrate survival and production of viable seed.

The problem thus lies in that hydroponic experiments often use unrealistically high dose treatments, where the characteristic differences between hyperaccumulators and non-

accumulators tend to disappear, because of saturation of the root-to-shoot translocation in the hyperaccumulator, or of the root's sequestration capacity in the non-accumulator. When used sensibly, it seems that hydroponic experiments can help to distinguish genuine hyperaccumulators, provided that the exposure levels are kept low (e.g. $<1 \mu\text{M}$). However, experimental confirmation using the natural soil is more straightforward and therefore preferable.

Similar comments apply to experiments in which one of the standard soil media is supplemented ('spiked') by the addition of large concentrations of soluble metal salts (nitrates, sulfates, etc.). The nature of the interaction between the amending solution and the base soil is generally largely unknown, and the resulting medium is unlikely to mimic a real metalliferous soil. This is analogue to artificial acidification of natural soil to increase metal-uptake (even if induced phytotoxicity is kept relatively low). Again great care needs to be taken in interpreting (and extrapolating from) the results of such experiments. In both cases, hydroponics and amended or acidified soils, we reject such experiments as capable of defining a species as a hyperaccumulator. Even when natural metalliferous soils are used, large-scale experimental screening for hyperaccumulators could yield misleading results if non-tolerant species are tested. When the tolerance limits of excluder species are exceeded, it is common to observe non-specific 'breakthrough' of metals into the shoot (Fig. 1; Baker 1981), yet this is not hyperaccumulation if the uptake results in death of the plant.

Hyperaccumulator databases

In order to provide a univocal platform for sharing knowledge of hyperaccumulators it is proposed to create an online database portal. Attempts to produce such databases have been few and global coverage is patchy. The most well known are Environment Canada's PHYTOREM database and the METALS (metal-accumulating plants) database originally maintained by the Environmental Consultancy, University of Sheffield (now ECUS Ltd, UK). Since 2009, the on-line Global Metallophyte Database (www.metallophytes.com), under the auspices of the International Serpentine Ecology Society (ISES) and future administration by the Centre for Mined Land Rehabilitation (CMLR) of The University of Queensland (UQ), has been put in place and aims to provide a global database available through the internet.

Conclusions

The use of the term 'hyperaccumulator' and the theoretical and practical implications of different methods of establishing 'hyperaccumulation status' have been evaluated critically, and we conclude the following as guidelines for future use of the term:

- (1) Nominal threshold criteria currently provide the only practical operational framework for recognizing hyperaccumulators until appropriate physiological definitions are defined in the future. When used sensibly, nominal criteria can guide the identification of extreme physiological behaviour. Furthermore, they are the only way to recognize hyperaccumulators in the field, without experimental cultivation, which has never been attempted for most reported hyperaccumulators.
- (2) Hyperaccumulation for nickel, zinc, cadmium, manganese, arsenic and selenium have been confirmed experimentally beyond doubt in a range of plant species.
- (3) Hyperaccumulation of lead, copper, cobalt, chromium and thallium have not (yet) been demonstrated beyond doubt in one or more plant species, whereas the use of the term for rare-earth elements requires critical evaluation.
- (4) Only plant leaves (or fronds) are to be considered in establishing hyperaccumulator status. Moreover, only metal or metalloids inside plant leaves indicates active (hyper)accumulation. Passive accumulation via air-borne deposition on plant leaves is not to be regarded as hyperaccumulation. Such contamination is a major cause of erroneous designation, particularly for Pb and Cr.
- (5) Growing plants from seed in their natural soil in the glasshouse or climate room is the most appropriate method for confirming hyperaccumulator status. This approach avoids airborne contamination and other uncontrolled irregularities of natural conditions in the field.
- (6) Hydroponic experiments often use unrealistically high dose treatments, which can result in spurious claims for supposed hyperaccumulation when ‘normal’ plants are exposed, resulting in immediate high shoot metal concentrations but also in inevitable plant death.
- (7) When exposure levels are kept low hydroponic experiments however can help to distinguish genuine hyperaccumulators by confirming characteristic traits such as hypertolerance to phytotoxic metal ions, hyperaccumulation in the shoot, high bioconcentration factors and high shoot/root metal translocation, and have been an effective methodology for physiological experimentation.
- (8) Experimental confirmation using natural soil is preferable over hydroponics, but the use of standard soil ‘spiked’ with soluble metal salts is unlikely to mimic natural metal-rich soils.
- (9) Hydroponics, metal-amended ‘spiked’ soils and artificially acidified (natural) soils in isolation are not capable of defining a species as a hyperaccumulator: natural populations must be studied.
- (10) Critical review suggests that criteria which have been commonly used to delimit hyperaccumulation of some metals are unnecessarily conservative. We propose that the criteria for hyperaccumulation of Se and Tl be lowered to 100 µg/g dried

leaf, the criteria for hyperaccumulation of Cu, Co, and Cr be lowered to 300 µg/g dried plant leaf, and the criterion for hyperaccumulation of Zn be lowered to 3,000 µg/g dried plant leaf.

- (11) Diffused reporting means that the exact number of hyperaccumulators is presently unknown. Therefore the adoption of standardized terminology and methods, and the use of an on-line database portal are vital.

