Are plant adaptations to growing on serpentine soil rare or common?
A few case studies from New Caledonia

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ABSTRACT

The relative commonness of a shift in soil preference (from non serpentine to serpentine soils and vice versa) in the New Caledonian flora is examined. A number of phanerogam genera occurring on the island of which modern phylogenies are available are used in this study (*Acianthus*, *Cupaniopsis*, *Guioa*, *Morinda* and in particular *Oxera*). It is concluded that the ability to grown on serpentine soil is either a plesiomorphic or a very homoplasious character for most groups in this study and that therefore the hypothesis that serpentine soils preserve the indigenous flora against competition with immigrant species can not be supported for these groups.

MOTS CLÉS
Nouvelle-Calédonie,
sols serpentineux,
Oxera,
adaptations.

RÉSUMÉ

Adaptations des végétaux à la croissance sur sols serpentineux : phénomène rare ou commun ? Étude de quelques cas en Nouvelle-Calédonie.

La fréquence relative des changements de préférence pour un type de sol (serpentineux ou non serpentineux), dans la flore de Nouvelle-Calédonie, est examinée. Des phylogénies récemment établies pour plusieurs genres de Phanérogames présents dans l'île (*Acianthus*, *Cupaniopsis*, *Guioa*, *Morinda* et en particulier *Oxera*) sont utilisées dans cette étude. On en conclut que la capacité de croître sur un sol serpentineux est un caractère plésiomorphe ou très homoplasique pour la plupart des taxons étudiés. Ainsi, pour ces groupes, l'hypothèse que les sols serpentineux jouent, pour la flore indigène, un rôle de protection contre les espèces immigrantes ne peut pas être confirmée.

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INTRODUCTION

New Caledonia is recognised as a global "hot spots" for biodiversity (MEYERS et al. 2000), in part because of its high diversity among the phanerogams (MORAT 1993b; JAFFRÉ 1992; THORNE 1965). The island has 165 families of angiosperms and gymnosperms, with a total of approximately 3021 native species, of which 76.9% are endemic (MORAT et al. 2001; LOWRY 1998). A number of different and sometimes conflicting hypotheses have been proposed to explain this high level of diversity. These include:

A) New Caledonia's Gondwanan origin and ancient isolation have preserved a number of taxa that went extinct elsewhere (THORNE 1965; HOLLOWAY 1979; LOWRY 1991; JAFFRÉ 1992; MORAT 1993a, 1993b).

B) The presence of a great variety of soil types and especially the fragmentation and isolation of sites with serpentine soil has contributed to a great variety of niches (THORNE 1965; CARLQUIST 1974; HOLLOWAY 1979; JAFFRÉ 1992; MORAT 1993a, 1993b).

C) Serpentine soils have preserved the "primitive" elements of the indigenous flora, which are adapted to living on these soils, protecting them against competition from more aggressive "advanced" immigrant species (usually from different families) which cannot live on serpentine soils (MORAT et al. 1986; LOWRY 1991; JAFFRÉ 1992; MORAT 1993b).

D) The variation in topographic relief and its corresponding diversity of climatic conditions have contributed to a great number of available niches (THORNE 1965; CARLQUIST 1965, 1974; MORAT 1993b).

E) The ability of some plants to disperse over long distances from areas such as New Zealand, New Guinea and East Australia to New Caledonia have enriched the local flora (THORNE 1965; MORAT et al. 1986).

F) New Caledonia' s climatic stability has protected the representatives of some lineages that have gone extinct elsewhere during radical climate changes (RAVEN & AXELROD 1972; HOLLOWAY 1979).

The geological history of New Caledonia during the last 30-40 million years has been dominated by the covering of the island, associated with the eastward movement of the continental plate, with a sheet of ultramafic rock (HOLLOWAY 1979; AITCHISON et al. 1995). Originally this 2000 m thick sheet covered almost the whole island, but has been eroded away and now occupies only about a third of the surface (MORAT et al. 1984; see also LOWRY 1998). These events must have had an enormous impact on the biota of the island through processes such as extinction, adaptation and fragmentation of populations.

