

## Mini-review

# The significance of metal hyperaccumulation for biotic interactions

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**Abstract.** Metal hyperaccumulating plants contain very high metal contents. Because of the general toxicity of metals, chemically-mediated biotic interactions involving hyperaccumulating plants may differ greatly from those of non-hyperaccumulators. Recent research has demonstrated a defensive function for hyperaccumulated metals against herbivores and pathogens. We predict that some herbivore/pathogen species have evolved metal tolerance, and suggest that resulting high metal levels in herbivores/pathogens may defend them against their own predators. Little is known regarding interference and commensal interactions involving hyperaccumulating plants. Decreased competition may occur through an interference interaction similar to allelopathy, in which enrichment of metal in the soil under a hyperaccumulator plant's canopy may inhibit another plant species, thus resulting in "elemental allelopathy". Metal enrichment of soil under hyperaccumulators also may result in commensalism if another plant species (possibly another hyperaccumulator) derives a benefit from growing in the metal-enriched soil under the canopy of a hyperaccumulating overstory plant. It seems likely that high-metal plant litter will host a specialized microflora of decomposers and may affect nutrient cycling rates. Mutualist biotic interactions also may be affected by the elevated metal contents of hyperaccumulating species. Mycorrhizal fungi may form mutualisms with hyperaccumulators, but the phenomenon is poorly-explored. The few cases investigated to date have not detected mycorrhizae. Pollination and seed dispersal mechanisms may require biotic vectors that might be affected by plant metal content. Hyperaccumulating plants may have solved this dilemma in three ways. First, some may rely on abiotic vectors for pollen or seed dispersal. Second, biotic vectors used by these species may have varied diets and thus dilute metal intake to non-toxic levels. Finally, biotic vectors may have evolved tolerance of elevated dietary levels of metals, and perhaps have become specialists on hyperaccumulator species.

**Key words.** Allelopathy – elemental defences – herbivory – mutualism – plant-animal interactions

## Introduction

Most plant species growing on soils that contain naturally high levels of metals have elevated concentrations of those metals in their tissues (Brooks 1987). However, some metal-tolerant plants markedly concentrate metal in their tissues. These plants, termed hyperaccumulators, contain in excess of 1000  $\mu\text{g g}^{-1}$  (dry weight) of metal for Ni, Cu, Co, Cr, or Pb, or 10,000  $\mu\text{g g}^{-1}$  for Zn or Mn (Baker & Brooks 1989). Nickel is the most commonly hyperaccumulated metal. Most of the 215 metal-hyperaccumulating species included in the review by Baker & Brooks (1989) hyperaccumulate Ni. They listed 145 hyperaccumulators of Ni, 26 of Co, 24 of Cu, 14 of Zn, four of Pb, and two of Cr.

Explanations for metal hyperaccumulation have been suggested by numerous authors but rarely have been tested experimentally. In Table 1 we present the six explanations offered for metal hyperaccumulation by plants, as summarized by Boyd & Martens (1992). One of these, the inadvertent uptake hypothesis, attributes no selective value to metal hyperaccumulation and suggests that this trait is a by-product of other physiological processes in hyperaccumulating plants. The remaining five hypotheses all propose that an ecological benefit accrues to metal-hyperaccumulating individuals. To date, only the defence hypothesis has been tested to any great extent, as we will discuss later in this paper.

Uptake and sequestration of toxic materials represents an interesting biological puzzle. The metals that are hyperaccumulated by plants generally are viewed as toxic in relatively low doses (Borovik 1990), which is one reason why metal hyperaccumulating plants have attracted scientific interest. The logical extension of this principle is that the metal levels in these plants might render them relatively toxic to other organisms with which they interact. In this paper, we identify those biotic interactions that are likely to be affected by the high metal contents of hyperaccumulating plant species, summarize current knowledge about each in relation to metal hyperaccumulation, and outline important questions that are worthy of future investigation.

