Australian Journal of Ecology (1998) 23, 528–538

Stand structure of the emergent conifer *Araucaria laubenfelsii*, in maquis and rainforest, Mont Do, New Caledonia

L. S. RIGG,[1] N. J. ENRIGHT[1] AND T. JAFFRÉ[2]
[1]*Department of Geography and Environmental Studies, University of Melbourne, Parkville, Victoria 3052, Australia and* [2]*Laboratoire de Botanique, ORSTOM, B.P. A5, Nouméa Cedex, New Caledonia*

Abstract Despite its small size, New Caledonia has a flora which includes 43 endemic species of conifer. This study examines the stand structure of the New Caledonian conifer, *Araucaria laubenfelsii* Corbasson, a species which occurs on ultramafic soils as an emergent tree in rainforest and in an unusual structural association with maquis vegetation. Fire and cyclone blow-down are the primary disturbances in the maquis, but fire is infrequent in the rainforests which is evident from the low proportion of fire scarred trees. Preliminary results show abundant seedlings and saplings of *A. laubenfelsii* both in maquis and forest. Size class distributions of individuals suggest that the species is continuously regenerating in the maquis and immature forests. Variability in the stand structure in maquis communities reflects the probable patchy nature of disturbance from small-scale fires and blow-down from tropical cyclones. In mature forests, *Nothofagus codonandra* (Baillon) Steenis is the dominant canopy species and 'other tree species' are continuously regenerating, while the size class distributions and basal area of *A. laubenfelsii* suggest that there is, at present, limited regeneration of this species. Tree ring counts indicate that individuals in forest areas grow at a slower rate than those in maquis, but attain greater age, probably as a result of greater protection from fire.

Key words: *Araucaria laubenfelsii*, maquis, rainforest, stand structure, tree rings, ultramafic.

INTRODUCTION

New Caledonia is a relatively small island group, (approximately 19 000 km^2), yet it possesses a rich and distinctive native flora of about 3000 species. Approximately 80% of all species are endemic and this number includes 43 conifers from four families: Taxaceae (one sp), Podocarpaceae (18 spp), Araucariaceae (18 spp), and Cupressaceae (six spp) (Jaffré 1995). This rich and unique flora is considered to be the result of the survival and evolution of species, many of Gondwanan origin, under circumstances of long isolation in comparatively constant climatic conditions, and a highly varied geology (Jaffré & Pelletier 1992). Approximately one-third of New Caledonia is dominated by ultramafic rocks, and soils on these parent materials are characterized by low levels of plant macronutrients, but high concentrations of certain metals, including nickel, manganese, and chromium (Jaffré 1980, 1995).

Two kinds of vegetation dominate the ultramafic areas; a sclerophyllous, light-demanding, evergreen shrubland to 2 m tall, known locally as 'maquis miniers' (Jaffré 1980), and rainforests, often with species of *Araucaria* or *Agathis* forming an emergent layer above the main forest canopy. Some areas of maquis also support a scattered emergent layer *Araucaria* or *Agathis* (but not angiosperm tree species), producing an unusual structural association. The density of this layer in maquis varies considerably; from areas with no trees, to those with very high stem densities. Jaffré (1995) has suggested that, on the Mont Do massif, *Araucaria laubenfelsii* is regenerating in maquis due to the absence of disturbance by fire since the area was set aside as a botanical reserve about 30 years ago. The regeneration status and ability of this species to persist within forest is unknown, while the hypothesis about its behaviour in maquis is untested. The issue of conifer–angiosperm coexistence in plant communities is a topical one (Bond 1989; Enright & Odgen 1995), and the diversity of unusual conifer–angiosperm plant assemblages in New Caledonia provides a unique opportunity to further explore and understand the mechanisms facilitating such coexistence.

