unrestricted gene flow between the different morphotypes. This makes the subdivision of the *C. alpinum* complex into distinct morphotypes uncertain on ultramafic soils.

The genetic differentiation among populations shows that *C. alpinum* has been able repeatedly to colonize ultramafic soils irrespective of genetic background. The hairy and glabrous morphotypes found in the two major groups of populations suggests a multiple origin of the different morphotypes. These results agree with what was found for ultramafic populations of the related plant *Silene dioica* (Caryophyllaceae), which in contrast to *C. alpinum* is a diploid obligate outcrosser.[12,17] A more thorough analysis of the postglacial colonization of *C. alpinum* populations on different soil types in Fennoscandia will be published elsewhere.

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Phytoenrichment of soil Ni content by *Sebertia acuminata* in New Caledonia and the concept of elemental allelopathy

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Elemental allelopathy, which depends upon elevated soil metal concentrations under metal-hyperaccumulating plants, may provide a competitive advantage for hyperaccumulators. We tested whether metal enrichment of litter and surface soil occurs under metal hyperaccumulators, using the New Caledonian Ni hyperaccumulator tree species *Sebertia acuminata*. We selected 11 *Sebertia* trees, pairing each with a nearby similar-sized tree of a non-hyperaccumulator species. We collected samples of litter, surface soil (0–5 cm depth), and subsurface soil (15–20 cm depth) from locations under the canopy of each tree. Elemental concentrations of litter and soils were quantified for 12 elements (Ni, Mg, Ca, K, P, Cu, Fe, Mn, Zn, Co, Cr and Pb). Litter under *Sebertia* contained significantly more Ni than litter under non-hyperaccumulator trees (31 000 *vs* 6300 µg/g, respectively), but was lower in Mg. Nickel was significantly higher in surface soil under *S. acuminata* trees (100 *vs* 65 µg/g), as was Pb (but Cr was lower). Subsurface soil differed significantly only for Pb, which was higher under *Sebertia* trees. Since, as the literature suggests, metal hyperaccumulators are more tolerant of elevated soil metal concentrations, litter and surface soil Ni levels under the canopy of *Sebertia* trees may provide an ecological advantage for metal-hyperaccumulating plants.

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Introduction

Plants can profoundly influence the soils on which they grow, in some cases by vertically redistributing elements in the soil profile.[1] Nutrient concentrations of soils under plant canopies can be affected by several plant characteristics, including litter pH, litter nutrient concentrations, and root characters.[2,3]

Some plants contain inordinately elevated concentrations of heavy metals. These plants, called hyperaccumulators,[4] are defined as having >1000 µg/g dry wt of Ni, Cu, Co, Cr or Pb, or >10 000 µg/g of Zn or Mn in their tissues.[5]

Research on the function(s) of hyperaccumulated metals in plants is only just beginning. Boyd and Martens[6] surveyed the literature on metal hyperaccumulation, finding much speculation on the ecological role(s) of hyperaccumulated metals but little research. Hyperaccumulated metals have been postulated to function in metal tolerance, drought tolerance, protection from herbivores, and/or interference between neighbouring plants. Besides tests of the defence hypothesis (reviewed by Boyd[7]), the other postulated roles of hyperaccumulated metals are relatively unexplored.

The interference hypothesis has, to our knowledge, never been tested. This interaction between hyperaccumulator and non-hyperaccumulator plant species, which Boyd and Martens[8] suggested was equivalent to 'elemental allelopathy', can only occur if the Ni concentration of soil beneath Ni-hyperaccumulating plants is significantly enriched. As envisaged by Wilson and Agnew,[9] this metal-enriched soil excludes less metal-tolerant plants and thus provides a competitive advantage for the hyperaccumulator. Boyd and Martens[8] also pointed

out that Ni enrichment of soil under hyperaccumulators could lead to commensal species interactions. These commensal relationships postulate greater odds of establishment or survival for seedling hyperaccumulators when they grow in the metal-enriched soil under the canopies of established hyper-accumulators. Phytoenrichment of metals in soils under metal hyperaccumulators has been only cursorily examined to date.[10-12]

