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Elemental levels and relationships in the Flacourtiaceae of New Caledonia and their significance for the evaluation of the 'serpentine problem'

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Summary Sixteen elements were determined in 156 specimens of 47 species of New Caledonian Flacourtiaceae including the genera Casearia, Homalium, Lasiochlamys and Xylosma. The data were used to study inter-elemental relationships, particularly those involving nutrient elements, magnesium and phytotoxic elements such as chromium, cobalt and nickel. Phytotoxic chromium was not accumulated to any marked degree by any taxon. Cobalt was inversely correlated with boron and sodium, and nickel with both nutrients as well as manganese. The data seemed to indicate the overriding controlling factor of reduced nutrient uptake caused by elements present in high concentrations in serpentinic substrates. It would seem that this reduced uptake is a major factor in the 'serpentine problem', at least as far as the Flacourtiaceae and the New Caledonian environment is concerned. By contrast, the toxic effects of elements such as nickel, cobalt and chromium seems less important.

Introduction

The 'serpentine problem' has attracted a great deal of scientific attention during the past 50 years. The problem relates to the general infertility of serpentine soils and the causes of this. The infertility has been linked to many factors[7] such as: physical properties of the soil; low levels of nutrients such as nitrogen, phosphorus, and potassium; reduced uptake of calcium due to the large amount of magnesium in the soil; the phytotoxicity of chromium, cobalt and nickel which all have high concentrations in serpentine soils.

To decide whether any one factor or combination of factors is

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responsible for the infertility of serpentine soils is very difficult to establish and the literature carries many conflicting reports on this problem. Recently however, Brooks and Yang[3] have determined 16 elements in about 20 serpentine-endemic species from the Great Dyke of Zimbabwe. From correlation analysis they established that there was a highly significant inverse relationship between magnesium in the plants and the concentrations of aluminium and cobalt, and the nutrients, boron, iron, manganese, phosphorus and sodium. These findings seemed to indicate antagonism to nutrient uptake caused by the high magnesium content of the soil.

We have recently extended our investigations on the serpentine problem by studying elemental uptake and relationships among the Flacourtiaceae of New Caledonia, a family with many serpentine-tolerant species in the genera Casearia, Homalium[6], Lasiochlamys and Xylosma.

The New Caledonian Flacourtiaceae are unusual in containing an inordinate number of hyperaccumulators of nickel defined as taxa with concentrations of this element exceeding 1000 μg/g (0.1%) in dried material. A total of 19 hyperaccumulators has been identified in this family. In the work described below, 16 elements were determined in 156 specimens of 47 species of Flacourtiaceae from New Caledonia. Correlation analysis was carried out on the data to determine whether uptake of plant nutrients was inversely related to the uptake of other element, particularly magnesium and phytotoxic non-nutrients.

Materials and methods

Plant material

Authenticated plant material from the herbarium at ORSTOM, Nouméa, New Caledonia (NOU) was used for the experiments. These species are listed in Table 1 together with collection localities and collector numbers. The collection localities are also shown in Fig. 1 which also shows the extent of the ultramafic rocks which cover about one third of the land area of the island.

Analytical methods

Samples (*ca.* 0.05 g) were placed in 5 ml borosilicate test tubes and ashed at 500°C in a muffle furnace. The ash was dissolved in 4 ml of 2 *M* hydrochloric acid prepared from redistilled 6 *M* constant-boiling reagent. The solutions were then analysed for 16 elements by plasma emission spectrometry (ICP) using an ARL 34000 instrument. The detection limit was of the order of 1 μg/g on the original plant ash for most elements and the precision was typically in the range 1–3%.

Results and discussion

The following findings depend largely on the use of correlation analysis to establish elemental relationships in plant material. In doing