The aim of this paper is to evaluate the impacts on the flora of some of the effects of these geological events. I would like to investigate the relative importance of one of the hypothesized causes of the high phanerogam biodiversity on New Caledonia (hypothesis C). How common have shifts in soil preference been (to and from serpentine) within various endemic plant clades? If a shift in soil preference from non serpentine to serpentine soils is a common event in the evolutionary history of a group, then it would suggest that serpentine soils may not have a special ability to protect species that can grow on them from direct competition involving species that are not tolerant of these substrates, in which case hypothesis (C) must therefore be rejected.

A number of authors (CARLQUIST 1965, 1974; JAFFRÉ et al. 1987; LOWRY 1998) have expressed doubt about the presumed ability of serpentine soils to preserve the "primitive" indigenous flora selectively against competition from more aggressive "advanced" immigrant species. They accept that serpentine soil may in theory hinder the colonisation of a given area. However, they believe that colonisation will eventually take place if sufficient time is available for plants to adapt to the new conditions. The protection of the original flora from competition with these new species would therefore be only temporary.

MATERIALS AND METHODS

In order to estimate the number of shifts in soil preference in a group, we need to document the soil preference of each species and to record the fidelity of these species to a particular soil type. A cladistic analysis of a group provides a basis for estimating the number of shifts in soil type preference in the evolutionary history of a group. Data about soil preferences were taken from recent revisions (see below). Taxa that can grown both on and off serpentine soil (taxa marked with a "d" in Figs. 1-5) have been treated in this study as uncertain and are thus considered to provide no information about the most likely character state at that node and below it. Those taxa about which no data were available have been marked with a question mark (?). Cladograms have been widely used to examine ecological traits (see BROOKS & MCLENNAN 1991; HARVEY & PAGEL 1991), which are inherited by plants in the same way as morphological characters and can therefore be used in the same way in a phylogeny. In this study I am only interested in the outcome of the adaptation process. I do not assume that one particular set of physiological and/or morphological adaptations which evolved in one group of plants to cope with the environmental pressures presented by serpentine substrates is homologous with those of other groups of plants examined. This would be unlikely given what we know about such adaptations. There are several known mechanisms that explain how plants can tolerate serpentine soils, some external such as preventing the uptake of a toxic level of metals, others internal e.g., the removal or naturalisation of the toxic elements (ANTONOVICS et al. 1971; VERKLEIJ et al. 1991). What I wish to compare here are the results of these adaptations, namely the "ability to grow on serpentine soil", not the specific method of adaptation. For this it does not matter whether these characters are homologous between the different groups of plants examined. What is important is that they all exhibit one type of adaptation or another to these soils.

Similarly I am not concerned with whether adaptive radiation occurred following or in association with a shift in soil preferences. The data presented here do not allow any inferences to be made about differences in the rate of evolution between plants growing on different soil types. It can only deal with the question of whether these shifts are common or rare in the evolution of a group and whether any patterns can be detected when comparing several groups of plants.

The genera used in this research have all been recently revised and analysed using cladistic methods. They also all have species that grow on different soil types in New Caledonia.

The genus *Oxera* is ideal for this research, as it has recently and been revised and cladisticaly analysed (58 morphological characters, CI = 0.43 and RI = 0.78) (DE KOK 1997; DE KOK & MABBERLEY 1999) and is a monophyletic group with many species growing on different substrate types (DE KOK 1997). Of the 23 New Caledonian taxa of *Oxera*, ten are restricted to serpentine soils, four occur only on soils derived from schists and one is restricted to calcareous soils (Table 1). This kind of substrate specificity is not necessarily a result of ecological constraints but could also be a result of historical factors. For instance, *O. microcalyx* is restricted to the Plateau de Dogny, which does not have serpentine soils. It could have evolved locally and therefore may never been exposed to serpentines. I did not have the opportunity to test this hypothesis using transplantation experiments.