**Table 1** Explanations advanced for metal (mainly Ni) hyperaccumulation in plants

Explanation	Papers suggesting explanation
Metal tolerance (sequestration)	Antonovics <i>et al.</i> 1971 Baker 1981, 1987 Krukeberg <i>et al.</i> 1993
Disposal from plant body	Ernst 1972 Wild 1978 Baker 1981 Farago & Cole 1988
Drought resistance	Severne 1974 Baker & Walker 1990 Robertson 1992 Mesjasz-Przybylowicz <i>et al.</i> 1996
Interference	Baker & Brooks 1989 Gabrielli <i>et al.</i> 1991 Wilson & Agnew 1992 Gabrielli <i>et al.</i> 1997
Inadvertent uptake	Severne & Brooks 1972 Baker & Walker 1989
Pathogen/herbivore defence	Reeves <i>et al.</i> 1981 Ernst 1987 Ernst <i>et al.</i> 1990

### Herbivory/disease/decomposition

A role for hyperaccumulated metals in resistance to herbivory and/or disease has been postulated a number of times (see Table 1). However, only recently have experiments been conducted to test whether hyperaccumulated metals harm or deter herbivores or pathogens. To date, there is a growing body of evidence indicating that metal-containing plants are protected to some extent from a variety of organisms, ranging from bacteria to fungi to insects (Table 2). Boyd & Martens (1992) suggested that metal hyperaccumulation represents an "elemental defence" that differs from other plant chemical defences ("secondary compounds") in two major ways. First, elemental defences involve a toxic element taken up from the soil, rather than a defensive chemical that is constructed by a plant's biochemical machinery.

Second, elemental defences cannot be degraded as can occur with secondary compounds, due to the elemental nature of the metal ions.

Most studies of the defensive function of hyperaccumulated metals have dealt with folivorous insects (*e.g.*, Ernst 1987; Martens & Boyd 1994; Boyd & Martens 1994; Pollard & Baker 1997). There are two different pathways by which defence is achieved. One is via acute toxicity of metal-containing plant tissue (Boyd & Martens 1994; Martens & Boyd 1994), in which ingestion of plant material results in mortality. Another is through deterrence, in which high-metal plant tissue is ingested to a lesser extent than low-metal tissue (when a choice is experimentally provided). Deterrence has been demonstrated by Boyd & Martens (1994) with the Ni-hyperaccumulator plant *Streptanthus polygaloides* Gray (Brassicaceae) and by Pollard and Baker (1997) using the Zn-hyperaccumulating *Thlaspi caerulescens* J. et C. Presl (Brassicaceae) (Table 2). In the most extreme case, that using larvae of *Pieris brassicae*, Pollard and Baker (1997) documented a complete refusal of the insects to even sample high-Zn leaves. The cues that prevented feeding in this case are unknown, but are worthy of further investigation. Failure of hyperaccumulated metals to deter herbivory has also been documented (Balkwill & Burt 1997; Martens & Boyd, *subm.*).

Much remains to be learned about the effects of metals in plant tissues upon herbivores/pathogens. While it is clear that the metal contents of some hyperaccumulators render them acutely toxic to some organisms, determination of minimum tissue metal concentrations required to negatively affect herbivores/pathogens has yet to be accomplished (Boyd 1998). There is little information regarding dose-response curves of metals to herbivores/pathogens that consume metal-containing plant tissue. Metal levels below the thresholds used to define hyperaccumulation might still have some defensive function. In this light, it is particularly intriguing that Ernst (1987) found that a Cu content of 400  $\mu\text{g g}^{-1}$  was acutely toxic to insect larvae

