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Spread of metals through an invertebrate food chain as influenced by a plant that hyperaccumulates nickel

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Summary. Hyperaccumulation of metals in the shoot system of plants is uncommon, yet taxonomically and geographically widespread. It may have a variety of functions, including defense against herbivores. This study investigated the effects of hyperaccumulation on metal concentrations across trophic levels. We collected plant material, soil, and invertebrates from Portuguese serpentine outcrops whose vegetation is dominated by the nickel hyperaccumulator *Alyssum pintodasilvae*. Samples were analyzed for nickel, chromium, and cobalt. Grasshoppers, spiders, and other invertebrates collected from sites where *A. pintodasilvae* was common had significantly elevated concentrations of nickel, compared to nearby sites where this hyperaccumulator was not found. Chromium and cobalt, occurring in high concentrations in the serpentine soil but not accumulated by *A. pintodasilvae*, were not elevated in the invertebrates. Therefore, it appears likely that a flux of nickel to herbivore and carnivore trophic levels is specifically facilitated by the presence of plants that hyperaccumulate this metal. The results may be relevant to the development of phytoremediation and phytomining technologies, which use plants to extract metals from the soil.

Key words. Hyperaccumulation – trace elements – phytoremediation – phytomining – *Alyssum*

Introduction

Hyperaccumulation of metals is known from about 400 species of flowering plants, which take up, transport and sequester metallic elements, achieving tissue concentrations that are toxic to most organisms (Baker *et al*. 2000; Reeves & Baker 2000). Several hypotheses have been advanced to explain the evolution of this trait (Boyd & Martens 1992), with most attention focused on the hypothesis that hyperaccumulated metals may act as defenses against herbivory (Boyd 1998; Boyd & Martens 1998; Pollard 2000; Pollard *et al*. 2000). With the exception of recent work by Wall and Boyd (2002), most studies to date have considered interactions between individual plants and herbivores, with little attention paid to the effects of hyperaccumulators on their communities or ecosystems.

The broader environmental consequences of hyperaccumulation are of practical importance because of developing technologies that would use metal-accumulating plants to cleanse contaminated soil, termed phytoremediation (Cunningham & Ow 1996; Chaney *et al*. 1997; Salt & Baker 2001; Schwitzguébel *et al*. 2002), or use such plants to extract commercially valuable metals from low-grade ores, termed phytomining (Brooks *et al*. 1998). A relatively unexplored risk of these techniques is that metals sequestered in plant tissues could be consumed by herbivores and thus mobilized into food chains (US Dept of Energy 1994; Chaney *et al*. 2000). One way to investigate the possibility of such mobilization is through studies of natural ecosystems whose vegetation is dominated by hyperaccumulating plants.

We conducted our study at Portuguese serpentine (ultramafic) sites, whose soils are typically high in nickel, chromium, cobalt, and magnesium, but relatively deficient in calcium, potassium and phosphate. Such sites possess distinctive vegetation with high levels of endemism (Brooks 1987; Chiarucci *et al*. 1998). *Alyssum pintodasilvae* Dudley (syn. *A. serpyllifolium* ssp. *lusitanicum* Dudley & Pinto da Silva; cf. Dudley 1986) is a member of the Brassicaceae (mustard family) that is endemic to serpentine outcrops in northeastern Portugal, where it can represent a very large proportion of the vegetation (Aguiar *et al*. 1998). Plants of this species are known to hyperaccumulate nickel in such systems (Brooks *et al*. 1981; de Varennes *et al*. 1996). The research reported here was designed to investigate the effects of this hyperaccumulation on the trace element levels in invertebrate communities.

Materials and methods

We collected replicate sets of soil, plant, and invertebrate samples from five sites where *A. pintodasilvae* makes up at least 50% of plant cover (designated Ap+) and five other areas where it is absent (designated Ap-). Collections were made on August 15–16, 1999,

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from two localities in northeastern Portugal in the vicinity of Bragança (N41°46'41.7", W6°45'4.2" near Samil and N41°50'34.8", W6°51'42.1" on the N103 at the Gondesende junction), with both Ap+ and Ap- sites in each locality. Site characteristics are described in Table 1.