Araucaria laubenfelsii is listed as a category 3 species (restricted or scattered range), in the IUCN Red Data Book world list of threatened conifer taxa (Farjon *et al.* 1993) and is of conservation concern as it has a restricted geographical range and is threatened by land degradation and increased fire frequency. This study seeks to determine whether *A. laubenfelsii* is

Accepted for publication February 1998.

regenerating in both the maquis and forest communities by analysing *A. laubenfelsii* stand structures. Specific hypotheses to be examined, at least in a preliminary manner, are: (i) that there is evidence for recruitment of *A. laubenfelsii* in maquis at Mont Do (Jaffré 1995); (ii) that *A. laubenfelsii* is killed by fire and is thus excluded from areas of maquis subject to recurrent disturbance by fire (Jaffré 1995); (iii) that the occurrence of *A. laubenfelsii* in maquis is restricted to certain compositional or environmental circumstances (here we seek an alternative explanation for the absence of a conifer layer in many maquis areas); and (iv) that density and recruitment of *A. laubenfelsii* in forest varies with stand structural characteristics which may reflect a successional (or environmental) gradient from sites strongly dominated by *Araucaria* to those rich in *Nothofagus* or mixed angiosperm species. Read *et al.* (1995) has previously proposed such an hypothesis to explain the distribution of monodominant (*Nothofagus*) versus high diversity mixed species rainforest stands in New Caledonia.

METHODS

Study area

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, 1800 km north of New Zealand (Fig. 1). The main island (La Grande Terre) has a central mountain chain with peaks ranging from 1000 to 1600 m a.s.l. The climate is tropical to subtropical and for most of the year the islands are exposed to trade winds from the northeast and southeast. The rainy season is from November to April and is characterized by warm temperatures, heavy rainfall and the occurrence of cyclones, while from May to October temperatures are cooler and there is less rainfall (METEO-France 1994). While the east coast receives > 3000 mm y^{-1}, the west coast may receive < 1000 mm y^{-1} (Latham *et al.* 1978; METEO-France 1994). The mean monthly temperature in the capital, Nouméa, is highest in February, 26.2°C, and lowest in August, 19.9°C (Jaffré 1980).

Approximately one-third (5500 km^2) of the main island is covered by ultramafic substrates (Fig. 1). These formations are principally periodites composed of harzburgites, dunites and pyroxenites, and the main soils derived from them include brown eutrophic hypermagnesian soils (sols bruns eutrophes hypermagnésiens) and ferralitic ferritic soils (sols ferralitiques ferritiques) (Latham *et al.* 1978; Jaffré 1980). The ferralitic soils are often characterized by a surficial iron hardpan and are known as 'sols cuirassés' (Jaffré *et al.* 1987). These typically have a low pH, a very low cation exchange capacity, are deficient in nitrogen, phosphorus, potassium and calcium, and have high levels of magnesium, nickel and manganese (Jaffré 1980; Brooks 1987).

The field sites described here were located in the Mont Do Botanical Reserve (Réserves Spéciales Botaniques), 21°45 S, 166°E. Mont Do reaches an altitude of 1025 m and the reserve occupies the top several hundred metres of the mountain, corresponding with the local extent of ultramafic bedrock. It receives an average annual rainfall of 1690 mm and the mountain top is frequently covered by clouds which increases the