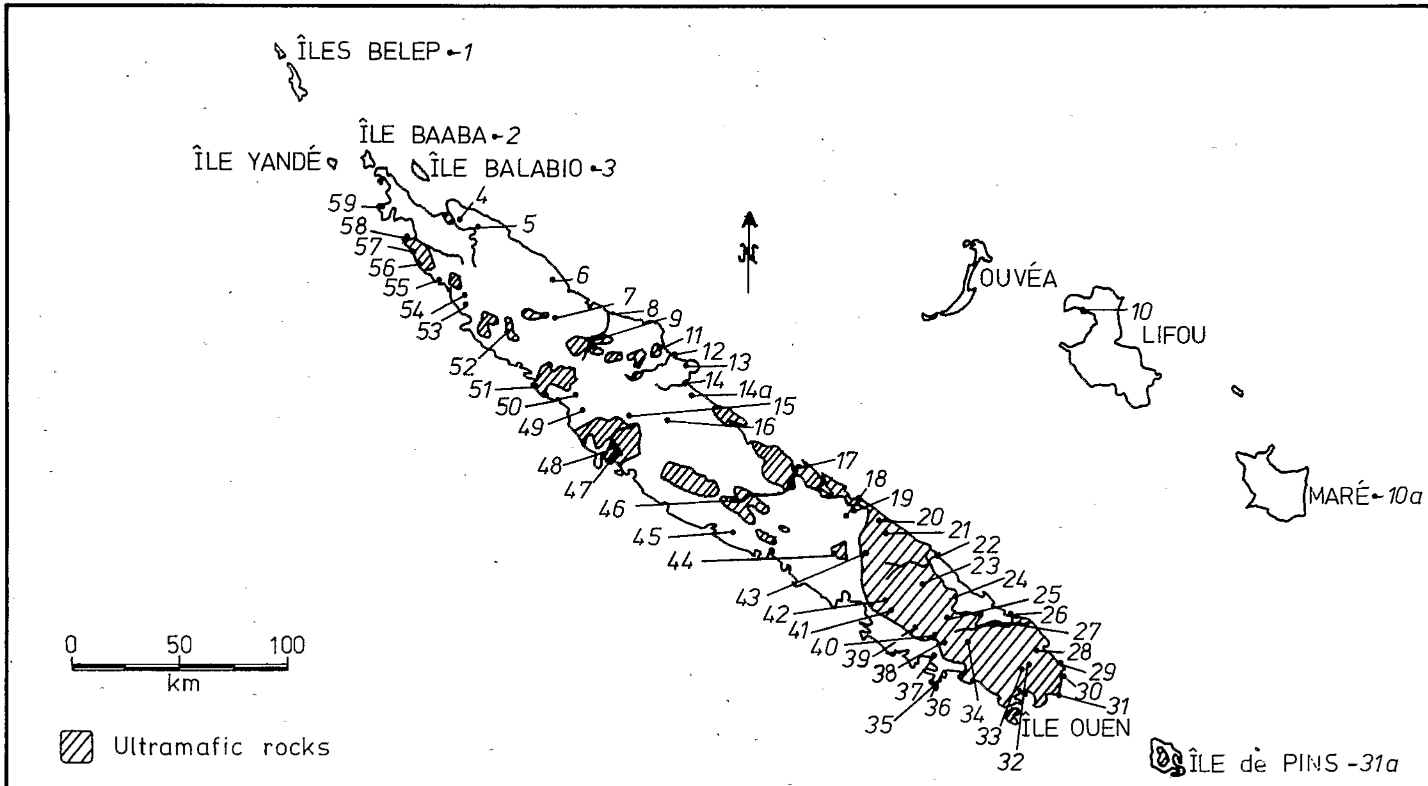

Fig. 1. Map of New Caledonia showing collection localities and areas of ultramafic rocks. *Numbers* refer to data in Tables 1 and 2.

