Environmental controls on species composition along a (maquis) shrubland to forest gradient on ultramafics at Mont Do, New Caledonia

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The landscape-scale pattern of distribution of maquis, maquis with emergent conifers (*Araucaria laubenfelsii*), and rain forest, on ultramafic substrate at Mont Do, New Caledonia, is investigated in relation to soil and plant chemistry, light and moisture. The structure and composition of these vegetation types reflects the impacts of disturbance on the one hand, and of physiological stresses on the other. Disturbance by fire is important in determining the presence and abundance of maquis and rain forest at the landscape level and is discussed in detail by Perry *et al.* elsewhere in this issue.[1] The impacts of light environments, water availability and soil chemistry on the succession of vegetation from maquis to forest are also important. The chemistry of iron-crust and eroded oxisol soils does not vary greatly between vegetation types, and does not appear to define the distribution of species at the local scale. Nevertheless, low concentrations of macronutrients (such as P) and slow rates of biomass accumulation associated with this ultramafic landscape may be important in slowing the rate of progression of the vegetation from maquis to forest. Chlorophyll fluorescence studies of seedlings, saplings and trees in maquis and forest provide strong evidence for severe reductions in photosynthetic efficiency in photosystem II on clear days for seedlings growing in maquis. The importance of increased water supply to plants establishing beneath emergent araucarians in maquis through cloud-combing is also illustrated.

Introduction

Vegetation on ultramafic (serpentine) soils is often highly distinctive in terms of species composition and community structure relative to that on adjacent, non-ultramafic soils.[2,3] In areas where forests grow on non-serpentine substrates, adjacent serpentine areas may have stunted vegetation characterized by high levels of sclerophylly,[4] supporting the notion that serpentine vegetation is structurally and morphologically distinct from non-serpentine plant communities.[5] This distinction seems less apparent in the wet tropics where high diversity rain forest is recorded for both substrate types. Indeed, the stunting of forests on ultramafic soils in Sabah (Malaysia) reported by Proctor *et al.*[6] was attributed more to the effects of altitude, cloud cover and high winds than to soil toxicity or low nutrient status.

In New Caledonia, ultramafic substrates cover approximately 5500 km^2 of the main island, with fire-prone shrublands (*'maquis miniers'*) occupying 75–85% of this area and closed rain forest most of the remainder.[7,8] The rate of endemism is about 75–80% in the native flora across all substrate types, but is highest in maquis on ultramafics (92.7%), and in rain forest regardless of substrate type (82–83%).[9,10] Much work has been reported on heavy metal uptake by plants on ultramafic soils in New Caledonia[7,11] and some on the vegetation associations which exist on these substrates,[7,8] including several recent studies of the population dynamics of long-lived tree species.[12–14] However, community to landscape-level analyses are rare and little has been published concerning variations in vegetation structure and floristics within the ultramafic zone in New Caledonia.[15] Here we examine factors influencing the distribution, and species composition, of maquis and rain forest vegetation on Mont Do, a serpentinitic outcrop to 1000 m in the Southern Province of New Caledonia.

Maquis may develop under a variety of climatic and edaphic conditions, from the dry lowlands of the west coast, where annual average rainfall is <900 mm, to the wet mountains of the Southern Massif with >4000 mm rainfall per year.[7] Maquis comprises almost entirely light-demanding species and forms relatively continuous communities dominated either by shrubs or sedges.[8] Dominant families in the maquis of New Caledonia include: Casuarinaceae, Cunoniaceae, Cyperaceae, Dilleniaceae, Epacridaceae, Myrtaceae, and Proteaceae.[16,17] These communities are fire-adapted with at least one quarter of the species able to resprout from rootstocks.[15] Where fire is very frequent, a fern cover of *Gleichenia dicarpa* R.Br., *Dicranopteris* sp. and *Pteridium esculentum* (G. Forst) Cockayne may dominate. In general, grasses are absent, but several genera of sedges from the family Cyperaceae are represented, including *Baumea, Costularia, Lepidosperma* and *Schoenus.*[16]

Two types of ultramafic maquis are recognized: primary and secondary.[9] Primary maquis is a presumed stable vegetation type which occurs in response to the low nutrient status of hypermagnesian soils in areas receiving <1300 mm rainfall annually, and limitations imposed by wind and cloud at some high altitude locations. Secondary maquis arises as a result of increased fire frequency associated with human activities over the past few hundreds (European phase) to thousands (Melanesian phase) of years. Such maquis may eventually revert to forest if fire is excluded. In low-altitude maquis, McCoy *et al.*[15] reported that successional change is slow; a closed maquis forms over a period of 40–75 years without fire, but it may take >250 years before a dense rain forest develops. They suggest that an emergent canopy of angiosperms dominated by *Gymnostoma* spp. in the early stages of succession facilitates the establishment of later successional rain forest species within the maquis by providing shade and litter, and reducing light and moisture stress on light-intolerant species. Other species, such as *Araucaria laubenfelsii* Corbasson and *Agathis ovata* (Moore) Warburg, may play a similar role in some mid- and high-altitude maquis.

