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Trace element hyperaccumulator plant traits: a call for trait data collection

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Abstract

Background and aims Hyperaccumulator plants exhibit extreme ecophysiological characteristics, which make them suited for phytoremediation. Understanding their ecological strategies might help identify the species and functions to be favored in phytoremediation, restoration, and conservation projects for metalliferous sites.

Methods Here, we identified the hyperaccumulator species in the worldwide plant trait database TRY and cross-referenced these trait syndromes associated with the ability of plants to concentrate metals. This allows us to link trace element hyperaccumulation with broader plant ecological strategies.

Results Hyperaccumulator plant species tend to have smaller leaves and poorer competitive ability compared to non-hyperaccumulator plant species. Contrary to expectations, we found no indication of hyperaccumulator plants being more resource-conservative on the leaf economics spectrum. However, these data remain fragmentary as only 2.7% of

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hyperaccumulator plant species have their traits published in the TRY database.

Conclusion The recent development of trait-based models to construct plant communities providing optimal ecosystem services (e.g., phytoremediation, restoration) requires further research to identify predictable trait-service relationships. We thus call for an international collaborative sampling effort to measure traits in more hyperaccumulator plant species.

Keywords CSR strategies · Functional traits · Hyperaccumulation · Metallophytes · Plant functions · Synthesis analysis

Introduction

Mining activities are major sources of pollution directly tied to human and environmental health issues worldwide. These activities severely threaten metalliferous ecosystems characterized by extreme environmental conditions (e.g., high metal concentrations, low resource availability), endangering some of the world's most biodiverse and endemic-rich communities (Myers et al. 2000; Baker et al. 2010; Ibanez et al. 2019). These ecosystems harbor a pool of species (i.e., metallophytes) with high ecological value and for use in contaminated land rehabilitation, phytomining, as well as metalliferous site restoration, and conservation (Whiting et al. 2004; Wójcik et al. 2017; Chaney et al. 2021; Quintela-Sabaris et al. 2020). Some metallophytes, called hyperaccumulators, are of particular interest because of their unique and extreme ability to accumulate trace elements (i.e., >100 times higher concentrations than most other plants) (van der Ent et al. 2013).

Although over 700 hyperaccumulator species have been identified so far (van der Ent et al. 2015b; Reeves et al. 2018), many questions concerning their ecological functions and potential applications remain unanswered (Lange et al. 2016), making it challenging to incorporate them into rehabilitation schemes (Reeves 2003; Kazakou et al. 2008; Kidd et al. 2015). Developing an approach to identify species and functions that can meet restoration or rehabilitation goals is, therefore, imperative. In this regard, a trait-based approach linking trace element accumulation strategies to plant morphology is a promising research avenue, given the wide array of plant traits that can be measured rapidly and the broad ecological processes

it can tackle (e.g., environmental filters, biogeochemical processes) (Laughlin 2014; Lange et al. 2016).

Metallophytes, including hyperaccumulators, often share common characteristics (morpho-physio-phenological traits), allowing for survival under the adverse conditions encountered on metalliferous sites (Violle et al. 2007; Baker et al. 2010). As a result, many generalizations have been made on their ecological traits and strategies, including (i) slow growth rates; (ii) investment in defense and secondary metabolites; (iii) multiple stress tolerances; (iv) extensive root system development; (v) high nutrient use efficiency (i.e., resource conservation strategy); (vi) investment in microbial nutritional symbioses (e.g., mycorrhizae or nitrogen-fixing bacteria); (vii) intolerance to shade and (viii) xeromorphic characteristics (Ernst 2006; Kazakou et al. 2008; Baker et al. 2010; Quintela-Sabaris et al. 2020; Paul et al. 2022). Moreover, because metalliferous soils are typically harsh environments with low vegetation cover and thus little competition over resources (Kazakou et al. 2008; Novakovskiy et al. 2021), metallophytes are generally categorized as stress-tolerators (*sensu* Grime 1988) with poor competitive ability and high capacity to conserve acquired resources (Wright et al. 2004; Ernst 2006; Baker et al. 2010; Maestri et al. 2010; Reich 2014; Lazzaro et al. 2021). These characteristics stand in contrast with fast resource-acquisitive species that invest in low-cost biomass to acquire resources rapidly but constantly invest in biomass replenishment, as more resources are lost to litter, predation, or parasitism (Reich 2014; Wright et al. 2004). As stress-tolerant species, hyperaccumulators are also expected to have smaller leaves and modest overall development (Pierce et al. 2017). Local studies have confirmed some of these trends with species, populations or ecotypes exposed to trace elements in soils (Kazakou et al. 2010; Adamidis et al. 2014; Lazzaro et al. 2021), as environmental factors may induce around 30% of intraspecific variability in traits (Albert et al. 2010). Nevertheless, it remains unknown whether these relationships hold at the global scale between hyperaccumulator and non-hyperaccumulator species. Although, it might be difficult to distinguish hyperaccumulator species from closely related non-hyperaccumulator species at such a large scale, traits-interspecific variability is generally high enough to distinguish broad tendencies. Moreover, since different metalliferous soils (e.g., ultramafic, calamine, seleniferous, Cu-Co rich soils) have distinct growth-limiting factors (e.g., fertility, climates) (Delhaye et al. 2019; Garnica-Díaz et al. 2022), and since luxuriant