**Table 2** Published information supportive of the defence hypothesis of metal hyperaccumulation

Paper	Plant species	Metal	Organism(s) affected
Ernst 1987	<i>Silene vulgaris</i> (Moench) Garke	Cu	<i>Hadena cucubalis</i> Schiff. (Lepidoptera: Noctuidae)
Boyd <i>et al.</i> 1994	<i>Streptanthus polygaloides</i> Gray	Ni	<i>Xanthomonas campestris</i> (Gram-negative bacterium) <i>Alternaria brassicicola</i> (Imperfect fungus) <i>Erysiphe polygoni</i> (Powdery mildew)
Martens & Boyd 1994	<i>Streptanthus polygaloides</i>	Ni	<i>Pieris rapae</i> L. (Lepidoptera: Pieridae)
Boyd & Martens 1994	<i>Thlaspi montanum</i> L. var. <i>montanum</i>	Ni	<i>Pieris rapae</i>
Pollard & Baker 1997	<i>Thlaspi caerulescens</i> J. et C. Presl.	Zn	<i>Schistocerca gregaria</i> (Forsk.) (Orthoptera: Acrididae) <i>Deroceras carvaneae</i> (Pollonera) (Pulmonata: Limacidae) <i>Pieris brassicae</i> L. (Lepidoptera: Pieridae)

(see Table 2), as this level of Cu is well below the 1000  $\mu\text{g g}^{-1}$  level that defines Cu hyperaccumulation (Baker & Brooks 1989). Boyd (1998) suggested that sublethal effects of metals (e.g., reduced herbivore growth rate, longer duration of pupation) may defend non-hyperaccumulating plant species, which often have elevated metal contents when growing on serpentine soils (Brooks 1987). The only study to examine this question to date is that of Boyd & Moar (subm.), who compared the defensive effects of Ni in hyperaccumulating and non-hyperaccumulating species of *Streptanthus*. They found statistically significant effects of foliar Ni concentrations as low as 93  $\mu\text{g g}^{-1}$  on larvae of beet army worm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), for which mean larval weight was reduced and time to pupation extended. Thus, metal-based defences might be more common among plants growing on serpentine soils than has been suspected previously.

The literature on plant chemical defences suggests that every defence is subject to some type of herbivore/pathogen counter-defence (Ehrlich & Raven 1967; Harborne 1988). Therefore, it is likely that some herbivores and pathogens are able to circumvent metal-based plant defences and that field observations will reveal evidence of herbivore and pathogen attack. Pertinent field observations are practically non-existent, as we know of only two studies published to date. Proctor *et al.* (1989) showed that the Philippine tree *Shorea tenuiramulosa* (Dipterocarpaceae), the leaves of which may contain up to 1000  $\mu\text{g g}^{-1}$  Ni, suffered as much leaf damage as non-hyperaccumulator species growing in the same habitat. The second study, by Noell and Morris (1997), dealt with the Ni hyperaccumulator *Stackhousia tryonii* Bailey (Stackhousiaceae). This western Australian plant may contain up to 21,500  $\mu\text{g g}^{-1}$  Ni in leaf tissue (Batianoff *et al.* 1990), and Noell & Norris (1997) documented epidermal wounds upon plants in the wild that they concluded were the result of feeding on leaf tissue by hemipterans. We predict that similar reports will accrue as investigators survey hyperaccumulators in the field for evidence of herbivore or pathogen attack.

We further predict that research will reveal three ways that circumvention of elemental defences may occur: (1) selective feeding on low-metal tissues, (2) use of a generalist diet to dilute metal-containing food, and (3) tolerance of high dietary metal content. Most studies that have examined the distribution of metal in hyperaccumulators find elevated metal contents in all plant organs (e.g., Jaffré & Schmid 1974; Jaffré *et al.* 1976; Reeves *et al.* 1981). However, because few studies exist, the distribution of metal among tissues is poorly known. Variation in metal content among tissues may provide an opportunity for an herbivore/pathogen to avoid metal toxicity. For example, Ni is reported to be transported in the xylem of crop plants (Mishra & Kar 1974) and, by extension, may be transported similarly by Ni hyperaccumulators. Recent study of a Ni hyperaccumulator documented xylem transport of Ni complexed with the amino acid his-

tidine (Kramer *et al.* 1996). The reliance of plants on xylem for Ni transport implies that phloem fluid may contain little Ni, and, since it is a rich source of carbohydrates, phloem fluid may be an undefended resource for organisms able to utilize it.