Soils were collected from the top 5 cm of the soil, adjacent to the plant root systems. Samples of *A. pintodasilvae* foliage were collected in sites where it was present, and separate samples of other representative plants were collected at all sites. Invertebrates were collected by sweep-netting along a 4 × 50 m strip transect, with two passes made along each transect. (In two cases where rocky terrain and thorny shrubs prohibited transect sampling, we sweep-netted in and around patches of *A. pintodasilivae* for a period of 4 minutes, which was determined to be the approximate time spent sampling the transects.)

Invertebrates were sorted into three groups: grasshoppers, spiders, and "other invertebrates." Mass requirements for metal analysis prevented us from dividing the groups further; for this reason many of the invertebrates were not taxonomically identified. Grasshoppers and spiders were separated because each was a relatively abundant group and because they represent exclusively herbivorous and carnivorous groups, respectively.

Plants and animals were dried, weighed, ashed at 500°C, and dissolved in 10% HCl. Soil samples were sieved, dried, weighed, and digested in concentrated HNO_3/HCl. Extracts were analyzed for Ni, Cr, Co, and Zn using flame atomic absorption spectrophotometry. There were few significant differences in Zn concentration among the samples, and they are not reported here.

Two-tailed Mann-Whitney U tests were used to test the significance of differences in mean metal concentration between sites where *A. pintodasilvae* was present and those where it was absent. This non-parametric test was employed because of large differences in variance between treatment groups, especially in cases where metal concentrations were near the limits of instrumental detection.

Results

Plants other than *Alyssum pintodasilvae* consistently had concentrations of Ni, Cr, and Co that were about 0.3% to 0.6% of the respective elemental concentrations in the soil in which they grew (Table 2). The mean Ni concentrations in *A. pintodasilvae* leaves were approximately 5,600 mg kg^{-1} (dry weight), more than 2.5 times the total concentration in the soil. On the other hand, concentrations of Cr and Co were only slightly if at all higher in *A. pintodasilvae* than in other nearby plants (Table 2), and about two orders of magnitude lower than their concentrations in soil.

Soils covered by *A. pintodasilvae* had higher concentrations of Ni, Cr, and Co than those where it was not present (Table 2). These differences were statistically significant for all three metals (Mann-Whitney U test: $P = 0.001$ for Ni, $P = 0.012$ for Cr, $P = 0.004$ for Co). The Ni content of plants other than *A. pintodasilvae* essentially mirrored these soil differences, with each element about 1.5 to 2 times more concentrated in the plants sampled from Ap+ sites than in those from Ap– sites.

More Ni was found in the bodies of grasshoppers, spiders, and other invertebrates from Ap+ sites than in their counterparts from Ap– sites (Fig. 1). The difference was statistically significant for all three invertebrate groups (Mann Whitney U test: $P = 0.009$ for grasshoppers, $P = 0.011$ for spiders, $P = 0.009$ for others). There were no significant differences ($P > 0.05$) between the Ap+ and Ap– sites in the amounts of Cr or Co in the bodies of any of the animals sampled.

Discussion

The metal concentrations of *Alyssum pintodasilvae* foliage confirm previous findings (de Varennes *et al*. 1996) that this species hyperaccumulates only nickel, and does not take up exceptional concentrations of other metals even if these are freely available. The differences in soil metals between the Ap+ and Ap– sites are consistent with the typical elemental composition of serpentine rocks (Brooks 1987), and suggest that while soils at both types of sites were derived from serpentine minerals, the former were more strongly ultramafic. Our data support this geological explanation rather than phytoenrichment of metals by hyperaccumulator leaf litter (Boyd and Jaffré 2001), in that Ni, Cr, and Co were all significantly higher in Ap+ soils, whereas *A. pintodasilvae* itself would enrich only the Ni. Conversely, it is unlikely that the elevated Ni levels measured in animals from Ap+ sites resulted from adhering dust and soil particles, as there was no concurrent elevation in Cr and Co in these animals, as would be expected from mineral contaminants.