tropical forests and fast-growing ruderals can develop on metalliferous sites (Baker et al. 2010; Delhay et al. 2016; Galey et al. 2017), it remains unclear whether these environments select for stress tolerators or whether alternative strategies could allow functionally distinct species to establish in these environments (Samojedny et al. 2022). Focusing on a global scale means that resolution at the species or population levels would be limited, but it is an essential step to evaluate the generalizability and predictability of a trait-based approach.

To identify one or multiple hyperaccumulation strategies within a worldwide trait spectrum, we systematically evaluate linkages between leaf traits/ecological strategies and trace element hyperaccumulation by cross-referencing the plant trait database TRY (Kattge et al. 2019) and the global hyperaccumulator database (Reeves et al. 2018).

Material and methods

Using the global plant trait database TRY (comprising data from >200,000 species), we gathered data on leaf area (LA - area of one leaf), specific leaf area (SLA - leaf surface area/dry mass ratio), and leaf dry matter content (LDMC - leaf dry mass/leaf fresh mass) (Kattge et al. 2019). These traits were selected to ensure broad species coverage (i.e., widely measured traits) while capturing essential components of plant strategies (Pierce et al. 2017). They are key traits on the economic spectrum strategies (Wright et al. 2004; Reich 2014) and help identify CSR strategies: Competitive (C), Stress-tolerant (S), and Ruderal (sensu Grime 1988). Moreover, traits related to nutrient acquisition, such as SLA and LDMC, might be associated with trace element accumulation (Lange et al. 2016). Species life forms were also obtained from the TRY database or the literature and subsequently categorized according to Pierce et al. (2013): trees, shrubs, forbs, graminoids, hydrophytes, and others (e.g., succulents, moss, and lichens). We further separated woody species (i.e., trees and shrubs) from non-woody species, as the presence of lignified tissues strongly covaries with the position of a plant along the resource acquisition-conservation spectrum (Pierce et al. 2013; Díaz et al. 2016). Potential hyperaccumulator species were first identified using the maximum concentrations of trace elements in leaves from the Global Hyperaccumulator Database (Reeves et al. 2018). The sources were validated to omit (i) non-peer-reviewed sources, (ii) data from hydroponic

and spiked soil experiments (van der Ent et al. 2015a), and (iii) records of foliar trace element concentrations below the hyperaccumulation thresholds (van der Ent et al. 2021). All species names were verified with the Taxonomic Names Resolution Service (TNRS), as recommended in TRY (Boyle et al. 2013; Kattge et al. 2019). All traits were averaged to species level, as is commonly done in global trait analysis (Díaz et al. 2016), and outliers were checked for possible data entry errors (Pérez-Harguindeguy et al. 2016). The final database contained 4523 species, of which 19 were hyperaccumulators (Table 1). The CSR strategies were calculated using the ‘StrateFy’ program based on LA, SLA, and LDMC species mean values (Pierce et al. 2017).