The question of metal phytoenrichment under the canopies of hyperaccumulator species is central to either elemental allelopathy or a commensal function for Ni hyperaccumulation. A major objective of this research was to examine Ni concentrations of litter and soils under a Ni hyperaccumulator species to determine if significant Ni enrichment can be demonstrated. To test this hypothesis, we selected perhaps the most renowned Ni hyperaccumulator species, the New Caledonian forest tree *Sebertia acuminata* Pierre ex Baillon (Sapotaceae). Commonly known as 'Seve bleue', it produces a blue latex that contains up to 26% Ni dry wt.[13] This extremely high Ni concentration led Reeves[14] to refer to the latex of *S. acuminata* as 'one of the most remarkable of all biological fluids.' Nickel values in leaves average 1.2%, and high levels of Ni are found in all parts of the tree.[13] It has been estimated that a single tree may contain as much as 37 kg Ni.[15] Promising preliminary soil analyses were reported by Schlegel *et al.*,[10,11] in which they proposed that Ni released from litter of *S. acuminata* accumulates in surface soil under tree canopies.

Study site

The field site for this research, conducted in late August 1995, is in the Parc de la Rivière Bleue on Grand Terre, the main island of the New Caledonian archipelago. Found near the southern end of the island, the park contains areas of humid tropical forest. Jaffré and Veillon[16] described the vegetation of this forest type, and Jaffré[17] provided an overview of the high level of floristic diversity found in New Caledonia. Our study was performed in a stand of humid forest located at the Kauri Geant, a site in the park notable for an exceptionally large *Agathis lanceolata* Lindl. tree. This site includes one of the study plots described by Jaffré and Veillon,[16] and is remarkable because six Ni hyper-accumulators co-occur in two layers of the vegetation.[16] The shrub layer contains *Psychotria douarrei* (Beauvis.) Däniker, *Hybanthus austrocaledonicus* (Vieill.) Schinz & Guillamin ex Melchior, and *Casearia silvana* Schltr. The overstorey contains *S. acuminata*, as well as the Ni hyperaccumulator tree species *Homalium guillaumii* (Vieill.) Briq. and *Geissois hirsuta* Brongn.

Methods

The study site was searched for *S. acuminata* trees, and 11 were selected for this study. Each *S. acuminata* tree was paired with a nearby, similar-sized tree of a non-hyperaccumulating species. The diameter at breast height (dbh) was measured for each tree included in the study. Each non-hyperaccumulating tree was as close as possible to its paired *Sebertia*, as long as canopies did not overlap. In practice, distances between trunks of trees comprising a pair ranged from *c.* 20 to 40 m. Samples of litter and soil were collected from under the canopy of each tree, from sites located as close as possible to the tree's trunk. Most sampled sites were within 2 m of the trunk of the target tree. Sampling locations were selected subjectively, choosing sites that were not under the canopy of a Ni-hyperaccumulating shrub species, for which the soil surface and litter showed no sign of recent disturbance by animals, and which were apparently free of large woody roots.

Litter samples included leaves and other fresh or decomposing plant material found on the soil surface, excluding large woody debris (such as pieces of branches) and humus material. Each litter sample was *c.* 100 ml in volume. After a litter sample was collected, any remaining organic material was removed to expose the surface of the mineral soil. A surface soil sample (to 5 cm depth) was collected, and then a lower soil depth sample was excavated from the same location at 15–20 cm depth. Each soil sample was *c.* 30 ml in volume. For a few locations, the presence of large woody roots forced us to collect the deeper soil sample from a location laterally displaced from the surface soil sample's location. This displacement was never greater than 15 cm. Thus, three samples were collected from each sampling location: a litter sample, a surface soil sample, and a subsurface soil sample. Two sampling locations were selected beneath each tree used in the study and samples were collected from each location.

Litter samples were dried for several days at 60°C, ground, and analysis was performed for 12 elements. One gram of each sample was dry-ashed at 485°C, further oxidized using 1 M HNO_3, and the residue re-dissolved in 1 M HCl. The latter solution was analysed for Mg, Ca, K, P, Cu, Fe, Mn, Zn, Co, Cr and Pb using an inductively-coupled argon plasma spectrometer (Jarrell-Ash, ICAP 9000). Nickel was determined by a separate procedure in which the sample was dry-ashed at 485°C, further oxidized using 1 M HNO_3, and the residue re-dissolved in 1 M HCl. The Ni concentration of the final solution was determined using an atomic absorption spectrophotometer.