Because *A. pintodasilvae* hyperaccumulates Ni selectively and to high concentrations, it is most likely that this species was the source of the elevated Ni detected in the invertebrates. Wall and Boyd (2002) came to a similar conclusion with regard to the effects of *Streptanthus polygaloides* on arthropods in California. We also detected higher Ni concentration in plants other than *A. pintodasilvae* at Ap+ sites compared to Ap– sites (Table 2), presumably because of the more strongly ultramafic soils at the former. While this difference was statistically significant (Mann-Whitney U test: $P = 0.013$), it was not of great magnitude, and the Ni concentrations in such plants were 10 to 100 times lower than those measured in the bodies of the animals. Thus, it seems unlikely that these other plants were responsible for the observed Ni concentrations in the animals. The specific results described here might differ had the collections been made on a different date, due to seasonal variations in metal uptake by the hyperaccumulator and differences in the floral and faunal characteristics of the sites.

The highest concentration of Ni that we observed in animals at Ap+ sites was in the "other invertebrates" category, with mean Ni concentration exceeding 1300 $\mu g\ g^{-1}$, a remarkably high value that would qualify as hyperaccumulation if it were in plant tissues. This heterogeneous category consisted primarily of several unidentified species of relatively large-bodied Heteroptera, along with various mantids, flies and ants. It is unlikely that all of them would accumulate high nickel concentrations; therefore, one or more species probably has a much higher concentration in order to bring the mean up to this value. Our ongoing studies are attempting to identify these insect taxa and assign nickel concentrations to individual species. In similar systems Schwarz & Wall (2001) have recently described a new species of Heteroptera that specializes on a Ni hyperaccumulator, *Streptanthus polygaloides* (Brassicaceae), in California, and accumulates 590-1020 $\mu g\ g^{-1}$ Ni in its tissues. On the other hand, a beetle that specializes on the South African Ni hyperaccumulator *Berkheya coddii* (Asteraceae) does not accumulate high Ni levels in its body tissues (Mesjasz-Przybylowicz *et al*. 2002).

Table 1 Characteristics of study sites in northeastern Portugal. Total soil nickel concentrations were determined from strong-acid digests. Plant lists indicate common taxa observed in the collection areas, but no attempt was made to comprehensively survey or quantify the vegetation. The most prominent species were sampled for nickel analyses based on ashed, acid-dissolved extracts. Nickel concentrations are given in parentheses after the name of the taxon. Grasses from each site were analyzed together as a combined sample. Other species observed but not analyzed for Ni are also listed

Site type*	Site name	Description	Soil Ni (µg g^{-1} d.w.)	Plants (µg Ni g^{-1} d.w.)
Ap+	Samil outcrop (3 transects)	Serpentine outcrop, vegetation mostly grasses and low shrubs	2962	*Alyssum pintodasilvae* (4520); grasses (9.0) including *Taeniantherum caput-medusae, Aegilops triuncialis, Agrostis capillaris, A. castellana x A. capillaris, Koeleria crassipes, Phleum bertolonii; Genista hystrix* (5.4); *Eryngium tenue* (14.3); *Centaurea micrantha* (23.8); *Trifolium cherleri; T. arvense*
Ap+	Gondesende south	Rocky area with grasses and scattered shrubs, sparse canopy of planted pine trees	524	*Alyssum pintodasilvae* (7859); grasses (5.8) including *Agrostis capillaris, A. castellana x A. capillaris, Dactylis hispanica; Genista hystrix* (3.1); *Daucus carota subsp. maritima* (12.0); *Armeria langei* subsp. *daveaui* (15.5); *Cytisus striatus; Pinus pinaster*
Ap+	Gondesende north	Very disturbed rocky area with grasses, scattered shrubs	851	*Alyssum pintodasilvae* (6578); grasses (4.7) including *Taeniantherum caput-medusae, Agrostis capillaris, A. castellana* x *A. capillaris, Bromus tectorum, Dactylis hispanica; Rubus* sp. (11.1); *Cytisus striatus* (13.9); *Daucus carota* subsp. *maritima* (12.0)
Ap–	Samil roadside (2 transects)	Disturbed roadside near serpentine outcrop	716	Grasses (1.1) including *Bromus hordeaceus, B. sterilis, B. tectorum, Hordeum murinum* subsp. *leporinum; Eryngium campestre* (4.7); *Plantago radicata* (8.7)
Ap–	Samil pasture	Cattle pasture near edge of serpentine outcrop	1960	Grasses (7.6) including *Holcus lanatus, Festuca rothmaleri, Bromus hordeaceus, Cynosurus cristatus; Carex muricata* subsp. *lamprocarpa* (3.48); *Trifolium repens; T. pratense; Plantago lanceolata*
Ap–	Gondesende roadside	Low grassy roadside near serpentine outcrop	374	Grasses (0.6) including *Taeniantherum caput-medusae, Bromus tectorum; Armeria langei* subsp. *daveaui* (9.3); *Daucus carota* subsp. *maritima* (8.3)
Ap–	Gondesende pasture	Cattle pasture approx. 100m from serpentine area	619	Grasses (0.4) including *Holcus lanatus, Festuca rothmaleri, Bromus hordeaceus; Daucus carota* subsp. *maritima* (6.2); *Mentha suaveolens* (6.8); *Trifolium repens; T. pratense; Plantago lanceolata*