Avoidance of an elemental defence via selective feeding appears to be the case with aphids feeding on the Ni hyperaccumulator *Streptanthus polygaloides* Gray (Brassicaceae). Boyd & Martens (submitted) grew Ni-hyperaccumulating plants (containing ca. 5000  $\mu\text{g g}^{-1}$  Ni) on potting soil amended with  $\text{NiCl}_2$  and grew non-hyperaccumulating *S. polygaloides* plants (40  $\mu\text{g g}^{-1}$  Ni) on unamended potting soil. Glasshouse experiments using the pea aphid (*Acyrtosiphon pisum* [Harris]; Homoptera: Aphididae), a horticultural pest presumably unadapted to feeding on serpentine-soil plants, revealed equal survival and reproduction on high- and low-Ni plants. These results imply that either the phloem fluid of high-Ni plants was not high in Ni or that the aphids were tolerant of Ni. Furthermore, collections of aphids feeding on high-Ni plants showed only a modest increase in Ni content in the aphid bodies, relative to the Ni content of aphids feeding on low-Ni plants (Boyd & Martens, subm.). In contrast, Ernst *et al.* (1990) collected aphids (*Brachycaudus lychnidis* L.) from a field-grown population of the Zn-tolerant plant *Silene vulgaris* (Moench) Garcke (Caryophyllaceae), which may contain up to 1400  $\mu\text{g g}^{-1}$  Zn in its leaves, and reported elevated (9000  $\mu\text{g g}^{-1}$ ) Zn in the aphids' bodies. It is unclear why the results differ in these two cases. Differences between the metals, the plant species, or the aphid species are all possible reasons for these contrasting results.

Another way in which herbivores might avoid metal toxicity is to mix high- and low-metal foods so that the total metal dose is non-toxic. This dilution strategy is likely to be most effective when the size of the herbivore is large relative to that of the plant. An example of this is suggested by Martens & Boyd (submitted), in which high- and low-Ni *Streptanthus polygaloides* plants were placed into a serpentine site to compare natural herbivory levels. Some plants were protected by wire mesh cages that excluded non-insect herbivores, whereas others were uncaged. Unprotected plants were eaten regardless of plant metal content. Damage patterns suggested that plants were grazed by a sizable vertebrate herbivore species (possibly a deer or rabbit species). Such relatively large generalists may destroy entire young plants with a few bites, but feed on many plant species and therefore dilute any high-Ni tissue that they may consume.

The third way that metal-based defences may be circumvented is through the ability of herbivores/pathogens to tolerate elevated levels of metals in the tissues they consume. To our knowledge, only a single study of animal, fungal, parasitic plant, or bacterial species that attack metal hyperaccumulating plants in the field has been conducted. Boyd & Martens (submitted) discovered plants of the Ni hyperaccumulator *Streptanthus polygaloides* (Brassicaceae) parasitized by

*Cuscuta californica* var. *breviflora* Engelm. (Cuscutaceae). Metal contents of the parasite ranged from 540–1220  $\mu\text{g g}^{-1}$  Ni, 73-fold higher than the metal contents of *Cuscuta* parasitizing a co-occurring non-hyperaccumulator plant species. These elevated tissue Ni contents showed that the *Cuscuta* plants were very Ni-tolerant, as a tissue Ni level greater than 10  $\mu\text{g g}^{-1}$  is usually sufficient to cause decreased growth of unadapted plants (MacNicol & Beckett 1985).

Metal tolerance is known from animal (Hopkin 1989; Klerks 1990), fungal (Brown & Hall 1990), and bacterial (Schlegel *et al.* 1992; Stoppel & Schlegel 1995) species, so it seems likely that many more metal-tolerant herbivores/pathogens will be discovered when the biotic associates of metal hyperaccumulators are studied. We further predict that, in parallel with some relationships between plants and herbivores mediated by organic-based secondary chemicals (see examples in Harborne 1988), the metal-based defences of some hyperaccumulating species will be sequestered by herbivores or pathogens to defend them against their own enemies. The above-cited example with *Cuscuta*, in which the parasite contained metal contents of up to 1220  $\mu\text{g g}^{-1}$ , was judged by Boyd & Martens (subm.) to be the first well-documented example of the transfer of elemental defences from a hyperaccumulating host to a seed plant parasite.