Table 1. Collection data for Flacourtiaceae of New Caledonia

#	Species	No.*	Collector numbers	Localities**
Casearia				
1	*C. coriifolia* Lescot and Sleumer	3 (3)	M32294; PS1599; V2050	44
2	*C. deplanchei* Sleumer	3 (3)	J970, 1003, 1504	47, 57
3	*C. kaalensis* Lescot and Sleumer	3 (3)	M1749, 40768, 41180	54, 55
4	*C. puberula* Guillaumin	6 (3)	B1133; J1480; M3939, 36182; S3471, V1006	11, 14, 27, 41
5	*C. silvana* Schlechter	6 (3)	J731; M11989, 21133; M05118; S4098; V3501	14, 17, 27, 35
Homalium				
6	*H. austrocaledonicum* Seeman	3 (3)	B807; J1368; M38984	55
7	*H. buxifolium* Däniker	3	J1437, 1488; M25289	59
8	*H. betulifolium* Däniker	3 (3)	B1286; J1512; V2889	41
9	*H. decurrens* (Vieillard) Briquet	6 (3)	J1391, 1555; M21310, 40564; N471; S1471	4, 57
10	*H. deplanchei* (Vieillard) Briquet	6 (3)	J1711; M10076, 20327, 34383, 35052; S1982	35, 71
11	*H. francii* Guillaumin	3 (3)	J1356; M25549, 28840	11
12	*H. guillainii* (Vieillard) Briquet	3 (3)	J1306, 1699; M14507	25, 27
13	*H. intermedium* (Vieillard) Briquet	3	M03780; M20462, 25524	4
14	*H. kanaliense* (Vieillard) Briquet	6 (3)	B1164; H3597; J834, 1337, 1710; M5041	28, 32, 47
15	*H. leratiorum* Guillaumin	3	M23829, 26450; VI1098	35, 49
16	*H. insulare* (Vieillard) Briquet	3	M27407, 27412; SU1185	4
17	*H. mathieuanum* (Vieillard) Briquet	1	J s.n.	1
18	*H. serratum* Guillaumin	3	J1684; M16897, 18105	20, 55, 58
19	*H. polystachyum* (Vieillard) Briquet	3 (3)	J1392; M30426; S2695	57
20	*H. rubrocostatum* Sleumer	1 (1)	J1708	48
21	*H. rubiginosum* (Vieillard) Warburg	2 (2)	M21715, 26355	17
Lasiochlamys				
22	*L. cordifolia* Sleumer	3	M25783, 26846; SU1353	14a
23	*L. coriacea* Sleumer	3 (1)	M13686, 20790, 26676	4, 11, 14
24	*L. fasciculata* (Guillaumin) Sleumer	3	M19630, 26829, 40559	4, 16
25	*L. koghiensis* (Guillaumin) Sleumer	3 (3)	M18186; V943, 1044	38, 39, 44
26	*L. mandjeliana* Sleumer	3	M19565, 25924, 37126	4
27	*L. planchonellifolia* (Guillaumin) Sleumer	3 (3)	M21076; M05337; S4998	34, 38, 44
28	*L. pseudocoriacea* Sleumer	2 (2)	MP4491; M21224	46
29	*L. reticulata* Schlechter) Pax and Hoff	3	M25758, 26805; SU1348	14a, 16
30	*L. rivularis* Sleumer	3 (3)	M32312; S843; V4208	27, 28
31	*L. trichostema* (Guillaumin) Sleumer	1 (1)	V2205	39
Xylosma				
32	*X. bernardianum* Sleumer	3	M19979, 21306, 33087	4
33	*X. boulindae* Sleumer	3 (3)	J1338, 2262, 2360	47
34	*X. confusum* Guillaumin	4 (4)	J1331; S5291, 5358, V3246	27, 43
35	*X. dothiense* Guillaumin	3 (2)	M22520; V1420, 3119	18, 19, 45
36	*X. kaalense* Sleumer	3 (3)	M16123, 39087; N0204	54
37	*X. lancifolium* Sleumer	3	M19215; S452, SE752	12

Table 1 (*continued*)

#	Species	No.*	Collector numbers	Localities**
38	*X. lifaunum* Guillaumin	3	S1275, 1276, 2208	10, 10a
39	*X. molestum* Sleumer	2 (2)	M17708, 17711	15
40	*X. nervosum* Guillaumin	3 (3)	M20176, 23041; V1129	20, 41, 42
41	*X. orbiculatum* (J. R. and G. Forster) G. Forster	3	S1023, 1817, 2210	10, 10a
42	*X. pancheri* Guillaumin	6 (3)	J50; M13153, 13154, 23181, 23669; S3332	2, 35, 36
43	*X. peltatum* (Sleumer) Lescot	3 (3)	M36784, 38024, 40264	29
44	*X. pininsulare* Guillaumin	2 (2)	M23474; S2098	31a
45	*X. serpentinum* Sleumer	3 (3)	J1667; M14977, 16175	57, 59
46	*X. tuberculatum* Sleumer	3 (3)	J1147; M17694, 22221	15, 48
47	*X. vincentii* Guillaumin	5 (3)	M12243, 16995, 25543; M05404; SE1693	11, 27

* number in brackets refers to specimens on serpentine.
** localities as indicated in Fig. 1.
B = Blanchon: H = Hoff: J = Jaffré: M = McKee: MO = Morat: MP = McPherson: NO = Nothis: PS = Pusset and Sevenet: S = Schmid: SE = Sevenet: SU = Suprin: V = Veillon: VI = Virot.

so a number of assumptions must be made. The first of these is that mature healthy plants were collected and that such plants will have a relatively similar chemical composition when growing over the same substrate. In using herbarium specimens there is of course no guarantee that the collector will have taken great care in selecting mature plants not showing signs of ill-health. Nevertheless, experienced collectors do not usually make this mistake, and as will be noted from Table 1, a small number of very reputable collectors were responsible for nearly all of the specimens. As regards compositional variability, it is well established that plants of the same species growing over the same substrate will have essentially the same chemical composition with relatively minor variations caused by such factors as aspect, drainage, health *etc*[1]. Indeed this relative lack of variability is the basis of biogeochemical prospecting[1].