* Ap+ sites were characterized by > 50% cover of *Alyssum pintodasilvae*; Ap– sites lacked this species.

Table 2 Nickel, chromium, and cobalt concentrations in plant and soil samples from Portuguese serpentine sites. Values shown are means ± standard errors, averaged across the 5 sites of each type

Site Type*	Sample	Concentration ($\mu g\ g^{-1}$ dry weight) Ni	Cr	Co
Ap+	Soil	2052.1 ± 264.4	748.0 ± 90.3	116.4 ± 11.0
Ap+	*Alyssum pintodasilvae*	5599.5 ± 1254.3	2.5 ± 0.6	6.8 ± 2.7
Ap+	All other plants	11.1 ± 2.1	2.1 ± 0.8	0.3 ± 0.2
Ap–	Soil	876.8 ± 137.8	503.2 ± 35.1	71.2 ± 6.5
Ap–	All plants	5.1 ± 0.3	1.4 ± 0.2	0.2 ± 0.1

*Ap+ sites were characterized by >50% cover of *Alyssum pintodasilvae*; Ap– sites lacked this species

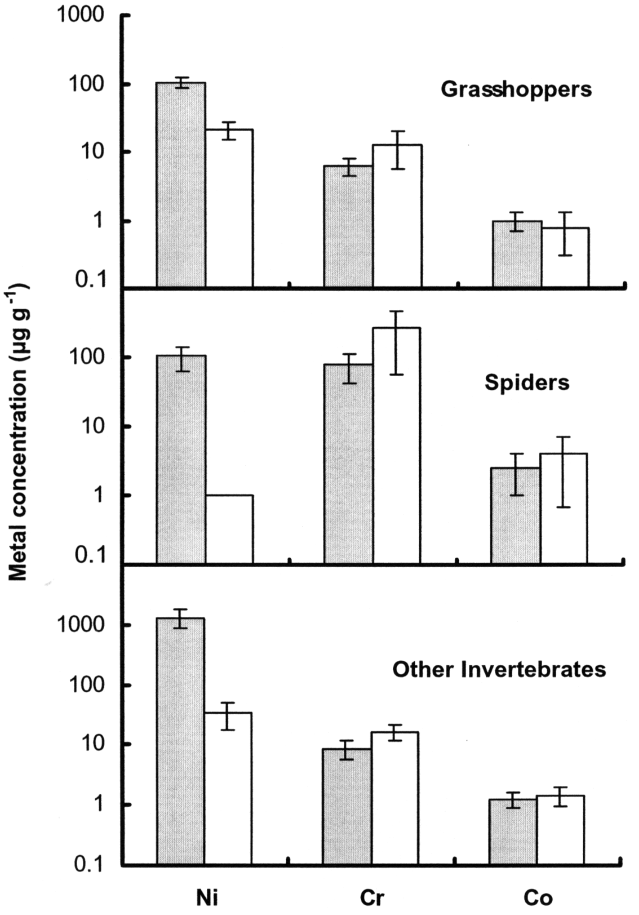

Fig. 1 Mean elemental concentrations of invertebrate samples from serpentine sites in northeastern Portugal. Shaded bars represent "Ap+ sites" in which the Ni-hyperaccumulator *Alyssum pintodasilvae* was the dominant vegetation. Open bars are "Ap– sites" where this species was not present. The vertical axes are scaled logarithmically in order to avoid obscuring lower values. Error bars indicate standard errors of means