The second genus used is *Morinda* L. (Rubiaceae). JOHANSSON (1994) revised the New Caledonian members, and produced a cladogram (18 morphological characters, CI = 0.58) that included the 11 New Caledonian species as well as some representatives from other Pacific islands. He believed that the cladogram provided only marginal support for the hypothesis that the occurrence of species on serpentine soil is a plesiomorphic character for the genus (JOHANSSON 1994).

The genus *Cupaniopsis* Radlk. (Sapindaceae) was revised and cladisticaly analysed (39 morphological characters, CI = 0.58) by ADEMA (1991). It has 27 species on New Caledonia which do not form a monophyletic group. Most New Caledonian species belong to one monophyletic assemblage, which he called the "upper group", containing 15 species, of which the New Caledonia taxa form the paraphyletic base. Five other New Caledonian species belong to a clade that he called the "middle group".

VAN WELZEN (1990) revised and cladisticaly analysed (67 morphological characters, CI =

TABLE 1. — Specificity for different soils of all New Caledonia ***Oxera*** taxa. M = mainly growing on this soil type, P = present on this soil type, X = only growing on this soil type.

***Oxera* species**	**Serpentine**	**Soils derived from schists**	**Calcareous**	**Other**
O. baladica Vieill. subsp. *baladica*	M	P	P	
O. baladica subsp. *nuda* (Virot) de Kok	X			
O. balansae Dubard			X	
O. brevicalyx (Mold.) de Kok	X			
O. coriacea Dubard	X			
O. coronata de Kok		X		
O. crassifolia Virot	X			
O. glandulosa Vieill.	X			
O. gmelinoides S. Moore	X			
O. inodora de Kok	P	?	?	?
O. macrocalyx Dubard subsp. *macrocalyx*	P	P	P	P
O. macrocalyx subsp. *sororia* (Däniker) de Kok	X			
O. microcalyx Guillaumin		X		
O. morierei Vieill.	P	M		
O. oreophila Guillaumin	X			
O. palmatinervia Dubard	X			
O. pulchella Labill. subsp. *pulchella*		X		
O. pulchella subsp. *grandiflora* (Dubard) de Kok		P	P	
O. robusta Vieill.	P	P	P	
O. rugosa Guillaumin	X			
O. sessilifolia Dubard		X		
O. subverticillata Vieill.	P	M		
O. sulfurea Dubard	P		M	M

0.50) the genus *Guioa* Cav. (Sapindaceae). It has nine species in one clade on New Caledonia.

The terrestrial orchid genus *Acianthus* R. Br. has been revised and cladisticly analysed (30 morphological characters, CI = 0.82) by KORES (1995). The 14 species which grow on New Caledonia belong to two separate monophyletic groups, containing six and eight species respectively.

RESULTS

In Fig. 1, the cladogram of *Oxera* (with the exception of *O. vanuatuensis* de Kok, a non-New Caledonian species) is presented. The sister group, *Faradaya* F. Muell., only grows on non-serpentine soil. The most parsimonious mapping of the substrate preference character would be to regard the ability to grow on serpentine soil as the plesiomorphic state. There would then have to be four reversals, one in the *O. pulchella* clade (*O. balansae, O. pulchella* subsp. *pulchella* and *O. pulchella* subsp. *grandiflora*) and one each for *O. coronata*, *O. microcalyx* and *O. sessilifolia*.

The cladogram of *Morinda* presented in Figs. 2A & B shows that the New Caledonian species do not form a monophyletic group. Of the 16 species represented, nine can grow on serpentine soil (six exclusively) and seven grow on other substrates. Two equally parsimonious solutions are possible in this group. One is to regard the ability to grow on serpentine soils as plesiomorphic, with four secondary losses of the character (Fig. 2A). The other is to consider the ability to grow on serpentine soil as a synapomorphy in *M. kanalensis* and *M. myrtifolia* and in the *M. glaucescens* group, with secondary loss in *M. phyllireoides* and *M. bucidifolia* (Fig. 2B).