Soil samples were dried, ground, and a sample extracted for Ni using the DTPA extractant of Lindsay and Norvell[18] adjusted to pH 7.0. DTPA was used because it better reflects plant-available soil Ni concentrations.[18] The DTPA extract was analysed for Ni using an atomic absorption spectrophotometer. If enough sample remained, a second extract was made using a double-acid extractant in order to quantify other elements. Soil samples were extracted in 20 ml of extractant (0.05 M HCl/0.025 M H_2SO_4) shaken with 5 g of dry soil for 5 min. This extract was analysed for Mg, Ca, K, P, Cu, Fe, Mn, Zn, Co, Cr and Pb using an inductively-coupled argon plasma spectrometer (Jarrell-Ash, ICAP 9000).

The above procedures created datasets for litter, surface soil, and subsurface soil elemental concentrations. Data for each element in each dataset were analysed by separate one-way analyses of variance (ANOVAs) to determine if tree type significantly influenced element concentration.

Results

Trees used for this study were well-matched in size for each pair and covered a wide range of tree sizes among pairs. Mean *S. acuminata* dbh was 44 cm (s.e. = 4.4) and ranged from 15–69 cm. Mean non-hyperaccumulator tree dbh was 42 cm (s.e. = 4.3), ranging from 15–72 cm. A paired sign test revealed no significant difference in the sizes of *Sebertia* and non-hyperaccumulator members of each sampled pair of trees ($P = 0.55$). In most cases the identity of the non-hyper-accumulators was unknown, but two of the eleven trees were *Schefflera gabriellae* Baillon (Araliaceae).

Elemental concentrations of litter samples varied due to tree type for only two elements (Table 1). The greatest difference was in Ni concentration, which was significantly (almost fivefold) higher for litter under *Sebertia acuminata* trees. It is noteworthy that the concentration of Ni in the litter from under *Sebertia* trees was about threefold higher than the value for Ca (Table 1). By contrast, litter under non-hyperaccumulator trees contained about twofold more Ca than Ni. A less extreme difference was observed for Mg concentrations, for which litter under *Sebertia*

Table 1. Elemental concentrations (µg/g dry wt) in samples of litter collected under *Sebertia acuminata* and non-hyperaccumulator tree species. Data are means (s.e.; *n*). *P*-values are the result of one-way ANOVA using tree type as the variable of interest. Asterisks denote elements whose values are significantly correlated with levels of Fe in the samples, and thus are likely to be influenced by soil adhering to the litter samples.

	Tree type		
Element	*Sebertia acuminata*	Non-hyperaccumulator	*P*-value
Ni	31 000 (4100; 20)	6 300 (860; 21)	<0.0001
Mg	2 600 (170; 21)	3 200 (190; 21)	0.021
Ca	12 000 (700; 21)	14 000 (1500; 21)	0.13
K	650 (37; 21)	710 (57; 20)	0.43
P	320 (15; 21)	310 (17; 21)	0.74
Fe*	3 700 (760; 21)	4 000 (810; 21)	0.74
Cu*	21 (1.9; 21)	22 (2.5; 21)	0.72
Mn*	240 (27; 21)	200 (23; 21)	0.36
Zn*	45 (2.7; 21)	39 (3.5; 21)	0.19
Co*	23 (2.4; 21)	22 (3.4; 21)	0.80
Cr*	94 (19; 21)	100 (20; 21)	0.75
Pb*	18 (1.3; 21)	16 (2.3; 21)	0.37

trees was about 80% that of litter collected under non-hyper-accumulator trees.

No significant differences between litter collected from under *S. acuminata* and non-hyperaccumulator trees were noted for the ten other elements quantified in Table 1. However, some of the metal values documented were very high for plant tissue samples, e.g. those for Fe and Cr. We are certain that some of these means reflect inclusion of soil along with the organic matter of the litter, as it was impossible to exclude all soil from these field-collected samples. Reeves[14] suggests that Fe measurements >500 µg/g and Cr measurements >50 µg/g for plant materials indicate soil inclusion. To determine which of the elements in Table 1 may have been influenced by soil inclusion, we performed a linear regression of each of the elements in Table 1 against the values for Fe. These regressions were significant (in all cases, *P* < 0.02) for most other metals (Cu, Mn, Zn, Co, Cr, Pb). The two exceptions were Ni and Mg, for which *P*-values were 0.63 and 0.25, respectively. Regressions for the remaining elements (Ca, P, K) also were not significant (*P* > 0.36 in all cases).

Surface soil layers varied significantly between *Sebertia* and non-hyperaccumulator trees for three elements (Table 2). Both Ni and Pb values were higher under *Sebertia* trees, whereas Cr levels were greater under non-hyperaccumulator trees. Values for other elements did not differ significantly with tree type (Table 2), although Zn did display a trend for greater concentration under *S. acuminata* trees.