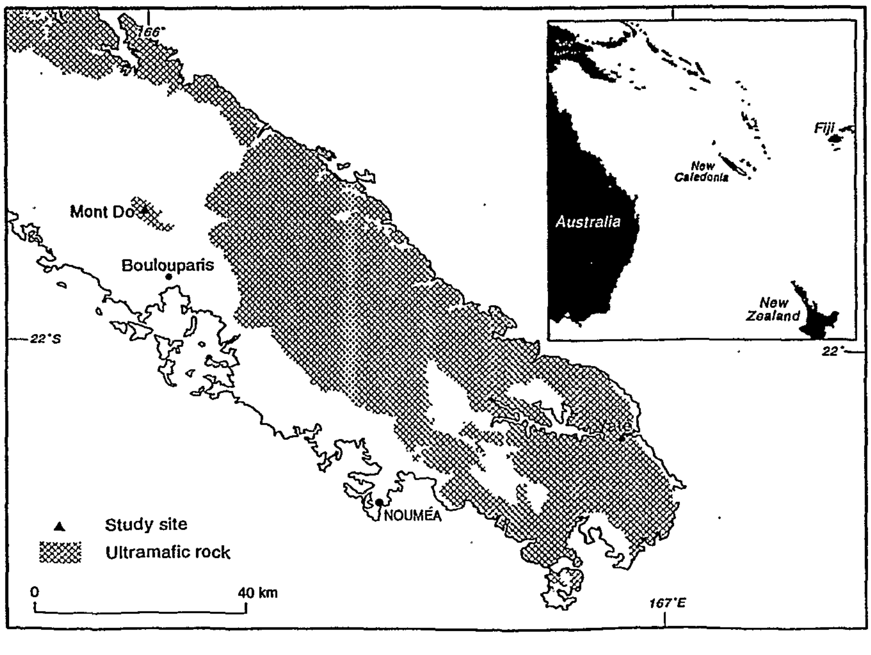

Fig. 1. Southern section of New Caledonia, showing study site and distribution of ultramafic substrate.

moisture available to plants due to cloud-combing by the vegetation, especially beneath emergent trees (L. S. Rigg pers. obs. 1995–96; Ekern 1964; Enright 1982). Based on 14 years of rainfall data (1980–94), the wettest month is February, receiving an average of 255 mm and the driest is September (45 mm).

The vegetation on Mont Do is a mosaic of rainforest, maquis, and maquis with emergent *A. laubenfelsii*. The maquis community is comprised of a diverse mixture of shrub species, including *Mydocarpus fraxinifolius* Brongn. & Gris, *Symplocos montana* (Vieill.) Brongn. & Gris, *Rapanea diminuta* Mez. and *Codia discolor* (Brong. & Gris) Guill., with some areas dominated by ferns such as *Gleichenia dicarpa* R. Br. and *Dicranopteris linearis* (Burm.) Underwood, or sedges (e.g., *Costularia nervosa* J. Raynal). Rainforests mostly occur as small stands or fragments in drainages, but continuous forest 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 *A. laubenfelsii* frequently forms an emergent layer.

Field sampling and analytical methods

All field sampling took place between February 1995 and July 1996. Seven permanent remeasurement plots (M1–M7), with a total area of 4 ha (ranging in size from 0.25 to 1 ha), were established in maquis covering a range of topographic positions and araucarian tree densities. In addition, thirteen 0.01 ha permanent plots were established in three rainforest fragments (F1–F3); three in F1, six in F2 and four in F3. Within permanent plots slope, and aspect were recorded, and all trees ≥5 cm diameter at breast height (d.b.h.) were tagged and d.b.h. was measured. The presence of fire scars was recorded for each tree.

Individuals ≥30 cm in height and <5 cm d.b.h. were classified as saplings (Veblen *et al.* 1981; Burns 1993), and individuals <0.3 m in height were classified as seedlings. In each maquis plot sapling density and height to apical tip was recorded within 10 (five in M6 and five in M7) randomly placed 100 m^2 subplots. Density and height of seedlings was measured in replicate 4 m^2 plots within sapling subplots in the maquis and in 1 m^2 subplots within the forest plots. In total, 130 seedling plots were sampled.

Sampling of the rainforest tree layer (stems ≥5 cm d.b.h.) was carried out in four forest fragments (F1–F4) using the point-centred-quarter method (PCQ) (Mueller-Dombois & Ellenberg 1974) with a minimum of 20 points per stand, each 10 m apart (15 m apart in F3). Forest fragment F3 had permanent plots established in the upper part of the fragment, while PCQ sampling was conducted at both upper slope (F3) and lower slope (F3a) locations. In order to increase the sample size of trees for stand structure analysis, a double measure PCQ was used in F2, F3 and F4, where both the nearest tree and the nearest *A. laubenfelsii* was recorded in each quarter. Forest fragment F1 was too small to allow the use of the PCQ method, while in F3a only the nearest individual was measured and recorded due to the absence of *A. laubenfelsii* from that part of the stand.