Decomposition of hyperaccumulator tissues also may be affected by high metal content. It seems likely that decomposers are faced with the same toxicity problems that face herbivores/pathogens, and we suspect similar evolutionary solutions also pertain (*i.e.*, selective consumption of low-metal tissues, dilution of metal in “diet”, metal tolerance). We know of no studies to date that have examined this phenomenon. Proctor *et al.* (1989) suggested that the serpentine flora of a Malaysian site excreted Ni into senescing leaves, indicating that elevated Ni levels in plant tissues may be a general problem for decomposers living on serpentine sites.

The ramifications of metal hyperaccumulation for the vital ecosystem processes of decomposition and nutrient cycling (*e.g.*, Komulainen & Mikola 1995) are currently unexplored. Elevated metal concentrations in plant biomass likely will lead to consequences for other portions of food chains, as has been shown in metal-polluted environments (*e.g.*, Roberts & Johnson 1978; Cheng *et al.* 1984; van Straalen & van Wensem 1986; Hopkin 1989). Metals hyperaccumulated by plants may accumulate at upper trophic levels and therefore have high “bioaccumulation indices”. For example, bioaccumulation indices reported by Pais & Jones (1997) show Cu, Co, and Zn with high indices, and Ni, Cr, and Pb with moderate indices. Of the seven metals hyperaccumulated by plants (Baker & Brooks 1989), only Mn has a low bioaccumulation index (Pais & Jones 1997). Therefore, there may be important ecosystem consequences due to the movement of metals along food chains in habitats harbouring hyperaccumulating plants.

## Interference

Interference is the second biotic interaction that may be affected by metal hyperaccumulation. Baker & Brooks (1989) suggested that interference may occur between hyperaccumulators and neighbouring plants but did not offer a mechanism. Metal-mediated interference was also suggested by Wilson & Agnew (1992), who speculated that elevated soil metal levels beneath hyperaccumulator canopies might prevent less metal-tolerant plants from invading patches of hyperaccumulators. Gabrielli *et al.* (1991), working with *Alyssum bertolonii* Desv. (Brassicaceae), predicted that Ni-enriched litter-fall would result in elevated soil Ni levels near hyperaccumulator plant canopies. They suggested that this, in turn, might negatively affect less Ni-tolerant plants and therefore result in a decrease in competition experienced by the hyperaccumulator. This mechanism is reminiscent of allelopathy, in which a plant species releases a chemical substance into its environment that negatively affects another (Rice 1974). However, inhibition in the case of a metal hyperaccumulator would be due to redistribution of an element in the soil, rather than manufacture of an organic compound. In this sense, we might call this “elemental allelopathy” between the hyperaccumulator and non-hyperaccumulator plants. However, for elemental allelopathy involving hyperaccumulators, autotoxicity (a negative effect of the chemical on the species producing it) is not likely to occur due to the high metal tolerance of hyperaccumulators. This is unlike some other cases of allelopathy, in which autotoxicity has been demonstrated (Newman 1978).

We know of no evidence that centers directly on the question of metal-based interference (elemental allelopathy). Schlegel *et al.* (1992) documented higher Ni levels in soil taken from under the canopy of the New Caledonian Ni hyperaccumulator *Sebertia acuminata* Pierre ex Baill. (Sapotaceae), compared to soil taken from under the canopy of non-hyperaccumulator species. Similarly, Baker *et al.* (1992) reported higher soil Ni concentrations near an isolated individual of a Ni-hyperaccumulating *Phyllanthus* species (Euphorbiaceae) in the Philippines. Thus, it appears that soil metal levels may be elevated near individual hyperaccumulator plants. The crucial evidence needed to substantiate the elemental allelopathy hypothesis is the demonstration that these elevated metal levels inhibit germination or growth of other serpentine plant species. To date this information has not been sought.