Generalized linear mixed models (GLM) with binomial distributions were used to link hyperaccumulation to leaf traits (i.e., LA, SLA, LDMC) and plant strategies (i.e., Grime’s C, S, and R scores). Model selection was based on AIC and pseudo- R^2 values and further validated with a likelihood ratio test. Traits were normalized before analysis: LA and SLA were log-transformed, and LDMC was logit-transformed. All analyses were performed in R (version 4.2.0) with the “stats” package (R Core Team 2020) and the ‘AICcmoavg’ package (Mazerolle 2020).

Results

The best predictors for hyperaccumulation were LA and LDMC, although the full model (i.e., LA + SLA + LDMC) performed equally well (no statistical difference between AIC). Both models explained only 5.7% of the variance (d.f. = 4522) and identified hyperaccumulators as having smaller leaves (LA, $P < 0.05$) (Fig. 1a). However, this was not observed in hyperaccumulating woody taxa specifically ($n = 4$) (Table S1), although this may simply result from low statistical power. Regarding the position of hyperaccumulators along the leaf economics spectrum a trade-offs between SLA and LDMC, we found no evidence for a conservative strategy with associated thicker leaves and high LDMC (Fig. 1a).

Hyperaccumulators also had significantly lower competitive ability (%C) ($P < 0.05$), which was the only predictor retained through model selection for all hyperaccumulators and non-woody hyperaccumulators. Nevertheless, the model explained minimal variance (i.e., 3.1% for all hyperaccumulators and 3.4%

Table 1 List of the 19 hyperaccumulators found on the global database TRY, their life forms, functional traits values, and hyperaccumulation elements

Family	Species	Life form	LA (mm ²)	SLA (mm ² g ⁻¹)	LDMC (mg g ⁻¹)	Trace element	Concentrations (mg kg ⁻¹)	Sources
Apocynaceae	<i>Carissa spinarum</i>	shrubs	339	9.46	0.47	Cu	700	(Rajakaruna and Bohm 2002)
Brassicaceae	<i>Arabidopsis halleri</i>	forbs	291	38.2	0.19	Zn	53,900	(Stein et al. 2017)
Brassicaceae	<i>Odontarrhena tortuosa</i> (syn. <i>Abyssum tortuosum</i>)	forbs	21.7	15.3	0.33	Cd	3640	(Teptina and Paukov 2015)
Brassicaceae	<i>Noccaea caerulea</i> (syn. <i>Thlaspi caerulea</i>)	forbs	114	30.3	0.15	Ni	1790	(Reeves et al. 2001; Schwartz et al. 2006)
Brassicaceae	<i>Noccaea montana</i> (syn. <i>Thlaspi montanum</i>)	forbs	164	18.3	0.15	Zn	53,500	(Boyd and Martins 1998)
Caryophyllaceae	<i>Minuartia verna</i>	forbs	3.66	22.5	0.29	Ni	4300	(Johnston and Proctor 1977)
Asteraceae	<i>Dieteria canescens</i> (syn. <i>Machaeranthera canescens</i>)	forbs	97.2	10.8	0.26	Zn	3200	(Fellet et al. 2012)
Asteraceae	<i>Gutierrezia microcephala</i>	shrubs	19.6	69.5	0.10	Tl	18,400	(Fellet et al. 2012)
Asteraceae	<i>Symphoricarum ascendens</i>	forbs	96.4	10.5	0.21	Se	3630	(Beath et al. 1941)
Asteraceae	<i>Symphoricarum ericoides</i>	forbs	63.9	14.0	0.24	Se	740	(Rosenfeld and Beath 1964)
Fabaceae	<i>Anthyllus vulneraria</i>	forbs	600	16.9	0.18	Se	1350	(Beath et al. 1941)
Lamiaceae	<i>Stachys recta</i>	forbs	739	28.1	0.22	Zn	1290	(Escarré et al. 2011)
Fabaceae	<i>Astragalus canadensis</i> (syn. <i>Astragalus carolinianus</i>)	forbs	675	15.6	0.27	Ni	2600	(Lisanti 1952)
						Se	1110	(Byers 1938)

Table 1 (Continued)