Rain forest on ultramafic substrates in New Caledonia is

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typically made up of a diverse mixture of angiosperms, but is sometimes dominated by one or more species of *Nothofagus* or *Araucaria*.[12,18] In these forests conifer species (e.g. *Araucaria* and *Agathis*) may form part of the canopy or are present as emergents. *Nothofagus* forests are found predominantly on ultramafic soils between 150 m and 1300 m a.s.l.,[12] and while many rain forest areas are devoid of *Nothofagus* spp., where they do occur they may form an almost mono-dominant canopy. These patches of dense *Nothofagus* are often surrounded by high diversity rain forest.[12]

As noted above, many ultramafic areas in New Caledonia are associated with a low, open maquis adjacent to high diversity, closed rain forest. Additionally, a number of species of *Araucaria* and *Agathis* occur as emergents in maquis, but no rain forest angiosperm tree species show similar behaviour. The relationship between these assemblages (maquis, maquis with emergent conifers, and rain forest with emergent conifers) is unclear, both in terms of the extent of their floristic similarity, and in the extent to which floristic and structural compositional differences are a consequence of landscape-scale disturbance processes such as fire, versus more site-specific differences in soil properties and other environmental factors which limit plant growth, especially of forest species. In frequently (or recently) disturbed maquis, plants are primarily dependent on skeletal mineral soils for nutrient and water uptake, and are subjected to high light intensities. In forest, most nutrients are cycled through the organic pathway (through litter decomposition), light levels are low and moisture availability may not be limiting.[19] Here, we address three questions concerning the nature of landscape level dynamics on ultramafic substrates at Mont Do:

1. How does plant species composition vary between maquis, maquis with emergent conifers, and rain forest?
2. How do non-disturbance-mediated environmental factors, including soil chemistry, light, and moisture, influence species composition and community structure? (Note: the role of disturbance is addressed explicitly by Perry *et al.*, elsewhere in this issue.[1])
3. What role does the emergent conifer *Araucaria laubenfelsii* play in the landscape?

In relation to soil chemistry, we speculate that nutrient uptake from mineral soils in maquis may lead to high levels of inadvertent uptake of metals, and the need for a high metal tolerance, while the cycling of nutrients through the organic layer in rain forests might create a pool of nutrients for recycling allowing the survival and growth of a broader range of species (although Chiarucci & De Dominicis[20] report enrichment of heavy metals in soils with high organic matter content). The changes in species composition between maquis and forest may be as much a consequence of changing metal tolerances as they are a reflection of the changed microclimatic or disturbance environment favouring recruitment of forest versus maquis species.

Study site

The New Caledonian archipelago is situated in the South Pacific between 20° and 23°S and 164° and 167°E, approximately 1500 km east of Australia and 1800 km north of New Zealand. The climate is subtropical to tropical, with a rainy season from November to April. The east coast of the main island (exposed to the trade winds for most of the year) receives >3000 mm yr^{-1}, while the west coast may receive <1000 mm yr^{-1}. Mean monthly temperature in the capital, Nouméa, is highest in February, 26.2°C, and lowest in August, 10.9°C.[7]

About one third of the main island is covered by ultramafic substrates,[16] the main area of which is in the south of the island. Ferralitic ultramafic soils (oxisols) dominate this area and are often characterized by a superficial iron crust known as *'sols cuirassés'* or cuirasse.[16] The formation of these soils began in the Miocene and periods of formation continued until the start of the Quaternary.[21] Ferralitic soils are found on the ultramafic massifs and are composed mostly of oxides and hydroxides of iron, with a large portion of the magnesium and silica leached from the profile.[7] These soils typically have a low pH, a very low cation exchange capacity, low nutrient levels, and high concentrations of nickel and chromium.[7,22]

This study took place on Mont Do (21°45 S, 166 °E), a botanical reserve (*Réserve spéciale de faune et de flore*) established in July 1981 to preserve and protect the mountain flora and fauna associated with the ultramafic substrate. Mont Do is part of the central mountain chain on the main island and is 1025 m a.s.l. at its highest point. The reserve occupies the top several hundred metres of the mountain, corresponding with the area of outcropping ultramafic bedrock. The mountain top receives an average of 1690 mm rainfall yr^{-1} (IRD, Nouméa) and is frequently covered by clouds.

The vegetation on Mont Do is a mosaic of rain forest and maquis. The maquis comprises a diverse mixture of angiosperm shrub species, including *Scaevola balansae* Guill., *Dracophyllum* spp., *Symplocos montana* (Vieill.) Brong. & Gris, *Rapanea diminuta* Mez., *Babingtonia leratii* (Schltr.) A.R. Bean (formerly *Baeckea leratii*) and *Codia discolor* (Brongn. & Gris) Guill., with some areas dominated by the ferns *Gleichenia dicarpa* and *Dicranopteris* sp., or by sedges, including species of the genera *Costularia, Lepidosperma* and *Schoenus.* Rain forests occur mostly as small stands or fragments in valleys, but there is one area of continuous forest which covers the southwestern side of the mountain. In some of the forest fragments, and in the continuous forest, *Nothofagus codonandra* (Baillon) Steenis, is the main canopy species, while *Araucaria laubenfelsii* frequently forms an emergent layer above the main canopy and also occurs as a scattered emergent in the maquis.

Methods

Field and laboratory methods

Species composition data were collected from 69 randomly located 100-m^2 plots within an area of approximately 1 km^2 directly east of the peak of Mont Do. The sampled vegetation included 60 plots in maquis with and without emergent *Araucaria laubenfelsii,* and nine plots in rain forest spread among three forest patches of assumed different successional stage/age since last major disturbance. Numbers of plots within each vegetation type were approximately proportional to their representation in the landscape. The Braun-Blanquet cover-abundance scale was used to describe species abundances in maquis and forest, while in the latter, total density was also measured for all individuals >30 cm height. Tree ring counts for stem cores taken from *Araucaria laubenfelsii* within each stand indicated approximate ages of 150 years for forest area 1 (F1), 300 years for F2 and 350–400 years for F3.[13]

Surface soil samples were collected from a sub-sample of 15 plots. Soil was collected from five random points within each plot and bulked into a single sample for chemical analysis. No samples were analysed for plots (n = 10) in areas completely covered in cuirasse since no surface soil was present. Samples were analysed for total concentrations of a broad range of metals (Al, Fe, Mn, Ni, Cr and Co), exchangeable cations (Ca^{2+}, Mg^{2+}, K^+, Na^+), cation exchange capacity (CEC), total P, pH, and %C. All analyses were performed by the Laboratoire commun d'analyse du Centre IRD (formerly ORSTOM) de Nouméa in accordance with their standard methods.[23]

Five plant species which occurred across the whole maquis to forest gradient were chosen for analysis of nutrient concentration in fresh leaf tissue. The sites sampled represented a postulated successional gradient with maquis representing the most recently disturbed site, and the continuous forest plots (F2 and F3) the most mature sites. Between these two 'endpoints' the other area sampled represented immature forest (F1). Individuals which occurred in both maquis and forest communities were chosen to see if differences in element concentration changed for each species along the shrubland to forest gradient. The species sampled were *Araucaria laubenfelsii* (Araucariaceae), *Codia discolor* (Cunoniaceae), *Polyscias pancheri* (Baillon) Harms (Araliaceae), *Styphelia cymbulae* (Labill.) Sprengel (Epacridaceae), and *Rapanea diminuta* (Myrsinaceae). From each of five replicate plants, approximately 20 g fresh weight of leaves was removed and stored on dry ice and then stored at –28°C until analysed at IRD, Nouméa.