A second assumption is that a good correlation implies a causal relationship between two variables. A causal relationship is difficult to prove for natural systems and the alternative is the reduce the number of variables by carrying out pot trials under controlled conditions. Such a procedure would have been quite impossible for the New Caledonian species if only because of the difficulties of propagation. The advantage of working in a natural laboratory, such as in field conditions in New Caledonia, greatly outweighs considerations that relationships established by correlation analysis might just possibly be non-causal.

Elemental levels in the Flacourtiaceae of New Caledonia

Elemental levels in dried leaves of the Flacourtiaceae of New Caledonia are shown in Table 2. The data are shown as mean (geometric) values for each species studied. In the case of nickel, a maximum value is also given. From the data it was possible to identify 12 hyperaccumulators of nickel all of which has been previously identified[6]. It should be mentioned that the hyperaccumulator *Xylosma peltata* (Sleumer) Lescot was originally described as *Lasiochlamys peltata* Sleumer. Apart from nickel and iron, none of the siderophiles (iron group elements) was accumulated to any inordinate degree. This indicates little or no contamination of the samples by the soil which typically has several thousand μg/g of chromium. Since chromium is not known to be accumulated to any degree by plants, the content of this element in plant material is often a good index of contamination.

Interelemental relationships in plant material

The results of correlation analysis of the data are shown in Table 3. Calculations were carried out on data converted to logarithms because the elemental abundance data were in general lognormally distributed. The calculations were moreover confined to only those specimens 95 known to be growing over ultramafic substrates. Analyses were indeed also available for a further 60 specimens not growing over ultramafic substrates. However, to have included these values would have produced misleading conclusions because of the very low concentrations of elements such as cobalt and nickel in these plants compared with the serpentinophytes. A preliminary survey of the data showed that a number of false correlations were obtained because the values were not normally distributed even after transformation to logarithms.

In general the siderophile elements (cobalt, chromium, iron, manganese, and nickel are correlated positively with each other as might be expected for passive uptake of these elements from the soil. The only significant negative correlation ($P < 0.05$) among these elements was that between manganese and nickel. This is particularly noteworthy however, since manganese is a plant nutrient.

Elemental relationships between plant nutrients and other elements show a number of important features. As mentioned previously[3], there was a strong trend of negative correlations between magnesium and other plant nutrients for serpentine-endemic plants from Zimbabwe and it was determined that magnesium was the most important edaphic controlling factor at that site. In the New Caledonian material however, magnesium is inversely correlated only with potassium, so that here at least, magnesium does not appear to be such an important controlling

Table 2. Mean (Geom.) elemental concentrations (μg/g dry weight) in 47 species of Flacourtiaceae of New Caledonia. Key for numbered species in Table 1