Tree cores were taken from 140 randomly chosen individuals in the maquis and forest plots. A Haglof (Langsele, Sweden) 12 inch case-hardened increment borer was used to take the cores at 0.3 m above the ground. Of the 140 cores, approximately 25 were taken from living trees with obvious fire scars. Six saplings were harvested at ground level to help determine the mean age at coring height, and three standing dead and two living trees were felled by chainsaw. Cores, stems and chain-sawed sections, were sanded and growth rings examined and counted using a stereo-microscope.

In each of the randomly located 100 m^2 sapling plots within the maquis ($n = 60$) presence and Braun-Blanquet cover-abundance were recorded for all shrub and ground layer species (including ferns), and for bare ground. Tree-sized individuals of *A. laubenfelsii* were not included, but saplings and seedlings (as a component of the shrub layer) were included. Slope, aspect and topographic position were recorded for each plot. Five subjective categories were used to describe topographic position; ridge top, shoulder slope, mid-slope, toe-slope and valley floor (scored 1–5, respectively).

The program DECODA (version 2.04; Minchin 1991) was used to perform the ordination procedure detrended correspondence analysis (DCA) on the cover/abundance data. Detrended correspondence analysis provides a multidimensional spatial arrangement of the data such that points close together in ordination space reflect similarity within the data. It also allows for the dominant gradients of change in species composition to be identified. Some authors have criticized DCA (Minchin 1987; Wartenberg *et al.* 1987) due to problems associated with detrending and rescaling. Despite these criticisms, it is considered an effective and powerful indirect ordination technique for ecological data (Gauch 1982; Peet *et al.* 1988; Kent & Coker 1992) and displays a high level of robustness. Kent and Coker (1992; p. 226) state that DCA as an ordination technique is '... as good as any other in most situations and better than most in many'.

Detrended correspondence analysis generates scaled axes with units reflecting the mean rate of species turnover, such that an axis length of 400 (i.e., 4 SD units) represents, on average, a complete turnover of species composition in the samples (Kent & Coker 1992). Sample scores on the first two axes generated from the ordination were correlated with the amount of bare ground, slope, and topographic position, using the Spearman's rank correlation. The summed basal areas of the trees in each plot, and the average sapling

Table 1. Spearman's rank correlation of selected environmental and independent vegetation variables with the first two axes from the detrended correspondence analysis (DCA)

Axis	% Bare ground	Slope (°)	Topographic position	Mean sapling height (m)	Total basal area of trees per plot
DCA 1	0.202	−0.209	−0.392*	0.066	0.412*
DCA 2	−0.265*	−0.033	−0.020	0.205	0.155

$n = 60$, *$P < 0.05$.

height, were also compared to scores on the first two axes of the DCA to determine which variables, if any, were correlated with the position of plots in the ordination space.

Size–class frequency distributions were constructed for the trees in forest and maquis plots using 5 cm diameter classes for all stands. In the maquis plots, *A. laubenfelsii* was the only species with stems ≥5 cm d.b.h., but in the forest, size class frequencies were determined for *A. laubenfelsii*, *N. codonandra* and a composite category for 'other tree species'. Differences in the size–class frequencies were compared between the stands and species (in the forest) using the Komolgrov–Smirnov two sample test (Siegel 1956). Seedling and sapling values were excluded from these tests so that they were not unduly influenced by the high proportion of individuals in the smallest size classes.