The relevant parts of the cladogram of *Cupaniopsis* are depicted in Fig. 3. The “Upper

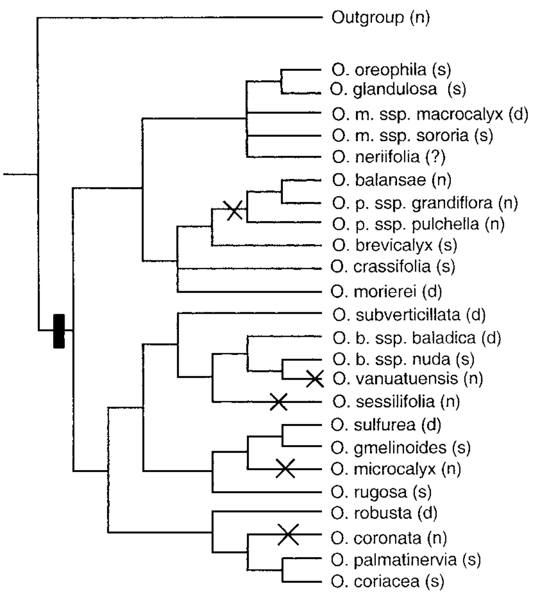

Fig. 1. — Simplified cladogram of ***Oxera*** (modified from DE KOK 1997), showing soil preferences. d = diverse soil preference, serpentine and non serpentine; s = strict soil preference: serpentine; n = strict soil preference: non serpentine; ? = soil preference unknown. **I** = Shift to ability to grow on serpentine; X = shift from ability to grow on serpentine (reversal).

group" contains 17 species, of which 14 grow on New Caledonia. Of these, five are only found on serpentine soils, two only on calcareous soils and six on varying kinds of soils (including serpentine). Of the two remaining species, no information on soil preference is available. This pattern of soil preference is most parsimoniously explained by considering the ability to grow on serpentine soils as plesiomorphic, with a secondary loss in the *C. pennelii* Guillaumin clade and the Pacific clade. In the New Caledonian clade of the "middle group", the ability to grow on serpentine soil is most likely apomorphic.

The New Caledonian clade of *Guioa* is depicted in Fig. 4. It consists of nine species of which seven grow on different kinds of soil (including serpentine), and two on non-serpentine soils. In this case, the most parsimonious explanation for the character distribution is that the ability to grow on serpentine soils is plesiomorphic, with one reversal in *G. crenulata* and one in *G. fusca.*

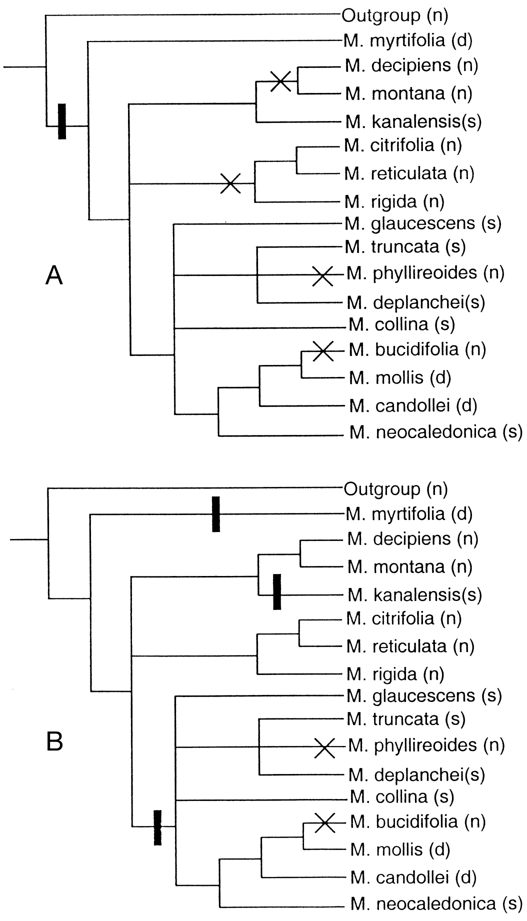

Fig. 2. — Cladogram of ***Morinda*** (modified from JOHANSSON 1994), showing soil preferences as in Fig. 1. **A**, version with ability to grow on serpentine soil as plesiomorphic; **B**, version with ability to grow on serpentine soils apomorphic.