Black and white hemispherical photographs of the forest canopy in each forest plot were taken in June 1997 with a fish-eye lens (Nikkor 8 mm f1.8) in order to estimate the photosynthetically-active photon flux density (PPFD, mol m^{-2} day^{-1}) in forest understories at 1 m above the forest floor. Light levels in each forest plot were estimated using the computer program HEMIPHOT.[24] Hemispherical photography has been found to produce comparable results to those obtained using light sensors and has been the preferred method for light estimation in many ecological studies (e.g. refs 25–27). Photographs were taken on overcast days as bright sun days can produce scattering of light through small holes in the canopy, making image analysis difficult.[24] Open-sky estimates of PPFD were used to characterize the light environment in the maquis at the same height above ground.

Chlorophyll fluorescence was measured for a sample of seedlings, saplings and trees of *Araucaria laubenfelsii* in maquis and forest, as the ratio of variable to maximum fluorescence (the Fv/Fm ratio). Fluorescence was measured for the adaxial leaf surfaces of fully expanded green leaves at approximately 2-h intervals through the day from pre-dawn to dusk for two leaves on each of six seedlings, saplings and trees in maquis and for the same number of seedlings and saplings in forest (site F2). The Fv/Fm ratio is a measure of photosynthetic efficiency of photosystem II. A full explanation of the characteristics of chlorophyll fluorescence and its application in physiological studies is given by Genty *et al.*[28] and Demmig-Adams and Adams.[29] This measure is regarded as an integrated index of overall stress on plant photosystem II, and provides indications of the extent of stress (reductions in photosynthetic efficiency) due to factors such as high light and low moisture availability, or unfavourable soil chemistry.[30]

The additional moisture supplied to the base of *Araucaria laubenfelsii* trees in maquis through interception of cloud water was assessed on three occasions using bulk precipitation collectors. Two plastic cups (6.2 cm diameter) were placed beneath the canopy of each of 25 randomly selected trees in maquis, and a further 25 cups were placed in the open, at least 5 m from the nearest tree. On the first two measurement occasions, collectors recorded rainfall as well as cloud combing, while on the third occasion the collectors were emptied after 2 days of periodic cloud combing but no rainfall. In the first trial some precipitation collectors overflowed. The second and third trials were considered reliable as the collectors did not overflow, and splash out of the collectors was not considered likely.

Analytical methods

Vegetation plot data (cover-abundance scores) were analysed by non-metric multidimensional scaling ordination (NMDS) with *post hoc* environmental vector fitting using the DECODA software package.[31] This method seeks the optimum spatial arrangement of samples in a specified number of dimensions based on rank order of Bray-Curtis dissimilarities. The significance of relationship between measured environmental (soil exchangeable and total metal concentrations, and estimated light environments), and independently estimated vegetation variables (species richness, Shannon-Weiner diversity), and the spatial arrangement of samples was then investigated by vector-fitting with significance determined by a Monte Carlo permutation test.[31]

One-way analysis of variance (ANOVA) was used to test for significance of difference in element concentrations in fresh leaves between species and between locations (maquis and forests 1–3), and in general vegetation and environmental parameters (e.g. diversity, canopy openness) between vegetation types and locations. Transformations were used as necessary to meet the normality requirements of the ANOVA method.

Results

Ordination

The NMDS ordination of 69 samples used all species occurring in more than one plot and gave stress values over the first four dimensions of 0.26, 0.15, 0.11 and 0.09, respectively. The 10 replicate two-dimensional solutions were all identical and this dimensionality was chosen to describe the vegetation data. Vegetation samples were spread across three half-changes on the first dimension, representing substantial (but not complete) species turnover along this axis, and 1.5 half-changes on the second. The first dimension reflected a clear gradient in plant species composition from plots characteristic of maquis on eroded oxisols with low scores, through plots characteristic of ridge-top (iron-crust oxisol) plots with emergent *Araucaria laubenfelsii,* to forest plots with high scores (Fig. 1). Species characteristic of maquis included *Gleichenia dicarpa, Costularia arundinacea* (Sol. ex Vahl) Kük, *Dracophyllum ramosum* Pancher, *D. verticillatum* Labill., *Babingtonia leratii* and *Scaevola beckii* Zahlbr. *Araucaria laubenfelsii* was present in all maquis plots as seedlings and/or saplings, but only in some as mature trees. However, mature individuals were present in all ridge top maquis plots on iron-crust soils. Here, additional woody species included *Codia discolor, Rapanea diminuta, Hibbertia emarginata* Guill., *Wickstroemia indica* (L.) Meyer, and *Styphelia cymbulae.* Forest plots included a broad array of tree species not found, or else infrequent, elsewhere in the samples, including *Nothofagus codonandra, Schefflera* spp., *Cunonia montana* Schltr., *Phelline lucida* Vieill. Ex Baillon, and *Falcatifolium taxoides* (Brongn. et Gris) de Laub.