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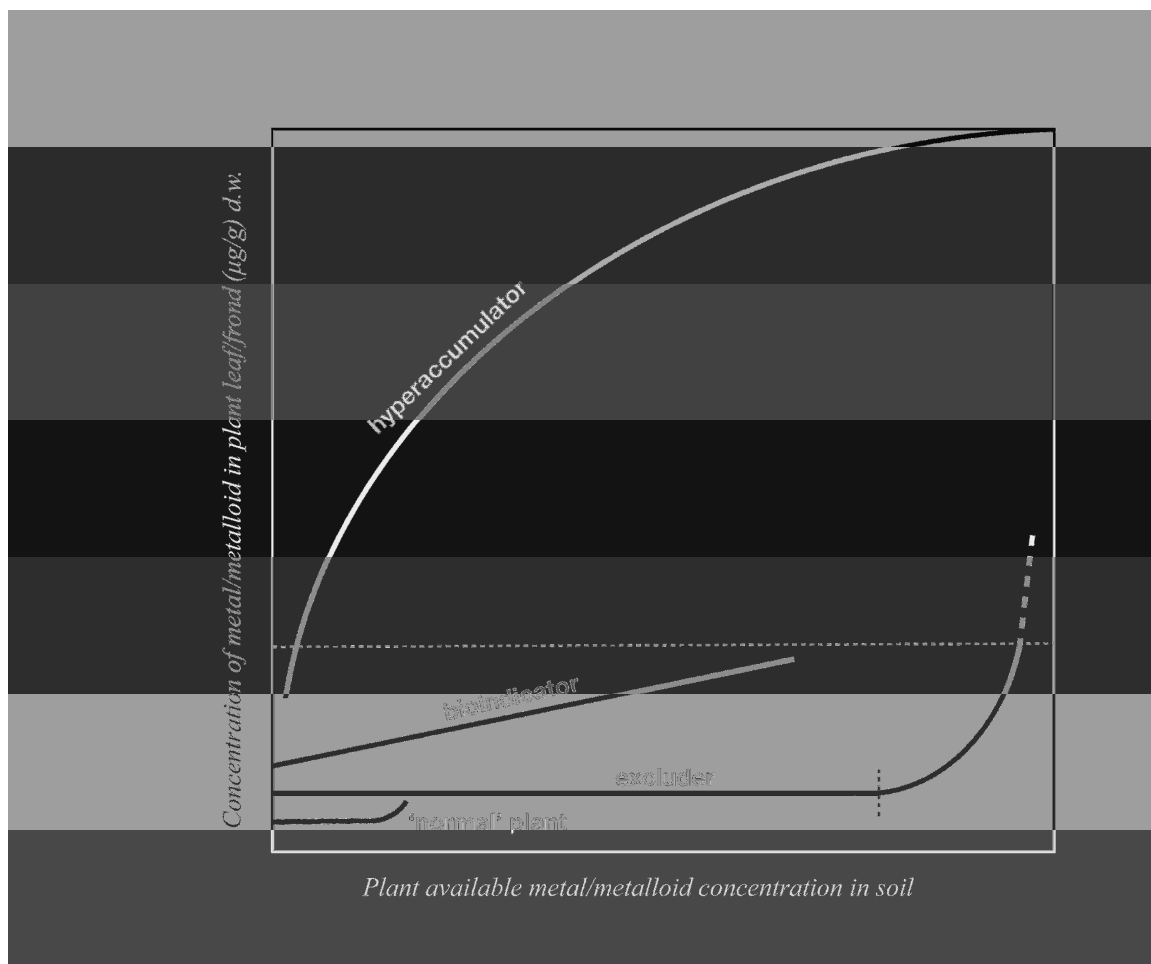
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CAPTION FOR FIGURE 1

Conceptual response diagram for uptake of metals and metalloids in plant leaves/fronds, adapted from Baker (1981). 'Normal' plants can only tolerate low concentrations of bioavailable metals/metalloids in soil, before they die due to acute phytotoxicity. Excluders however can grow over a wide range of phytotoxic available metals before physiological mechanisms cannot control and allow unregulated uptake, resulting in death of the plant. Bioindicators take up metals over a wider range than 'normal' plants and the concentrations in plant leaves reflect that of the soil, until phytotoxicity prevents further growth and causes death of the plant. Hyperaccumulators are able to withstand much higher concentrations of bioavailable metals than 'normal' plants, bioindicators and excluders, and because of competitive disadvantages and greater sensitivity to fungal and pathogen infections, most do not occur over non-metal-enriched soils, depicted by the latent start of the line in the diagram. The dotted baseline indicates the hyperaccumulator threshold for the different metals and metalloids: 100 µg/g for Cd, Se and Tl, 300 µg/g for Cu, Co and Cr, 1000 µg/g for Ni, As, and Pb, 3000 µg/g for Zn, and 10,000 µg/g for Mn. Note that the response line for hyperaccumulators represents the possible behaviour of such plants, individual plant concentrations are scattered around the line, and most hyperaccumulators occupy only a small portion of the line (above the hyperaccumulation threshold).





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