#	Al	B	Ca	Co	Cr	Cu	Fe	K	Mg	Mn	Na	Nickel max.	Nickel mean	P	S	Sr	Zn
1	12	665	14555	4	3	2	66	10789	3289	139	7852	218	32	579	492	149	29
2	12	432	6761	4	2	6	46	7621	2891	121	6213	209	70	923	700	181	19
3	28	646	16672	3	4	4	155	1897	6745	89	5248	57	29	601	753	77	20
4	33	544	9772	4	3	2	111	3715	5546	391	9614	684	15	1030	701	134	78
5	17	602	11092	3	2	2	89	6081	2648	159	8279	762	12	776	632	76	50
6	10	136	10233	6	2	11	112	3388	6310	117	2455	244	195	1000	3090	110	50
7	15	89	3837	3	2	2	39	4291	4416	58	573	3	2	918	1422	84	15
8	43	114	4721	4	22	4	933	4742	4416	113	2466	206	141	1486	1644	43	87
9	10	179	12589	8	2	2	94	3296	4457	773	2825	191	73	787	1786	65	13
10	11	228	13804	4	3	4	105	4036	3508	50	2793	238	238	1347	1324	91	20
11	21	101	7745	4	6	2	95	4345	2449	35	2123	2574	1644	1146	1598	55	39
12	11	231	4395	6	2	5	50	6887	2427	133	3443	5115	407	1164	1376	48	38
13	100	186	7723	3	2	18	145	2328	3524	1021	4150	9	4	1358	1904	126	25
14	20	122	6095	27	4	7	83	10304	3999	124	1205	4389	1230	769	1409	92	68
15	45	114	18664	9	2	8	90	2182	4130	631	2152	24	19	1298	2183	74	101
16	45	275	5598	29	2	18	55	5346	3475	1121	4932	7	5	1479	1774	56	77
17	9	172	16539	11	2	11	78	3210	5215	1204	4362	9	9	530	1227	182	32
18	172	151	9333	5	4	13	283	7910	3357	25	1778	94	27	2183	1480	39	69
19	38	162	16181	4	3	22	108	6486	3864	955	2118	18	12	1469	1982	251	32
20	47	231	5109	4	6	9	295	9338	1749	51	2477	94	318	387	611	56	46
21	36	130	11474	3	5	8	263	6166	4285	36	1820	498	398	1807	1164	135	36
22	72	344	7943	3	2	7	87	2765	2361	2228	4125	13	11	644	886	190	53
23	52	127	13232	4	4	5	109	525	4188	198	2158	2782	28	431	885	206	30
24	38	184	14309	3	2	10	59	8017	1483	365	1982	6	5	670	809	142	48
25	44	120	11535	3	3	6	122	4710	2286	41	2061	562	473	637	1807	110	53
26	38	81	10399	4	3	7	53	3105	2360	410	1905	6	4	705	832	256	43
27	19	113	11015	5	2	7	76	9484	2500	53	1726	127	64	383	1200	78	28
28	59	121	8141	5	5	6	158	7870	1954	110	2149	91	34	574	869	80	41
29	87	50	9931	3	2	4	169	3733	3365	1384	1629	28	15	420	1778	211	56
30	23	147	16885	16	4	8	73	2535	3673	182	2104	140	95	408	2014	195	44

Table 2 (*continued*)

#	Al	B	Ca	Co	Cr	Cu	Fe	K	Mg	Mn	Na	Nickel max.	Nickel mean	P	S	Sr	Zn
31	94	348	13276	3	6	8	361	5454	4477	96	3193	99	67	895	1519	222	96
32	144	334	10023	4	3	14	236	5212	1280	24	4575	3	3	678	1216	78	34
33	18	144	11866	7	2	5	63	1531	1641	51	2084	1688	1510	340	824	91	40
34	28	337	14565	4	4	11	122	9026	2576	61	4529	1114	199	689	895	150	65
35	25	87	15776	6	3	7	75	1230	2992	243	1799	1317	155	871	867	41	37
36	93	214	16827	13	20	8	1030	1914	1312	63	2642	1265	2460	478	1429	174	65
37	43	161	27353	8	3	6	61	8985	787	100	1814	115	38	1042	2576	223	99
38	32	242	28054	3	2	12	37	4046	2703	49	4305	3	3	2472	1012	36	19
39	30	112	10914	23	3	6	47	2032	2506	92	1738	1021	1281	612	953	60	40
40	53	237	9683	4	4	4	259	2972	1778	52	2438	235	461	920	511	94	39
41	38	275	16331	4	3	5	47	7063	1945	8	6223	4	3	2089	1489	140	11
42	44	242	16255	4	4	5	163	3926	3112	31	4036	757	201	832	855	81	63
43	20	141	11298	3	2	6	47	13002	2065	42	1742	1217	662	421	1148	90	36
44	23	104	8650	4	4	7	194	12218	2742	25	943	695	598	1151	820	168	73
45	46	107	10972	4	4	5	181	5585	1936	32	1330	530	58	818	947	74	51
46	23	160	9638	4	3	6	62	7047	1178	43	2038	1876	673	650	1178	72	71
47	22	171	13900	4	2	6	51	3890	2723	72	2158	2377	234	586	838	105	29

Table 3. Elemental relationships in serpentine-tolerant species of New Caledonian Flacourtiaceae. Significances calculated from correlation coefficients. Negative values indicate inverse relationships