The second dimension separated the forest plots, with F2 having low scores on axis 2, and plots from F1 (the youngest stand) and F3 having intermediate to high scores on this axis, suggesting no clear successional gradient from F1 to F3 as initially speculated. Forest plots in F1 were strongly dominated by *Araucaria laubenfelsii* (up to 150 years old) with few other tree species represented by individuals >5 cm (diameter at breast height) dbh, and none >10 cm dbh. The litter layer was thin and did not completely cover the mineral soil. Plots in F2 and F3 were not separable according to levels of species richness and diversity (Table 1), but F3 had a deeper and more continuous litter layer underlain by a humus layer about 5 cm thick (containing

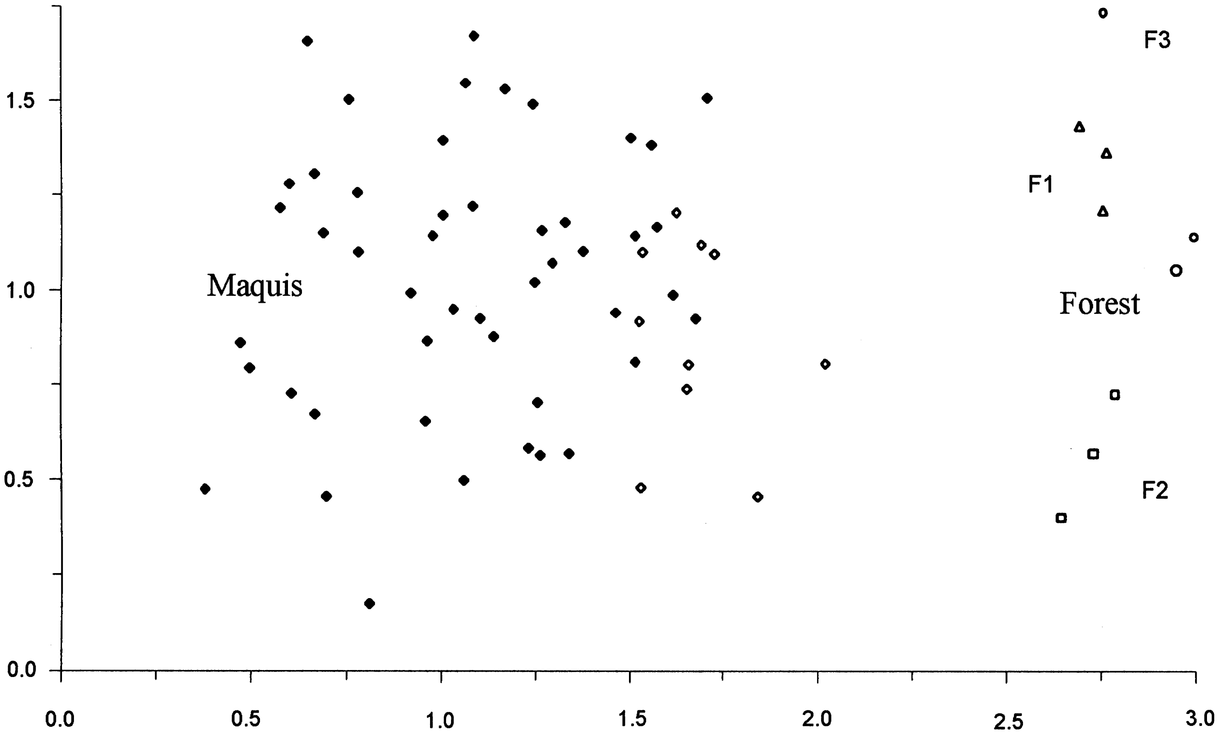

Fig. 1. Two-dimensional non-metric multidimensional scaling ordination of 69 vegetation samples from maquis and rain forest on Mont Do, New Caledonia. Symbols are: closed diamonds for maquis on eroded oxisols, open diamonds for maquis on iron-crust oxisols of ridge tops, open triangles for forest area 1, open squares for forest area 2. and open circles for forest area 3. Axes are scaled in units of half-change in plant species composition.

Table 1. Plant species richness (*R*, spp./100 m^2), Shannon-Weiner diversity (*H*'), and cover, for maquis and forest sites at Mont Do, New Caledonia. Values are mean ± s.e. (sample size in brackets). Row values followed by the same letter are not significantly different ($P < 0.05$, ANOVA with *post hoc* SNK and Bonferroni correction).

	Maquis (30)	Maquis + emergents (20)	Maquis on iron crust (10)	Forest 1 (3)	Forest 2 (3)	Forest 3 (3)
R^a	7.53 ± 0.27a	8.65 ± 0.37a	10.80 ± 0.47b	15.00 ± 0.58c	21.33 ± 3.84c	16.33 ± 1.76c
H'	1.48 ± 0.06a	1.60 ± 0.05a	1.97 ± 0.07b	2.22 ± 0.02c	2.37 ± 0.20c	2.33 ± 0.10c
Cover	56.4 ± 4.5a	94.6 ± 7.4b	100.5 ± 6.5b	173.3 ± 10.6c	169.0 ± 15.5c	166.0 ± 22.7c

[a] Richness and diversity are calculated for plot data after excluding *Araucaria*.

abundant fine roots), and *Nothofagus codonandra* was abundant in the canopy.

Species richness and diversity per 100 m^2 was lowest in maquis plots without mature *Araucaria laubenfelsii* trees, increasing for maquis plots with trees, ridge top and young forest (F1), to highest values in forest areas F2 and F3 (Table 1; note: *A. laubenfelsii* occurrence in samples was removed for purposes of these comparisons). Richness was 2–3 times higher in forest than in maquis on eroded oxisols, and 1.5–2 times higher than on iron-crust oxisols of ridge sites. The index of vegetation cover (sum of Braun-Blanquet cover-abundance scores) increased in the same manner, although all forest areas showed similar cover scores.