In *Acianthus* sect. *Macropetalus* (Fig. 5A) four species can grow on serpentine soil, of which one is restricted to it. *Acianthus* sect. *Univiscidiatus* (Fig. 5B) includes six species that can grow on serpentines, of which four exclusively grow on these soils. One species does not occur on serpentine soil and the soil preference is unknown in the last species. In both groups the most parsimonious explanation for the observed character distribution is that the ability to grow on serpentine soils is plesiomorphic.

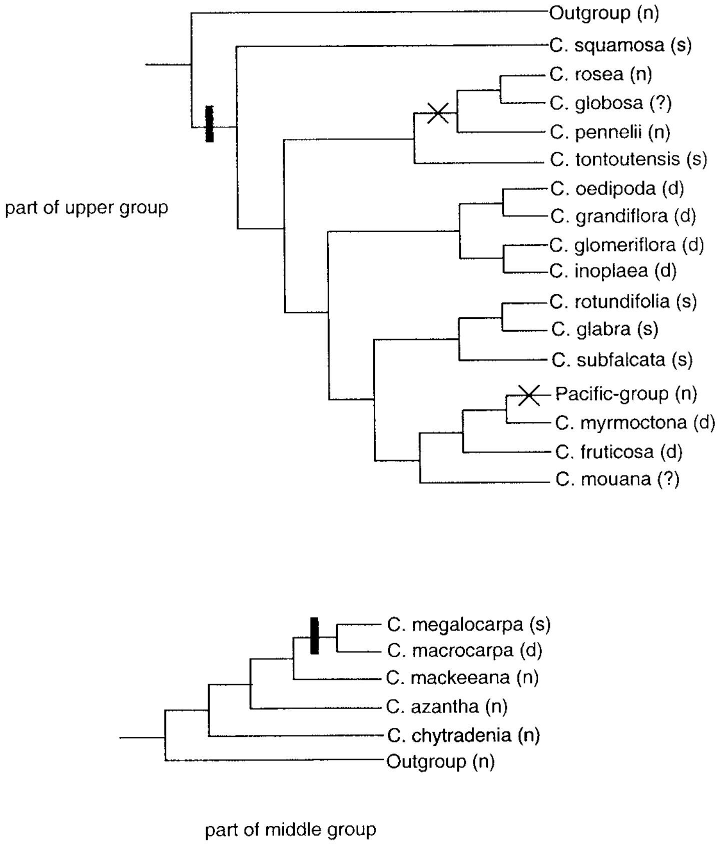

Fig. 3. — ***Cupaniopsis*** (modified from ADEMA 1991), showing soil preferences as in Fig. 1.

DISCUSSION

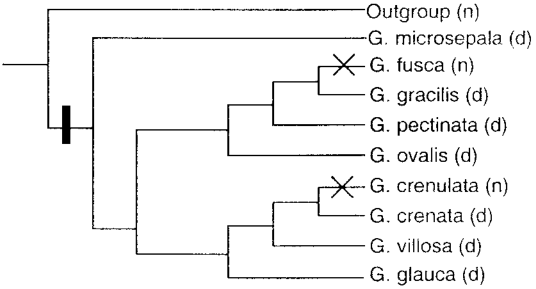

Fig. 4. — ***Guioa*** (WELZEN 1990), showing soil preferences as in Fig. 1.