High Ni concentrations in both grasshoppers and spiders suggest that the presence of hyperaccumulating plants affects the flux of Ni to both herbivore and carnivore trophic levels. This parallels findings recently published by Boyd and Wall (2001) showing that nickel accumulated by a herbivore feeding on hyperaccumulating plants can be passed on to the bodies of carnivores. Their study mostly involved feeding experiments in captivity, in which animals were reared on a single diet with no choices. Our data extend this finding to a natural situation, in which both herbivores and carnivores were feeding freely on foods with a variety of metal concentrations. In one case, Boyd and Wall (2001) reported the nickel concentration in wild-caught crab spiders (*Misumena vatia*, Araneae: Thomisidae) from *Streptanthus polygaloides* on California serpentines. The maximum Ni concentration they reported, 110 $\mu g\ g^{-1}$, was similar to our mean value for spiders of 103.1 $\mu g\ g^{-1}$. This similarity is made more intriguing by the fact that our samples were also primarily made up of thomisid crab spiders, especially *Xisticus cristatus* but also some *M. vatia*.

The mean Ni concentration that we found in spiders (103.1 $\mu g\ g^{-1}$) was very close to that in grasshoppers (103.3 $\mu g\ g^{-1}$). If these figures are taken as representative of general concentrations of Ni in herbivore and carnivore trophic levels, their ratio represents a biomagnification index (Laskiowski 1991, Boyd & Wall 2001) of B = 0.998. Values of this index near unity indicate that, once an element enters the food chain, it is transferred but is not further concentrated or "magnified." In this respect our result agrees with previous findings for nickel and most other metals (Heliövaara & Väisänen 1987, Outridge & Sheuhammer 1993, Barceloux 1999, Chaney *et al.* 2000).

We did not attempt to determine what portion of the nickel measured in the arthropods had been assimilated into body tissues, as opposed to residing in gut contents. Apart from the difficulty of separating these tissues, we also wanted the results to be relevant to predators that consume whole prey, including the gut contents. The limited data on toxicological effects of dietary nickel toward vertebrates suggests that foraging in systems such as this could harm insectivorous animals. Grasshoppers are a major component of arthropod biomass (Devkota & Schmidt 2000), and the concentrations of Ni observed in their tissues approach the level at which mammals and birds become unable to regulate their absorption and excretion of this element (Outridge & Sheuhammer 1993). The concentrations found in the "other invertebrates" category could be acutely toxic to wildlife (Cain & Pafford 1981).

Although our study was intended to mimic the situation of a phytoremediation monoculture, it differs in several ways. Most importantly, the hyperaccumulator *A. pintodasilvae* is endemic to this vegetation, and herbivores and carnivores have had the opportunity to adapt, in both the physiological and evolutionary senses, to its presence. Short-term introduction of metal accumulating plants to communities in which they do not normally occur could have different consequences. There is mounting evidence that hyperaccumulated metals may act as defenses against herbivory, either by acute toxicity (Boyd & Martens 1994, Boyd 1998) or by deterrence of feeding (Pollard & Baker 1997, Jhee *et al.* 1999). Even in systems without hyperaccumulators, grasshoppers have been shown to avoid feeding on plants contaminated by heavy metal pollution (Migula & Binkowska 1993). Thus, in systems that are not co-adapted, trophic transfer of metals may be less common than demonstrated in our studies. On the other hand, our results point out the possibility that a technique used to clean up pollutants in the environment could potentially spread these materials through food chains at hazardous concentrations instead. We recommend that phytoremediation and phytomining schemes incorporate regular sampling and monitoring of metal concentrations in both invertebrate and vertebrate herbivores at the sites. Such data may determine whether measures such as trapping, exclusion, or insecticide treatments are warranted to avoid herbivory on metal-rich plant material. Herbivores represent a potential loss of yield as well as an entry point into food chains; therefore, these steps could increase both the safety and the efficiency of phytoremediation.

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