Vector-fitting of environmental and derived vegetation variables on vegetation sample locations in NMDS ordination space revealed a number of significant correlations (Fig. 2). Canopy openness and estimated PPFD (from hemisphere photographs) decreased as scores along axis 1 increased, i.e. with movement from maquis to ridge to forest areas (see also Table 2). On the other hand, exchangeable Mg, K and Ca, cation exchange capacity and % C in the surface soil (0–5 cm) all increased along this axis, as did cover and richness. Total surface soil Al also increased with movement from maquis to forest (Table 3). Correlations with vegetation sample locations along the second axis were weaker, although soil pH and total P both increased. In general, total metal concentrations in surface soil samples were not as strongly correlated with sample locations as were exchangeable metal concentrations. None of the potentially toxic metals (Co, Cr, Ni, Mn) were significantly correlated with the revealed pattern of variation in plant species composition. Total concentration does not necessarily provide a good measure of plant

Table 2. Mean (± s.e.) canopy openness (%), estimated photosynthetic photon flux density (PPFD mol m^{-2} day^{-1}) and leaf area index (LAI) for each vegetation type at Mont Do, New Caledonia, estimated from hemisphere photographs taken at a height of 1 m above ground[8] (see text for details). Figures in brackets represent sample sizes. Row values followed by the same letter are not significantly different ($P < 0.05$, ANOVA with *post hoc* SNK and Bonferroni correction).

	Maquis (1)	Forest 1 (3)	Forest 2 (3)	Forest 3 (3)
% Openness	100.0	17.05 ± 0.67a	8.11 ± 1.14b	9.98 ± 0.86b
PPFD	50.4	15.76 ± 0.79a	8.45 ± 0.40b	9.35 ± 0.42b
LAI	n/a	1.93 ± 0.06a	3.01 ± 0.33b	2.62 ± 0.11b

*Vegetation <1 m in height is not included in LAI estimates.

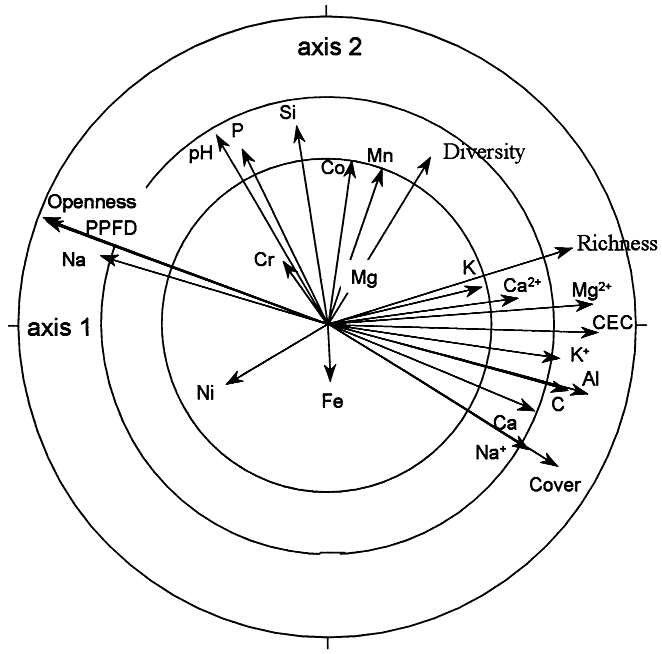

Fig. 2. Environmental and vegetation vectors fitted to the two-dimensional NMDS ordination of vegetation samples from Mont Do, New Caledonia. Arrows indicate the direction of positive correlations between fitted variables and the location of vegetation samples in ordination space. Vector length indicates the level of significance of correlations (inner circle $P < 0.05$, middle circle $P < 0.01$). Exchangeable cations are labelled with their charge (e.g. Ca^{2+}) to differentiate them from total soil concentrations for the same element (e.g. Ca).

available concentration, however, and this result must be interpreted with caution in the absence of exchangeable concentration for these metals.

Soil and leaf chemistries

Total element analyses for surface soil samples from areas supporting maquis and forest showed little variation between vegetation types (Table 3). All samples were strongly dominated by Fe (35–40%), Cr (3.5–4%) and SiO_2 (0.5–1%) with no significant difference between samples from maquis or forest. Only two metal elements showed significant differences between vegetation types; Al was nearly twice as high in forest as in maquis, while Na was 2–3 times higher in maquis. The Ca:Mg ratio was low in soils from all vegetation types, but was an order of magnitude lower in the maquis sites (0.013) than in the forest sites (0.112–0.162), primarily due to a very low concentration of Ca in the former.

Table 3. Total metal element concentrations (%) in surface soils (0–5 cm) for maquis and forest areas at Mont Do, New Caledonia. Values are mean ± s.e. (sample sizes in brackets). Asterisks indicate rows where differences between groups are significant (one-way ANOVA, $P < 0.05$).

	Maquis (6)	Forest 1(3)	Forest 2 (3)	Forest 3 (3)
Si	0.77 ± 0.04	0.57 ± 0.03	0.36 ± 0.16	0.96 ± 0.19
Al*	1.52 ± 0.09	2.27 ± 0.27	2.58 ± 0.09	2.65 ± 0.03
Fe	36.7 ± 0.2	37.3 ± 3.9	39.5 ± 1.4	35.6 ± 3.6
Mn	0.16 ± 0.03	0.14 ± 0.02	0.19 ± 0.06	0.45 ± 0.21
Ca*	0.01 ± 0.00	0.08 ± 0.04	0.07 ± 0.02	0.07 ± 0.03
Mg	0.53 ± 0.04	0.50 ± 0.10	0.46 ± 0.17	0.66 ± 0.07
K	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
Na*	0.02 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
Ni	0.25 ± 0.05	0.13 ± 0.02	0.23 ± 0.02	0.22 ± 0.06
Cr	4.00 ± 0.40	3.68 ± 0.68	3.62 ± 0.04	3.89 ± 0.43
Co	0.02 ± 0.00	0.01 ± 0.00	0.02 ± 0.00	0.05 ± 0.03

Table 4. Exchangeable metal concentrations and cation exchange capacity (m.e. 100 g^{-1}), % carbon, total phosphorus (ppm) and pH in surface soils (0–5 cm) for maquis and forest areas at Mont Do, New Caledonia. Values are mean ± s.e. (sample sizes in brackets). Asterisks indicate rows where differences between groups are significant (one-way ANOVA, $P < 0.05$).