In the minds of some botanists serpentine soils seem to possess almost magical properties. Not only are they said to preserve in isolation so called "primitive" taxa, they can at the same time act as an evolutionary laboratory. This paradox seems to be based on two different views of the ability of plants to adapt to serpentine. The first is held by those who are more concerned with vegetation patterns or with the results of the adaptation process (biogeographers). Their general view is that plants do not "easily" adapt to living on serpentine soils, and that adaptation events will thus be rare in the history of a particular group. The second view is largely expressed by people who work at the population level, who hold that plants can "easily" adapt to serpentine soils, and can do so in a very short time span. In fact, the discovery of populations of common European plants growing on the slag heaps from metal mines, and which have developed a tolerance to

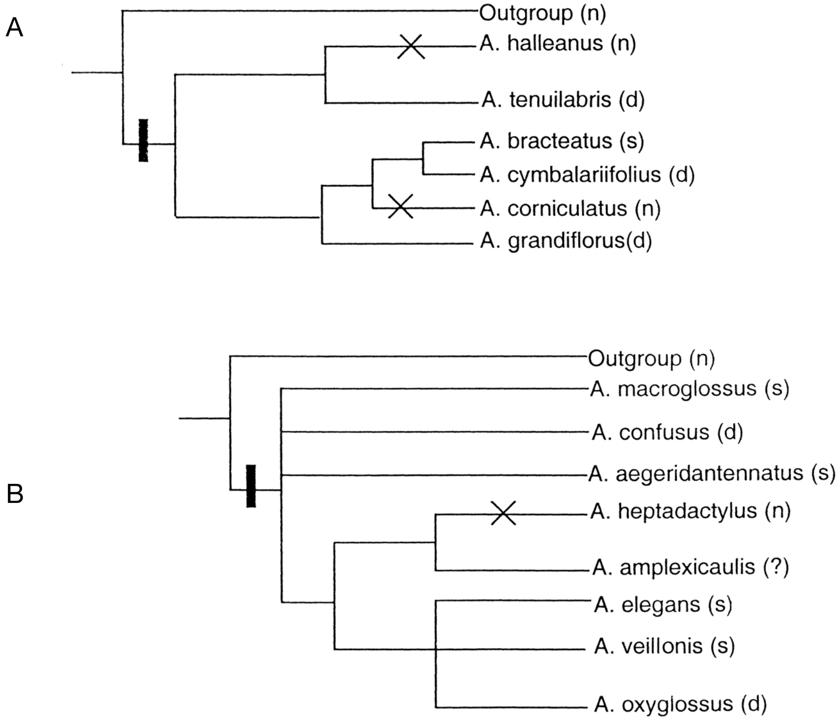

Fig. 5. — Modified from VAN KORES 1995, showing soil preferences as in Fig. 1. **A**, ***Acianthus*** sect. ***Macropetalus***; **B**, ***Acianthus*** sect. ***Univiscidiatus.***

heavy metals in the serpentine-like soil, is one of the best documented cases of evolution in action (ANTONOVICS et al. 1971).

When workers try to explain the high level of phanerogam diversity of areas such as New Caledonia, they often invoke arguments that are taken from both of these views. The resulting explanations are therefore often in conflict with one another.

In the genera examined here, the ability to grow on serpentine soil is most parsimoniously regarded as a plesiomorphic character in six groups (*Oxera*, *Guioa* and in the two clades each in *Cupaniopsis* and *Acianthus*). In *Morinda* both hypotheses appear to be equally parsimonious. The clade comprising the "middle group" of *Cupaniopsis* is the only case where treating the ability to grow on serpentines as the apomorphic state is more parsimonious. It is surprising to find that this character seems to be plesiomorphic in clades of such diverse families as Labiatae, Rubiaceae, Sapindaceae and Orchidaceae. Other independent studies of some taxa (Liliaceae s.l., Linaceae and Cruciferae) from serpentine areas of Europe and North America also show that the ability to grow on these substrates is either plesiomorphic and/or very homoplasious (FIEDLER 1992; MAYER & SOLTIS 1994; PROCTOR 1999). It seems that this adaptive shift is either common in plants and/or that a great number of groups representing many families are pre-adapted to growing on serpentines. This is in line with the ideas of JAFFRÉ et al. (1987), who proposed that the flora on serpentines in New Caledonia is derived in part from early pre-adapted pioneer species. These species were adapted to grow on soils derived from substrates such as schists, which have some chemical characteristics in common with highly weathered serpentine soils, or in some cases the pioneers evolved from species which were already adapted to serpentine soils.