For the subsurface soil layer, concentrations of only one element varied significantly beneath *Sebertia* and non-hyper-

accumulator trees (Table 3). Values for Pb were significantly higher under *S. acuminata* trees, although the mean for soil under *Sebertia* was only 1.2 times higher than that for non-hyper-accumulator trees. Mean Ni concentration was higher beneath *S. acuminata* trees, but this difference was not statistically significant (*P* = 0.11).

Discussion

Our data showed Ni enrichment of both litter and surface soil under *Sebertia* trees (relative to non-hyperaccumulator trees). Mean Ni levels for litter under non-hyperaccumulator trees were relatively high (6500 µg Ni/g). This is probably due to inclusion of litter from understorey hyperaccumulator species in those samples. The understorey at this site contains two other Ni hyperaccumulators (*Psychotria douarrei* and *Hybanthus austro-caledonicus*), which produce leaves with Ni concentrations of up to 47 000 µg/g[19] and 13 600 µg/g.[20] Even though we avoided sampling in locations directly under the canopy of either of these species, we did note nearby individuals in many cases.

High Ni levels in soil under Ni hyperaccumulators may be explained in two ways. One is phytoenrichment. The other explanation is that hyperaccumulator seedlings may become preferentially established on high-Ni microsites that occur naturally due to variation in the Ni concentration in the soil parent material. Definitive separation of these hypotheses requires more detailed investigation, but our evidence supports plant-driven Ni phytoenrichment. If these trees established on microsites in which the parent material was higher in Ni, then we predict that deeper soil layers under the hyperaccumulators would contain elevated Ni levels. This difference would be less marked for surface soils, whose characteristics would be ameliorated to some extent by biotic activity.[1] We found the opposite pattern: significantly higher Ni levels were found for surface soil under *Sebertia*, and there was no significant difference for soil at greater depth. In combination with the very marked enrichment of Ni in the litter layer, our data suggest that Ni phytoenrichment is the primary reason for elevated surface soil Ni concentrations under *Sebertia* trees.

Phytoenrichment of soil Ni by hyperaccumulator species may be a widespread phenomenon. Elevated Ni levels under hyperaccumulator plants have been reported previously. Baker et al.[12] reported soil chemical trends underneath *Phyllanthus palawanensis* from the Philippines. They found that surface soils were higher in Ni close (5 cm) to a single specimen of this species, compared to soil samples collected farther away (40 and 100 cm distant). Krämer et al.[21] documented twofold higher soil Ni levels for soil next to roots of *Thlaspi goesingense*, relative to soil next to

Table 2. Elemental concentrations (µg/g soil) in upper soil layer (0–5 cm depth) samples collected under *Sebertia acuminata* and non-hyperaccumulator tree species. Ni was extracted with DTPA, whereas other elements were double-acid extracted (see Methods). Data are means (s.e.; *n*). *P*-values are the result of one-way ANOVA using tree type as the variable of interest.

	Tree type		
Element	*Sebertia acuminata*	Non-hyperaccumulator	*P*-value
Ni	100 (10; 23)	65 (8.2; 20)	0.0078
Cr	0.67 (0.044; 9)	0.89 (0.086; 10)	0.036
Pb	2.5 (0.23; 9)	1.6 (0.081; 10)	0.0009
Mg	970 (140; 9)	980 (140; 10)	0.97
Ca	600 (120; 9)	580 (120; 10)	0.91
K	68 (8.4; 9)	66 (7.7; 10)	0.90
P	8.3 (0.71; 9)	7.6 (0.72; 10)	0.52
Cu	0.37 (0.032; 9)	0.37 (0.036; 10)	0.91
Fe	9.2 (1.0; 9)	12 (0.96; 10)	0.11
Mn	85 (7.6; 9)	130 (35; 10)	0.24
Zn	5.3 (0.87; 9)	3.7 (0.18; 10)	0.064
Co	5.2 (0.35; 9)	7.4 (2.0; 10)	0.30

Table 3. Elemental concentrations (µg/g soil) in lower soil layer (15–20 cm depth) samples collected under *Sebertia acuminata* and non-hyperaccumulator tree species. Ni was extracted with DTPA, whereas other elements were double-acid extracted (see Methods). Data are means (s.e.; *n*). *P*-values are the result of one-way ANOVA using tree type as the variable of interest.