	Maquis (6)	Forest 1 (3)	Forest 2 (3)	Forest 3 (3)
pH	4.39 ± 0.07	3.96 ± 0.03	4.06 ± 0.08	4.27± 0.17
%C*	1.95 ± 0.30	15.67 ± 5.51	12.03 ± 1.99	13.40 ± 3.05
Ca^{2+}	0.187 ± 0.105	1.570 ± 1.191	1.167 ± 0.295	1.790 ± 0.744
Mg^{2+}	0.175 ± 0.065	1.540 ± 0.513	1.393 ± 0.103	1.707 ± 0.216
Ca:Mg	0.787 ± 0.232	0.809 ± 0.219	0.857 ± 0.200	0.955 ± 0.449
K^+	0.018 ± 0.005	0.170 ± 0.103	0.163 ± 0.023	0.180 ± 0.040
Na^+	0.003 ± 0.003	0.170 ± 0.106	0.180 ± 0.021	0.160 ± 0.020
CEC	4.17 ± 0.94	13.29 ± 3.29	14.02 ± 0.46	15.28 ± 1.13
P*	320 ± 61	283 ± 11	136 ± 1	169 ± 13

Surface soil pH ranged from 3.96 in forest F1 to 4.39 in maquis. Although highest in maquis, there was no clear trend across sites and the differences were not significant. Soil carbon was an order of magnitude higher in forest sites than in maquis, as were exchangeable Ca, Mg, K, and Na, and CEC (Table 4). Nevertheless, the Ca:Mg ratio was approximately constant across all sites at 0.8 to 1.0. Total soil P showed the opposite trend to that described for cations, with maquis and young forest (F1) soils having significantly higher levels of P than mature forest (F2 and F3) soils.

Mean total element concentrations in living leaf tissue for 5 species occurring in maquis and the three forest areas (F1–F3) showed no significant differences between locations as defined by vegetation cover type, except for P and Na, which were higher in maquis and F1 than in the older forest patches (Table 5). In the case of P, this pattern paralleled that found for P in surface soil samples. The Ca:Mg ratio ranged from 4.5 in two of the forest areas to 5.2 in maquis, but differences were not significant. Concentrations of Ni, Co and Cr were low throughout and Mn was the only micro-nutrient found in high concentrations in leaf tissues (0.15–0.32%). Grouped by species (regardless of location), a number of differences in patterns of metal accumulation became apparent (Table 6). *Codia discolor* (Cunoniaceae) was the only species to accumulate (in small amounts) Ni, Co and Cr, while *Polyscias pancheri* (Araliaceae) showed hyperaccumlation of Mn (>1% concentration in some samples). In the latter case, Mn concentration was twice as high for leaf samples from forest plants as from maquis plants.

Chlorophyll fluorescence

The patterns of chlorophyll fluorescence for seedlings, saplings and trees of *Araucaria laubenfelsii* from dawn to dusk on a sunny June (winter) day revealed extreme photo-inhibition for seedlings in maquis (Fig. 3). The Fv/Fm ratio for seedlings was already low (0.5) at dawn, indicating acute stress and failure to recover overnight, and declined further during the course of the day to values <0.3. Recovery by dusk was minimal. Saplings in maquis commenced the day with Fv/Fm ratios close to normal for a healthy plant (i.e. approaching 0.8) but fell quickly during the morning to a minimum mean value of 0.51 by early afternoon. Recovery began during mid-afternoon but was not completed by the time measurements ceased two hours after sunset. Mature trees started the day with normal values (0.84), showed a slight decline during the day, followed by full recovery by early evening.

Seedlings and saplings in the forest understorey of forest area F2 commenced the day with Fv/Fm ratios >0.8 and these remained approximately constant throughout the day, indicating no stress on photosystem II. Forest trees were not sampled due

Table 5. Living leaf tissue element concentrations (%) and Ca:Mg ratio for five plant species from each vegetation type; data pooled across species. Values are mean ± s.e. (sample sizes in brackets). Asterisks indicate rows where differences between groups are significant (one-way ANOVA, $P < 0.05$).

	Maquis (30)	Forest 1 (30)	Forest 2 (22)	Forest 3 (18)
Ca	0.855 ± 0.059	0.892 ± 0.060	0.866 ± 0.063	0.754 ± 0.069
Mg	0.210 ± 0.019	0.233 ± 0.020	0.206 ± 0.018	0.178 ± 0.014
Na *	0.442 ± 0.086	0.438 ± 0.074	0.327 ± 0.044	0.268 ± 0.039
K	0.568 ± 0.048	0.514 ± 0.051	0.521 ± 0.075	0.559 ± 0.088
P *	0.030 ± 0.001	0.027 ± 0.001	0.024 ± 0.002	0.024 ± 0.001
Co	0 ± 0	0 ± 0	0 ± 0	0.001 ± 0.000
Cr	0 ± 0	0 ± 0	0 ± 0	0.001 ± 0.000
Fe	0.005 ± 0.001	0.004 ± 0.000	0.005 + 0.000	0.004 ± 0.001
Mn *	0.154 ± 0.033	0.228 ± 0.076	0.325 ± 0.085	0.236 ± 0.056
Ni	0.002 ± 0.001	0.002 ± 0.000	0.004 ± 0.002	0.003 ± 0.001
Ca:Mg	5.29 ± 0.61	4.56 ± 0.41	4.88 ± 0.48	4.54 ± 0.46

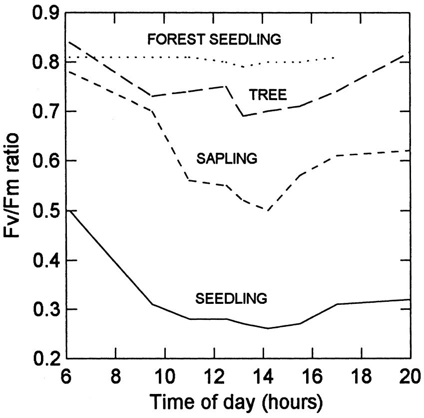

Fig. 3. The extent of photo-inhibition, as measured by chlorophyll fluorescence parameter Fv/Fm, exhibited by seedlings, saplings and trees of *Araucaria laubenfelsii* in maquis, and *A. laubenfelsii* seedlings in rain forest, at Mont Do, New Caledonia, on a sunny day in June 1997.

to the problem of access to canopy foliage but are likely to have followed the same trend as for trees in maquis since their canopies are emergent and exposed to full sunlight during the day.