Family	Species	Life form	LA (mm ²)	SLA (mm ² g ⁻¹)	LDMC (mg g ⁻¹)	Trace element	Concentrations (mg kg ⁻¹)	Sources
Meliaceae	<i>Walsura pinnata</i>	trees	27.1	16.2	0.40	Ni	8000	(van der Ent et al. 2019)
Plantaginaceae	<i>Linaria alpina</i>	forbs	15.0	22.7	0.17	Ni	1990	(Vergnano Gambi and Gabrielli 1979)
Plumbaginaceae	<i>Armeria maritima</i>	forbs	95.1	15.0	0.19	Zn	5500	(Szarek-Lukaszewska et al. 2004)
Polygonaceae	<i>Rumex acetosa</i>	forbs	1510	29.1	0.15	Cu	4230	(Frago et al. 1980)
Rubiaceae	<i>Psychotria grandis</i>	trees	9760	16.5	0.22	Cu	1100	(Tang et al. 1999)
Saxifragaceae	<i>Saxifraga paniculata</i> (syn. <i>Saxifraga aizoon</i>)	forbs	83.5	8.75	0.24	Zn	11,000	(Johnston and Proctor 1977)
						Pb	5540	(Johnston and Proctor 1977)
						Ni	11,900	(Reeves 2003)
						Ba	2320	(Fehlauer et al. 2022)

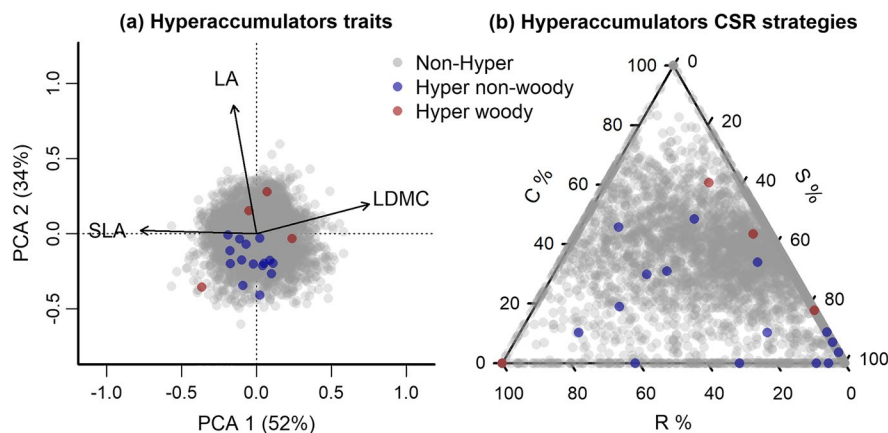


Fig. 1 Representation of hyperaccumulators' traits (a) and CSR strategies (b). Comparing all non-hyperaccumulators (gray circle, $n=4503$), non-woody hyperaccumulators (blue circle, $n=15$), and woody hyperaccumulators (red circle,

$n=4$) species available on TRY database. *Abbreviations:* leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), competitive (C), stress-tolerant (S), and ruderal (R)

for non-woody hyperaccumulators). Furthermore, no model could distinguish woody hyperaccumulator traits due to the small sample size ($n=4$) and large dispersion. Overall, hyperaccumulators remained scattered across the CSR ternary plot and were poorly associated with any specific strategy (Fig. 1b). Finally, the CSR classification through leaf traits alone might be questionable for some species such as *Gutierrezia microcephala*, which is classified as a 100% R strategist, despite being usually described as a successional perennial species from desert habitats (Parker 1982).

Discussion

Our preliminary results confirmed a weak trend for hyperaccumulator species to have smaller leaves, a trait often observed in flora from 'harsh' environments, such as metalliferous soils (Adamidis et al. 2014; Lazzaro et al. 2021; Sharma et al. 2021). Hyperaccumulator species were also relatively poorer competitors with more S and R strategies (e.g., shade-intolerant) (Ernst 2006; Baker et al. 2010). This is in line with the underrepresentation of competitive broadleaf species from hyperaccumulators. However, contrary to expectations (Kazakou et al. 2008; Adamidis et al. 2014), they were not consistently associated with the resource conservation end of the leaf economics spectrum. Nevertheless, it should be kept

in mind that all models performed poorly, which can be caused by a weak ecological signal at a global scale but also, potentially (and maybe primarily), by a lack of quality data on traits and strategies of hyperaccumulators.