Differences in sapling density within maquis and forest plots were examined using the Kruskal–Wallis test (data were not normally distributed and logarithmic transformation did not improve the distribution). Sapling density differences between maquis and forest were determined using a two-tailed Mann–Whitney *U*-test (Zar 1984). Analysis of variance was performed on log-transformed seedling density data to explore the density differences within the maquis and forest, with the Scheffé test (Zar 1984) for post-hoc multiple comparison. Seedling densities between forest and maquis were compared using a *t*-test (two-tailed). Regression analysis was used to assess the relationship between the number of growth rings and tree diameter at breast height. Homogeneity of slope tests (Zar 1984) were performed to determine the significance of difference in d.b.h./ring-count relationships between plots in maquis and forest.

RESULTS

Ordination of maquis community data

A total of 23 species were used in the DCA ordination (Fig. 2). Three species were excluded from the analysis due to their infrequent occurrence in the 60 plots. Eigenvalues for the first four axes in the ordination were 0.248, 0.138, 0.090, and 0.069, respectively. Only results for the first two axes are described here since they explain approximately 45 and 24% of the variance, while the third and fourth axes explain little of the variation and are unlikely to be readily interpretable or ecologically meaningful.

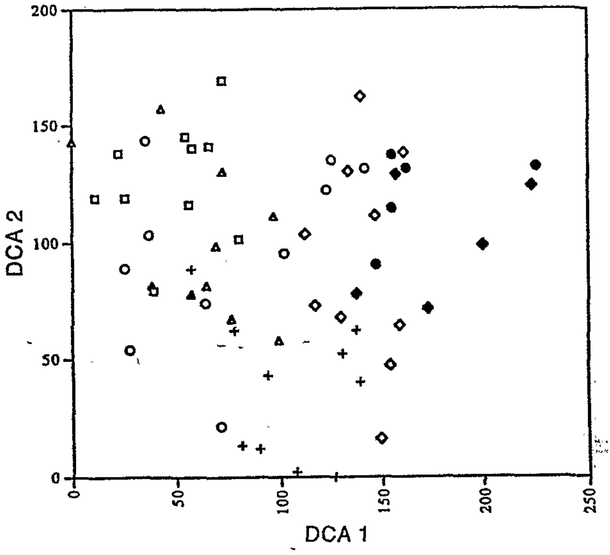

Fig. 2. Ordination (detrended correspondence analysis) of species cover/abundance data for 60 100 m^2 maquis plots within seven permanent plots (M1–M7) on Mont Do, New Caledonia. (□) M1, (◇) M2, (○) M3, (△) M4, (+) M5, (◆) M6, (●) M7.

The site ordination (Fig. 2) shows plots from M6 and M7 with high scores on the first axis and plots from M1, M3 and M4 with low scores. The length of the first axis is about 2.5 SD meaning that there is considerable, but not complete, turnover of species among the samples on this axis. On the second axis, plots from M5 have consistently low scores while those from M1 have high scores. The length of the second axis is <2†SD.

Scores on the first axis are positively correlated ($P < 0.05$) with the total tree basal area in the plot and negatively correlated ($P < 0.05$) with topographic position. This indicates that plots with high scores on the first axis, such as those from M6 and M7, occur along ridge tops and shoulder slopes, and have either higher stem densities of tree-sized *A. laubenfelsii* or have larger individuals in the plots (Table 1). Scores on the second axis correlate negatively with percentage bare ground. Plots with low scores on this axis, such as M5, have large areas of bare ground (Table 1).

The species ordination shows that *A. laubenfelsii* seedlings and saplings are associated with the woody shrubs *M. fraxinifolius*, *Dracophyllum ramosum* Panch. ex Brongn. & Gris, *Dracophyllum verticillatum* Labillardière, *C. discolor*, *R. diminuta*, *Costularia arundinacea* (So. ex Vahl.) Kük., *Scaevola beckii* Zahlbruckner, and *Beackea leratii* Schltr. These species are common in the maquis on Mont Do and are present in most plots. Based on the scores from the first axis of the species ordination there are some species which do not occur with others. For example, when the fern, *Gleichenia dicarpa*, and the sedge, *C. nervosa*, are abundant, woody species such as *Wikstroemia indica* (L.) C. A. Meyer and *Hibbertia emarginata* Guillaumin are usually absent. *Araucaria laubenfelsii* falls in the centre of the species ordination and is likely to be found in association with all species to some extent.