## Mutualism

Mutualism is the third category of biotic interactions that might be affected by metal hyperaccumulation. There are two types of mutualism we shall consider here, mycorrhizae and animal-mediated pollen or seed dispersal.

Mycorrhizae, associations between fungi and plant roots, provide plants with enhanced nutrient uptake

while the fungus receives energy-rich organic compounds (Allen 1991). A number of Ni hyperaccumulators are members of the Brassicaceae, a family that forms few mycorrhizal associations (Allen 1991), and these might be expected to lack them. However, the non-hyperaccumulator *Streptanthus glandulosus* Hook. (Brassicaceae) has been reported to possess mycorrhizae (Hopkins 1987) and so the topic may simply be poorly explored. We know of only two published studies that have examined Ni hyperaccumulating species for mycorrhizal associations. Lioi & Giovanetti (1989) examined *Alyssum bertolonii* Desv. (Brassicaceae) from Italian serpentines, and Goncalves *et al.* (1997) examined *Alyssum serpyllifolium* Desf. from Portuguese serpentines. Both failed to find mycorrhizae.

Metal tolerance is well-known in fungi (Brown & Hall 1990) and serpentine soils are populated by fungi that tolerate the generally elevated metal contents of these soils. Some of these fungal species are mycorrhizal (Maas & Stuntz 1969). We speculate that some hyperaccumulators may form mycorrhizae and, in some cases, the mycorrhizal fungi may play a role in metal uptake. Brown & Hall (1990) report that vesicular arbuscular mycorrhizae may enhance metal uptake of non-hyperaccumulating species when soil metal levels are low. However, we should note that mycorrhizae also have been reported to increase metal tolerance of some non-hyperaccumulating species by decreasing metal uptake. For example, Bradley *et al.* (1982) reported that mycorrhizae assisted *Calluna* in avoiding Cu and Zn toxicity.

Pollen and seed dispersal may involve biotic and/or abiotic vectors. Biotic vectors may engage in mutualism, in which the animal usually obtains a food resource from the plant. This food resource commonly consists of nectar, pollen, or fruit pulp (Howe & Westley 1988). If a hyperaccumulating plant produces these resources and if they have high metal contents, then animal mutualists of these plants must either be tolerant of the metal or dilute it through a mixed diet. A third solution to this problem is for the plant to rely on abiotic vectors or non-mutualistic animal vectors for pollen or seed transport.

There is little available information on seed and pollen dispersal mechanisms for hyperaccumulating plants. We know of no studies that have specifically measured metal contents of pollen, nectar, or the non-seed portions of fruits produced by metal hyperaccumulating species. Some studies have measured metal contents of entire flowers and/or fruits, and have usually recorded elevated metal levels in those structures (*e.g.*, Jaffré & Schmid 1974; Jaffré *et al.* 1976; Reeves *et al.* 1981). An exception from the Philippines was found by Baker *et al.* (1992) for *Walsura monophylla* Elm. (Meliaceae), reported to have 7000  $\mu\text{g g}^{-1}$  Ni in leaves but only 54  $\mu\text{g g}^{-1}$  in fruits. This very limited available evidence suggests that metal exclusion from reproductive structures might occur in some hyperaccumulators. We expect that seed and pollen dispersal studies of hyperaccumulating species will reveal examples of each of the mechanisms outlined above (non-mutualistic or

abiotic vectors, diet-diluting vectors, and metal tolerant vectors).

### Commensalism

Commensalism is an interaction that benefits one organism and is of neutral value to another. In the context of hyperaccumulating plants, epiphytism seems the commensal interaction most likely to be affected by plant metal content. We can find no reference to epiphytes in the literature dealing with hyperaccumulating plants, possibly because few detailed field studies of hyperaccumulators have been conducted in humid habitats where the phenomenon is most noticeable. The few studies that deal with humid tropical forests on serpentine give little or no mention to this aspect (*e.g.*, Proctor *et al.* 1988; Proctor *et al.* 1989; Baker *et al.* 1992). Proctor *et al.* (1988) estimated covers of epiphytes on the boles of trees in Malaysia, but did not report values for individual species. Their study included *Shorea tenuiramulosa*, a tree that can accumulate up to 1000  $\mu\text{g g}^{-1}$  Ni in its leaves.