The high variability in hyperaccumulator traits/strategies could also suggest that many alternative strategies have convergently evolved to promote trace element accumulation through various pathways. The accumulation strategy may change according to the metalliferous biogeochemical systems (i.e., ultramafic soil with Ni and Co or calamine soils with Zn, Pb, and Cd) or even the trace element accumulated. For example, co-occurring Ni and Co may be stored in different tissues and cell parts (i.e., vacuolar or exocellular sequestration) (Tappero et al. 2007; Rue et al. 2020; Paul et al. 2020b) or one specific trace element may accumulate in different tissues depending on the species and interactions with other trace elements (Broadhurst et al. 2009; Paul et al. 2020a). This may translate into alternative strategies of hyperaccumulation, relying on distinct plant traits/strategies. Detecting such alternative strategies at a global scale will require many more points than the 19 hyperaccumulator species from which we could gather reliable data in this study. Collecting more data on hyperaccumulator species is also necessary to address the non-independency between species and include some factors in further analysis (e.g., climate, phylogeny, habitat, life cycle, soil fertility)

(Broadley et al. 2001; Cappa and Pilon-Smits 2014; Joswig et al. 2022).

International trait data collection

Our preliminary study does not provide conclusive evidence for trait syndromes associated with trace element hyperaccumulation. We believe this may be primarily due to the lack of statistical power, given the poor representation of hyperaccumulators in the TRY database. A systematic review is currently underway to increase the hyperaccumulator species list. However, hyperaccumulator plant species remain underrepresented in trait databases, as they are often rare and localized species (Violle et al. 2015).

The lack of trait representation calls for a coordinated international effort to gather trait data on hyperaccumulators, particularly from locally endemic species. Non-hyperaccumulator metallophyte species should also be sampled to distinguish hyperaccumulation strategies and traits from those specifically involved in trace element tolerance. Future investigations could also focus on Ni hyperaccumulator species as they represent ~70% of identified hyperaccumulator species (Reeves et al. 2018) and would remove the noise associated with different metal accumulation.

Only a few leaves are necessary to inexpensively measure key leaf economic traits (LA, SLA, and LDMC). These leaves can be obtained from field specimens, gardens, or controlled experiments (if controls on metalliferous soil are available). Detailed protocols can be found in the *New handbook for standardized measurement of plant functional traits worldwide* (Pérez-Harguindeguy et al. 2016) and the TRY database (WEB cited protocols) (Kattge et al. 2019). Ideally, this approach should include more traits (i.e., plant height, seed mass, and stem-specific density) and nutrient leaf concentrations (P, K, N) (Lange et al. 2016). In addition, root traits (e.g., dry matter content, diameter, depth, P concentration) should also be considered to extend this approach, as they seem correlated with trace element accumulation and stress-tolerant strategies (Gervais-Bergeron et al. 2021; Lambers et al. 2015). To participate in this international sampling effort, we ask for measurements of metallophyte traits and their publication on the TRY database. To join this initiative or for further questions, contact the corresponding author.

Conclusion

This study is the first attempt to link plant traits to their ability to concentrate trace elements. Our results did not provide evidence for hyperaccumulators being necessarily characterized by a resource-conservative trait syndrome or a stress-tolerating strategy (according to Grime's framework and a classification based on leaf morphology alone). We believe that our inability to unravel trait syndromes among hyperaccumulators is rooted at least partly in a lack of reliable trait data. However, it may also well be that leaf morphology is a poor predictor of a plant's ability to concentrate trace elements at such a large scale (e.g., decoupled ecophysiological processes or limiting factors). Filling the gaps will be essential to guide applied land reclamation efforts and preserve metalliferous environments. We thus call for an international collaborative sampling effort to measure and share on TRY the traits of hyperaccumulator and metallophyte species.

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Author's contribution Béatrice Gervais-Bergeron, Pierre-Luc Chagnon and Michel Labrecque conceived the ideas and designed methodology. Data were collected and analysed by Béatrice Gervais-Bergeron. The first draft of the manuscript was written by Béatrice Gervais-Bergeron, Adrian L.D. Paul, Pierre-Luc Chagnon and Michel Labrecque. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The data presented in this study are available on the repository of the University of Montreal, at <https://doi.org/10.5683/SP3/QKNQ08>.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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