Seedling and sapling size and densities

Araucaria laubenfelsii seedling density in maquis plot M7 was significantly higher (6.9 m^{-2}) than in any other maquis plot ($P < 0.01$). Seedling densities in plots M1 to M6 ranged from 0.8 to 3.2 m^{-2}, with no significant differences between them (Table 2). M4 had the tallest seedlings, averaging 0.17 m, while mean seedling height in the other six maquis plots varied from 0.10 to 0.12 m, but none of these differences were significant.

Seedling densities were significantly greater ($P < 0.01$) and seedlings were taller in the forest, than in the maquis (Table 2). Significant differences ($P < 0.05$) in seedling densities were found between all three forest plots, with seedlings most abundant in F1 (Table 2). In F1 and F2, seedling densities were at least 10 times those found in all maquis plots except M7. F3 was the exception with only 3.5 seedlings m^{-2}. Forest seedlings were slightly taller on average than seedlings found in the maquis, with mean seedling heights varying between 0.13 and 0.16 m, but these differences were not significant.

Table 2. Density m^{-2} (± SE) for seedlings and saplings in sample plots, Mont Do, New Caledonia. Values are derived from data collected in June 1995. In the three forests extra 1 m^2 plots were sampled for seedling densities (a total of 15 plots in F1, 30 plots in F2, and 24 plots in F3)

	Seedling density (m^{-2})	Sapling density (m^{-2})
M1	3.2 ± 0.81	0.16 ± 0.06
M2	0.8 ± 0.19	0.15 ± 0.08
M3	2.5 ± 0.66	0.05 ± 0.03
M4	1.3 ± 0.23	0.09 ± 0.05
M5	0.8 ± 0.20	0.03 ± 0.02
M6	1.8 ± 0.69	0.29 ± 0.07
M7	6.9 ± 1.31	0.42 ± 0.18
F1	42.2 ± 4.77	4.3 ± 1.05
F2	27.5 ± 3.06	3.32 ± 0.94
F3	3.5 ± 0.79	2.87 ± 1.07

Sapling densities were more variable between the two community types than were seedling densities. Density values were calculated based on five to ten, 100 m^2 subplots in each maquis plot, but in M3, the six subplots at the bottom of the slope were void of either saplings or trees of *A. laubenfelsii*. This plot had the lowest sapling density (0.03 m^{-2}). In the other maquis plots sapling densities ranged from 0.05 to 0.29 m^{-2}. Plot M7 was again an exception with 0.42 saplings m^{-2} and there was a significant difference in sapling densities among maquis plots ($P < 0.01$).

Sapling densities were significantly greater ($P < 0.05$) in the forest than in the maquis, with a maximum of 4.3 saplings m^{-2} in F1 (Table 2) and no significant difference between forest plots. The mean height of saplings in the maquis ranged from 0.47 m in M5 to 0.75 m in M6. The mean heights of saplings in F2 and F3 were comparable with those found in the maquis plots, but in F1 mean height exceeded 1 m. A two sample (with unequal variance) *t*-test comparing the height/d.b.h. ratios for maquis (71.8 ± 5.5) versus forest (120.0 ± 19.8) showed a significant difference ($P = 0.01$) indicating that for a given d.b.h., saplings in the forest were taller, and those in the maquis were shorter, but had thicker stems.