Another possible explanation for the plesiomorphic nature of the ability to grow on serpentine soils involves the geological history of New Caledonia. Almost the entire island was covered with a sheet of ultramafic rock about 30 million years ago (see LOWRY 1998). If there were plant-life on the island, then most species would have grown on serpentine soils. When, as a result of erosion, more non-serpentine substrate became available, which must then have been colonised partly from the serpentine areas. The idea presented by MORAT et al. (1984) that parts of the pre-Eocene flora possibly survived in the few areas of non-serpentine substrate available to them is interesting. If any pre-Eocene elements survived off the serpentine substrate, then the ability to grow on serpentines must be either absent or apomorphic in those groups. Some genera used in this study (*Cupaniopsis* and *Guioa*) are likely to be of Gondwanan origin and could well have been present on the island when it broke away from Gondwana (ADEMA 1991; VAN WELZEN 1990) and thus when it was subsequently covered over by ultramafic rock. For two out of three of the New Caledonian clades studied, however, the ability to grow on serpentine soil is plesiomorphic, which makes it more likely that, if they were present on the island at that time, they survived on the serpentine part of the island.

If plants can “easily” adapt to serpentines, then one could argue that the species level may not be the most appropriate one at which to examen this adaptation. Analysis of a highly homoplasious character at too high a taxonomic level causes it to appear to be plesiomorphic. In the genus *Oxera,* there is some indication that this is the case. Of the 23 taxa in New Caledonian, only 15 grow on a single soil type, whereas the eight others occur on various types, some primarily on one specific soil type, but others on various substrates in some parts of their range. Two examples are *O. baladica*, subsp. *baladica* which usually grows only on serpentine soils, but is also found on other substrates on the geologically very complex Mt. Koghi; and *O. sulfurea*, which normally does not grow on serpentine soils, but is sometimes found on them on the Plaine des Lacs. However, if the species level is not appropriate to study the evolutionary history of this character, then adaptation to serpentine soils must be very homoplasious.

CONCLUSIONS

How common or rare is a shift in soil preference (from non-serpentine to serpentine or vice versa) within a group of endemic New Caledonian plant clades? Although shifts from non-serpentines to serpentine soils appear to be relatively common in the studied clades, the reverse is less so. This mainly reflects the fact that the character (the ability to grow on serpentine soil) is plesiomorphic for most groups (five out of six of the clades examined), suggesting that some form of pre-adaptation within these diverse plant groups seems likely. This begs the question whether there are any plant groups that are not pre-adapted and are therefore absent from serpentine areas. If so, there should be a difference in floristic composition between serpentine and non-serpentine areas on New Caledonia. However, MORAT et al. (1984, 1986) have shown that the floristic affinities of both areas with neighbouring landmasses are very similar.

The hypothesis that an adaptive shift to growing on serpentine soil is a common event best fits the present data. For one, it is in line with what is known about this kind of adaptation from populations found on mine sites in the Northern Hemisphere (ANTONOVICS et al. 1971). It would also explain why serpentine and non-serpentine areas on New Caledonia have very similar floristic composition and relationships with possible source areas (MORAT et al. 1984, 1986). It would also be consistent with the anecdotal evidence within *Oxera,* where many species have their main distribution on non-serpentines, but some populations are also known to grow on serpentine substrates (see Table 1). In order to distinguish between these two hypotheses (pre-adaptation or frequent adaptive shifts) more research on New Caledonia is needed.

Whatever the explanation behind the patterns observed on the cladograms presented here (pre-adaptation or homoplasy), this research does not support the idea that serpentine soils can provide protection to (primitive) taxa growing on serpentine soils from direct competition of invading (advanced) ones. If a great number of plant groups are pre-adapted or can readably adapt to growing on serpentine soils, then over time serpentine soils can and will be colonised successively by new groups which would bring them in direct competition with those established earlier.

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