	Tree type		
Element	*Sebertia acuminata*	Non-hyperaccumulator	*P*-value
Ni	72 (7.4; 23)	55 (7.8; 21)	0.11
Pb	1.7 (0.15; 16)	1.4 (0.050; 15)	0.032
Cr	0.77 (0.045; 16)	0.74 (0.024; 15)	0.54
Mg	610 (63; 16)	580 (62; 15)	0.74
Mn	64 (7.8; 16)	68 (11; 15)	0.76
Zn	4.8 (0.36; 16)	6.1 (0.84; 15)	0.16
Co	3.9 (0.40; 16)	3.9 (0.52; 15)	0.94
Ca	180 (45; 16)	120 (28; 15)	0.30
K	29 (3.8; 16)	26 (1.3; 15)	0.46
P	5.8 (0.41; 16)	5.3 (0.36; 15)	0.44
Cu	0.47 (0.022; 16)	0.46 (0.026; 15)	0.65
Fe	10. (0.66; 16)	11 (0.60; 15)	0.43

roots of non-hyperaccumulator plants in the same ultramafic plant community.

Phytoenrichment of soils by metal hyperaccumulators is likely to have important ecological consequences. These may include elemental allelopathy, nurse plant effects, and soil biotic effects. We will discuss each of these in turn, in the hope of guiding further research into each phenomenon.

Elemental allelopathy is a negative effect of high soil metal concentration on less metal-tolerant plant species. As noted previously, one of the hypotheses advanced to explain the evolution of metal hyperaccumulation, as summarized by Boyd and Martens,[6] was interference with other plant species. This hypothesis requires that metal hyperaccumulators be more metal-tolerant than other serpentine soil plant species. If so, high metal soils around hyperaccumulators will be less hospitable microsites for non-hyperaccumulators. This elemental exclusion of non-hyperaccumulator individuals may lead to lessened competition (for soil resources or light) and thus benefit the hyperaccumulator.

There is some evidence that metal hyperaccumulator species are more tolerant of metals than non-hyperaccumulators. Early work by Morrison et al.[22] showed greater root elongation for four Ni hyperaccumulating species of Alyssum grown at high soil Ni concentration, relative to a non-hyperaccumulating congener. Using root elongation tests, Gabbrielli et al.[23] showed greater Ni tolerance in the Ni hyperaccumulator A. bertolonii Desv. relative to the non-hyperaccumulator Silene italica L. Krämer et al.[24] reported higher biomass for a hyperaccumulator species of Alyssum than for a non-hyperaccumulator, when grown on high-Ni substrates. Shen et al.[25] reported greater Ni tolerance in T. caerulescens when compared to the non-hyperaccumulating species T. ochroleucum. Finally, Boyd et al.[26] concluded that the Ni hyperaccumulator species Streptanthus polygaloides Gray was more Ni tolerant than the non-hyperaccumulator species S. breweri Gray. These reports all suggest that a competitive advantage may accrue to metal hyperaccumulators when grown together with non-hyperaccumulators on high-metal soils, but field- or greenhouse-based experiments should be conducted to explore this ecological consequence of phytoenrichment.

Commensalism is another possible consequence of metal phytoenrichment.[8] This is likely to be similar to a 'nurse plant effect', in which an individual of one species modifies the environment in its immediate vicinity in a way that favours the establishment of individuals of another species.[27,28] At sites that support more than one species of hyperaccumulator, similar positive interactions may occur based on shared tolerances of metal hyperaccumulator species for high soil metal concentrations. For example, at our study site, overstorey hyperaccumulator individuals (Sebertia acuminata, Homalium guillaumii, Geissois hirsuta) may create metal-enriched microsites that favour the establishment of individuals of understorey hyperaccumulator species (Psychotria douarrei, Hybanthus austrocaledonicus, Casearia silvana).

It is also possible that recruitment of juveniles of a hyperaccumulator species might be favoured under a parent plant's canopy. Even an annual hyperaccumulator species, such as S. polygaloides, might over time create high-metal soil patches that favour recruitment of the species in future years. In this case, the relationship would not be commensalism but one of 'plant parental care'[29] mediated by metal phytoenrichment.

Finally, we suggest that soil metal phytoenrichment has a major impact on soil biology in microsites located under metal-hyperaccumulator plant canopies. Given that litter and surface soils are significantly enriched in Ni, the decomposer fauna and microflora of these microsites will likely have adapted to these high-metal microenvironments. Besides the work of Schlegel et al.,[10,11] who suggested that the entire bacterial flora in such locations was metal-adapted, this ecological consequence of metal hyperaccumulation remains to be explored.

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