	Al	B	Ca	Co	Cr	Cu	Fe	K	Mg	Mn	Na	Ni	P	S	Sr
B	NS														
Ca	NS	NS													
Co	NS	$-S$	NS												
Cr	S^{**}	NS	NS	NS											
Cu	S	NS	NS	NS	NS										
Fe	S^{**}	NS	NS	NS	S^{**}	NS									
K	NS	S^{**}	$-S^{**}$	NS	NS	NS	NS								
Mg	NS	NS	NS	NS	NS	NS	NS	$-S^{*}$							
Mn	NS	S^{*}	S^{*}	NS	NS	NS	NS	NS	S^{**}						
Na	NS	S^{**}	NS	$-S^{*}$	NS	NS	NS	NS	NS	NS					
Ni	S	$-S$	NS	S^{**}	S^{*}	NS	S	NS	NS	$-S$	$-S^{**}$				
P	NS	S	NS	NS	NS	NS	NS	S^{*}	S^{*}	NS	NS	NS			
S	NS	$-S^{**}$	NS	S	S^{*}	S	S	NS	S	S	$-S^{*}$	NS	S^{*}		
Sr	NS	S^{*}	S^{**}	NS	NS	NS	NS	NS	NS	S^{**}	NS	NS	NS	NS	
Zn	S	S	NS	NS	S^{**}	NS	S^{*}	S^{*}	NS	S	NS	S^{**}	S^{**}	S	NS

S^{**} = very high significant ($P < 0.001$)
S^{*} = highly significant ($0.001 > P > 0.01$)
S = significant ($P > 0.01$)

factor. It has however been emphasized by Jaffre[4,5] that in respect of the mineral nutrition of plants growing in soils derived from ultramafic rocks in New Caledonia, many different soil types must be considered. These range from the extremes of magnesium-rich brown soils on the one hand to impoverished iron-rich soils on the other. The latter are deficient in all of the major elements including magnesium.

Since the infertility of serpentine soils has also been linked to the presence of phytoxic elements such as cobalt, chromium and nickel (see introduction), relationships involving these elements and nutrients are also of importance. The chromium content of the plants is not inversely related to the concentration of any nutrient, as might be expected from an element which is highly unavailable to plants. Cobalt is inversely related to boron and sodium, whereas nickel is inversely related to both of these nutrients as well as manganese.

In summary, it appears that the elements associated with uptake of the nutrients boron, potassium, manganese and sodium, are mainly cobalt and nickel both of which have often inordinately high concentrations in serpentine soils.

In the present study as well as in the previous work[3], it appears that there are no elemental relationships indicating restriction of calcium uptake by excessive uptake of other elements. However the work certainly supports the theory that reduced uptake or availability of nutrients is an important controlling factor in a serpentine flora.

As regards the theory that the presence of phytotoxic elements is a major controlling factor, our data do not show that this is important, at least in the Flacourtiaceae of New Caledonia. Not only are cobalt and chromium not accumulated to any significant degree, but many taxa can tolerate large concentrations (up to 0.5% dry mass by *Homalium guillainii*) of the supposedly phytotoxic nickel.

Our work has not answered the question as to whether reduced nutrient uptake may not arise merely from their low concentrations in the New Caledonian soils (Table 2), but clearly this factor cannot but be exacerbated by the antagonism to nutrient uptake demonstrated by several other elements present in high concentrations in these soils.

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References

1 Brooks R R 1983 Biological Methods of Prospecting for Minerals. Wiley, New York, 322 p.
2 Brooks R R, Lee J, Reeves R D and Jaffré T 1977 Detection of nickeliferous rocks by analysis of herbarium specimens of indicator plants. J. Geochem. Explor. 7, 49–57.

3 Brooks R R and Yang X H 1984 Elemental levels and relationships in the endemic serpentine flora of the Great Dyke, Zimbabwe and their significance as controlling factors for the flora. Taxon 33, 392–399.

4 Jaffré T 1976 Composition chimique et conditions de l'alimentation minérale des plantes sur roches ultrabasiques (Nouvelle Calédonie). Cah. ORSTOM Sér. Biol. 11, 53–63.

5 Jaffré T 1980 Etude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle Calédonie. Trav. Doc. ORSTOM No. 124, 273 p.

6 Jaffré T, Kersten W, Brooks R R and Reeves R D 1979 Nickel uptake by the Flacourtiaceae of New Caledonia. Proc. Roy. Soc. Lond. Sec. B 205, 385–394.

7 Proctor J and Woodell R J 1975 The ecology of serpentine soils. Adv. Ecol. Res. 9, 255–370.