Fog interception

Overall the amount of water collected beneath *Araucaria laubenfelsii* trees in maquis was more variable than that in open areas of maquis without trees, and was significantly greater during periods of ground level cloud but no rain. There was no significant difference between the volumes of water collected beneath trees and in the open during the first two trials (Table 7). Although the second trial did not show a significant increase in water interception beneath trees, the average amount collected was both greater and more variable than in the open. The amount of cloud interception and rainfall collected beneath individual trees was also highly variable, with one tree measuring 20 mm difference between the two rain gauges placed beneath it. The third trial revealed substantial cloud-combing of moisture by trees in the absence of rainfall. Water equivalent to 12 mm of rainfall was collected beneath trees on this occasion, while collectors in open sites remained essentially empty.

Discussion

Maquis, maquis with emergent *Araucaria laubenfelsii,* and rain forest with *A. laubenfelsii* can all occur within areas of just a few hectares on oxisols derived from serpentinites at Mont Do. Ordination results reveal a dominant gradient of species compositional relatedness running from maquis without emergent trees, through maquis with mature trees, to rain forest, suggestive of a successional gradient from maquis to forest through time. McCoy *et al.*[15] have proposed a similar explanation for the distribution of lowland maquis, *Gymnostoma* forest and rain forest on iron-crust oxisol soils of the Goro Plateau region of southern New Caledonia based on the age and shade tolerance of species in these vegetation types.

Maquis without trees dominates eroded oxisol soils on moderate to steep slopes at Mont Do. These stands are rich in ferns and sedges that facilitate fire spread when an ignition event occurs. While seedlings, and occasionally saplings, of *Araucaria laubenfelsii* are found in these shrublands, none appears likely to survive to maturity if fires recur within about 50 years.[13] Species richness was found to be higher in 100-m^2 maquis sample plots where individual *Araucaria laubenfelsii* trees occur as emergents. This increased diversity was due to the presence of additional woody shrub and early successional forest tree species beneath the tree canopy. The abundance of *Araucaria laubenfelsii,* and species richness, increased further within maquis vegetation on iron-crust oxisols characteristic of ridge top locations at Mont Do. Here, rockiness and break of slope are likely to reduce fire spread, so that many araucarian seedlings can establish and grow to a size (5–10 cm dbh) at which death from stem scorch is unlikely because of the protection afforded the cambium layer by thick bark.[32] The presence of *Araucaria laubenfelsii* trees within maquis thus reflects local site differences indicative of a lower risk of fire. In addition, mature trees themselves provide an environment that favours recruitment of other woody species and the beginnings of a succession to forest.

Variations in nutrient and other metal concentrations in soils under maquis and forest were minor, returning values typical of those found for oxisols on ultramafics elsewhere in New Caledonia,[18] with Fe, Al and Si common, but Mg much reduced relative to values found in nearby hypermagnesian soils. The oxisols

Table 6. Living leaf tissue element concentrations (%) and Ca:Mg ratio for five plant species from each vegetation type; data pooled across vegetation types. Values are mean ± s.e. (sample sizes in brackets).

	Codia discolor (16)	*Styphelia cymbulae* (20)	*Polyscias pancheri* (17)	*Rapanea diminuta* (17)	*Araucaria laubenfelsii* (20)
Ca	0.798 ± 0.052	0.628 ± 0.035	0.748 ± 0.064	1.118 ± 0.063	1.083 ± 0.077
Mg	0.231 ± 0.014	0.086 ± 0.004	0.317 ± 0.019	0.191 ± 0.010	0.259 ± 0.014
Na	0.129 ± 0.019	0.090 ± 0.012	0.457 ± 0.036	0.542 ± 0.026	0.232 ± 0.017
K	0.372 ± 0.018	0.357 ± 0.025	0.805 ± 0.079	0.319 ± 0.021	0.697 ± 0.075
P	0.027 ± 0.001	0.018 ± 0.001	0.032 ± 0.001	0.025 ± 0.002	0.032 ± 0.001
Co	0.002 ± 0.001	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Cr	0.001 ± 0.000	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Fe	0.006 ± 0.000	0.004 ± 0.000	0.006 ± 0.001	0.004 ± 0.000	0.004 ± 0.000
Mn	0.098 ± 0.010	0.252 ± 0.012	0.763 ± 0.122	0.020 ± 0.004	0.113 ± 0.013
Ni	0.011 ± 0.002	0.001 ± 0.000	0.002 ± 0.000	0.001 ± 0.000	0.001 ± 0.000
Ca:Mg	3.89 ± 0.67	7.50 ± 0.50	2.39 ± 0.15	6.09 ± 0.47	4.44 ± 0.46

Table 7. The sum of cloud water interception and rainfall (mm ± s.d.) measured beneath trees of *Araucaria laubenfelsii* ($n = 50$) and in open areas ($n = 25$) in maquis at Mont Do, New Caledonia, on three occasions during June 1998.

Trial No.	Beneath tree	In open	Minimum beneath	Maximum beneath
1 Rain and cloud	38.5 ± 13.3	40.8 ± 9.7	12.4	53.7
2 Rain and cloud	15.4 ± 8.5	14.0 ± 1.0	3.7	34.5
3 Cloud only	12.0 ± 13.0	0.1 ± 0.2	0.6	50.7

were moderately to strongly acidic in reaction and the exchangeable Ca/Mg ratio was close to 1. By contrast, hypermagnesian soils have a pH >7.5 and a very low Ca/Mg ratio.