The occurrence of epiphytes on leaves of the Ni hyperaccumulating shrub *Psychotria douarrei* (Beauvis.) Däniker (Rubiaceae) was reported by Boyd *et al.* (subm.). They surveyed leaves of varying age on individuals of this tropical moist forest understory shrub from New Caledonia. Epiphyte load was quite high and increased significantly with increasing leaf age. Mean cover of epiphytes on upper leaf surfaces ranged from 0.11% in young (expanding and recently expanded) leaves to 62% for the oldest leaves (Boyd *et al.* subm.). The latter high cover value implies that hyperaccumulated Ni was not a deterrent to colonization of *Psychotria douarrei* leaves by epiphytes.

Whether epiphytes from hyperaccumulators contain elevated metal levels is almost completely unexplored. To our knowledge, the only investigation into this question to date is the work of Boyd *et al.* (subm.) cited above. They documented 400  $\mu\text{g g}^{-1}$  Ni in an epiphyte sample consisting of leafy liverworts removed from leaves of *P. douarrei*. Although this is a notable Ni content, it is much less than the content of *P. douarrei* leaves. The oldest (and most heavily epiphytized) leaves of this shrub contained a mean value of 32,000  $\mu\text{g g}^{-1}$  Ni. The interplay of epiphytes and host plant chemistry is well-known (*e.g.*, Gustafsson & Eriksson 1995) and suggests this is a topic worthy of further exploration. Chemicals that mediate host-epiphyte interactions are most likely to be located in the outermost tissues of the host (Gustafsson & Eriksson 1995). Studies examining the localization of metal in hyperaccumulators have concluded that much metal is sequestered in epidermal or subepidermal cell walls or vacuoles (Ernst & Weinert 1972; Vazquez *et al.* 1994; Mesjasz-Przybylowicz *et al.* 1996; Gabrielli *et al.* 1997). These findings suggest that epiphytes would experience higher metal levels when growing on hyperaccumulator leaves. To our knowledge, only one study has attempted to measure the release of metal via

leaching of leaves from a hyperaccumulator. That work, with the Ni hyperaccumulator *Hybanthus floribundus* (Lindl.) F. Muell. (Violaceae) from western Australia, concluded that Ni is not readily leached from the leaves (Severne 1974).

Elevated metal contents in the soil under hyperaccumulators could also lead to another commensal interaction. This interaction would be similar in principle to the “nurse plant” effect observed for cacti in arid environments (e.g., Franco & Nobel 1989). It could occur if the high soil Ni levels under hyperaccumulator plants were required for establishment and growth of another plant species. We know of no evidence showing positive effects of high levels of soil metals upon growth or survival of hyperaccumulators in the field. However, we suggest that New Caledonian humid forests, which contain both overstory tree hyperaccumulators and understory shrub hyperaccumulators (Jaffré & Veillon 1990), would be excellent places to search for this phenomenon.

## Epilogue

It is clear that our ecological understanding of metal hyperaccumulating plant species is rudimentary. There are many fascinating and scientifically important questions about the consequences of metal hyperaccumulation for biotic interactions that need to be addressed. Furthermore, these questions have important practical implications for some of the applied uses of metal hyperaccumulators that are being contemplated. For instance, hyperaccumulators are being investigated for use in phytoextraction of metals from metal-polluted soils (e.g., Brown *et al.* 1994; McGrath *et al.* 1993) and for phytomining (Nicks & Chambers 1995). Large-scale uses of hyperaccumulators for these purposes will be more readily achieved if we first understand the ecological consequences of metal hyperaccumulation for co-occurring organisms.

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