Ultramafic soils are generally deficient in calcium and have an abundance of magnesium, resulting in a low Ca/Mg quotient.[33] It is suggested that vegetation growth is negatively affected by the excess of magnesium rather than low levels of calcium, as Mg in high concentrations is toxic for many plants, especially when Ca is low (as Ca ameliorates the effects of Mg).[33–35] In ultramafic areas many plants are tolerant of high levels of Mg coupled with low Ca.[33] However, it has also been postulated that the benefits of high Mg concentrations may outweigh its potential toxicity as it has the ability to ameliorate the toxicity of other metals such as Ni.[33] Nevertheless, conditions for plant growth on ultramafics in New Caledonia may be considerably less limiting on strongly leached oxisols (such as those at Mont Do) than on hypermagnesian soils, and soil chemistry may not be a major factor in the distribution of maquis and forest at the local scale. McCoy[30] reports markedly greater photo-inhibition in plants on hypermagnesian soils than on oxisols in New Caledonia, perhaps reflecting greater soil chemical constraints on plant growth.

Leaf tissue nutrient and other metal concentrations for five plant species common to both maquis and forest all had Ca/Mg ratios >2 and only one species (*Polyscias pancheri*) showed strong metal accumulation (for Mn). The uptake and accumulation behaviour of plants was uniform across vegetation types in relation to all measured elements apart from P and Na, which were higher in maquis and young forest than in mature forest sites. In the case of P, this pattern reflected that for total P in the top 5 cm of the soil profile. The lower apparent availability of P in forest than in maquis sites is difficult to explain, and the possible, larger store of P in the forest litter layer (not measured) cannot be invoked to explain the anomaly, since the concentration of P in living foliage should reflect overall availability of P from both organic and inorganic sources. Rather, P may be close to in limiting supply in these forests, the available P being shared by a much larger living biomass in forest sites than in maquis.

There is no evidence that accumulation of elements at the forest floor and their cycling through the decomposition pathway may favour species unable to grow in the maquis. Nor is there evidence of increasing accumulation of metals as reported by Chiarucci and De Dominicis[20] for ultramafic sites in Tuscany. While the amount of organic carbon in surface soils of forest sites is much greater than in the maquis soils, Al is the only element to show a marked increase between maquis and forest soils. Given that fresh leaves show no clear patterns of increasing or decreasing metal concentrations across vegetation types, forest litter layer analyses (although not performed) are also unlikely to show any such pattern. Rather, it seems likely that changing species composition between maquis and forest is a consequence of different amounts of time for community development in the absence of disturbance (from fire), the capacity of different components of the available plant species pool to cope with stresses caused by variations in light and moisture availability, and the presence of *Araucaria laubenfelsii* trees in the maquis which facilitate the entry of other woody species through their moderating influence on light and moisture stress.

Leaf fluorescence studies show that *Araucaria laubenfelsii* seedlings in the maquis are subject to acute photo-inhibition on clear-sky days, and that recovery does not occur overnight, so that stress may become chronic during lengthy sunny spells. Similar depressions in Fv/Fm have been reported by Adams *et al.*[36] and Garcia-Plazoala *et al.*[37] Seedling death is a likely consequence of prolonged stresses of this kind, and almost certainly reflects the combined effects of photosystem damage and insufficient moisture supply to the foliage on these gravelly, excessively well-drained substrates, or eroded soils where runoff exceeds infiltration. As plants increase in size the level of photo-inhibition decreases, as was shown for saplings, so that by some stage between sapling and tree size, individuals show only slight photo-inhibition and are regularly able to recover overnight. This implies that moisture may be the most important limiting factor, with water supply increasing, and/or cloud-combing more effective, with increasing plant size and age. Given that *Araucaria laubenfelsii* is the only tree species which occurs in the maquis, we speculate that other rain forest tree and shrub species would show even greater levels of photo-inhibition, reflecting their adaptation to recruitment beneath a forest canopy. This assertion is supported by the pattern of increasing woody species richness associated with the occurrence of isolated araucarian trees in maquis.

That water supply may be important in the recruitment of forest species is further implied both by the pattern of distribution of forest patches across the landscape — in gullies and on south-facing (cool) slopes — although these are also likely to represent fire-protected sites, and by the cloud combing results detailed here. During periods when low-level clouds sweep across the mountain, but no rain falls, isolated trees of *Araucaria laubenfelsii* harvested water and delivered it to the soil beneath the canopy, thus increasing effective rainfall in these locations. Ekern[38] showed that *Araucaria heterophylla* (Norfolk island pine) was able to harvest the equivalent of 760 mm rain per year from clouds on Lanai in Hawaii, sufficient to irrigate a commercial pineapple crop on this dry island.

We conclude that the landscape scale pattern of distribution of maquis and rain forest on ultramafic substrate at Mont Do, New Caledonia, reflects the impacts of disturbance on the one hand, and of physiological stresses on the other. Disturbance by fire is important in determining the presence and abundance of maquis and rain forest at the landscape level.[1] The effects of light environments, water availability and soil chemistry on the succession of vegetation from maquis to forest are also important. While it has been argued that the chemistry of these ultramafic soils does not appear to vary greatly between vegetation types, they may, nevertheless, be important in slowing the rate of progression of the vegetation from maquis to forest (slow rates of biomass accumulation associated with low rates of macronutrient supply). McCoy *et al.*[15] considered that the transition from maquis to rain forest on iron-crust oxisols in the Goro area of southern New Caledonia might take in excess of 250 years due to low nutrient availability. Added to this is strong evidence for severe damage to photosystem II on sunny days for seedlings growing in maquis, and for the importance of increased water supply in facilitating the recruitment of forest species beneath emergent araucarians in maquis.

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