Density and basal area of trees

Stem densities of *A. laubenfelsii* individuals ≥5 cm d.b.h. ranged from 40 to 316 ha^{-1} in the maquis (Table 3); and 63 (F3a) to 2200 ha^{-1} (F1) in the forest (Table 4). All of the forest fragments sampled were >1 ha in size, except F1, which was approximately 0.25 ha. Densities for *N. codonandra*, which occurred only in F3 and F3a, were 1254 and 628 ha^{-1}, respectively. The stem densities for 'other species' ranged from 1033 ha^{-1} in F1 to 2400 ha^{-1} in F2 (Table 4).

In the maquis, total basal area for *A. laubenfelsii* ranged from 1.5 to 11.4 m^2 ha^{-1} (Table 3). Basal area in forest plots was consistently higher than that in the

Table 3. Density and basal area of *Araucaria laubenfelsii* in maquis, Mont Do, New Caledonia

	Density ha^{-1} (m^{-2})	Basal area ha^{-1} (m^{-2})
M1	79	2.7
M2	51	1.5
M3	42	2.3
M4	40	2.0
M5	53	2.0
M6	316	5.8
M7	262	11.4

maquis, except for F3a which had a value of 1.49 m^2 based on a sample of only two stems. In the vicinity of F3a, *N. codonandra* was the dominant canopy species and very few *A. laubenfelsii* were encountered along the 200 m transect sampled.

Total basal area for all species in the forest plots varied between 32.4 and 76.9 $m^2 ha^{-1}$. F1 had the lowest total (32.4 $m^2 ha^{-1}$), although 85% of the basal area was *A. laubenfelsii*, while the other 15% was comprised of a large number (30% of the total density ha^{-1}) of small stems of other species. In F1, F2 and F4 the average basal area per stem for *A. laubenfelsii* was 130, 380, and 300 cm^2, respectively (Table 4). *Araucaria laubenfelsii* comprised 63 and 40% of the total basal area in F2 and F4 and in neither case was *N. codonandra* prominent.

The two areas sampled in Forest 3 contained *N. codonandra*. This forest covered the southwestern face of the mountain from approximately 1000 to 800 m a.s.l. *Araucaria laubenfelsii* was prominent on the ridges and spurs between drainage lines within the forest. In F3 and F3a, *N. codonandra* comprised 65 and 67% of the total basal area of the forest and *A. laubenfelsii* only 15 and 3% of the basal area, respectively (Table 4). In general, there were fewer but larger stems of all species in F3 than in the other forest stands. The average basal area per stem in F1 was the lowest at 100 cm^2, F2 and F4 were similar with 170 and 160 cm^2, while F3 and F3a had the largest stems with respective values of 250 and 230 cm^2.

Stand size structure

The largest tree found in the maquis was 58.3 cm d.b.h. in plot M1. No other maquis plot contained trees >50 cm d.b.h. The maximum d.b.h. of trees found in forest plots was 40.1 cm in F1, 64.9 cm in F2, and 68.8 cm in F3. In all maquis plots the density of indi-

Table 4 Basal area (BA) and density (D) of trees in five forest plots, Mont Do, New Caledonia. Values for F1 are based on counts from plot data, while the other values are calculated from PCQ data

	Araucaria laubenfelsii			*Nothofagus codonandra*			Other species			All species		
	n	BA ($m^2 ha^{-1}$)	D (ha^{-1})	*n*	BA ($m^2 ha^{-1}$)	D (ha^{-1})	*n*	BA ($m^2 ha^{-1}$)	D (ha^{-1})	*n*	BA ($m^2 ha^{-1}$)	D (ha^{-1})
F1	66	27.5	2200	0	0	0	31	4.9	1033	97	32.4	3233
F2*	80	36.2	963	0	0	0	79	21.0	2400	159	57.2	3363
F3*	92	11.83	209	40	49.8	1254	52	15.8	1628	184	76.9	3091
F3a	2	1.49	63	28	38.6	628	58	17.5	1821	88	57.6	2512
F4*	77	18.21	616	0	0	0	79	28.4	2246	156	46.6	2862

*Values calculated based on PCQ double measure, see methods.

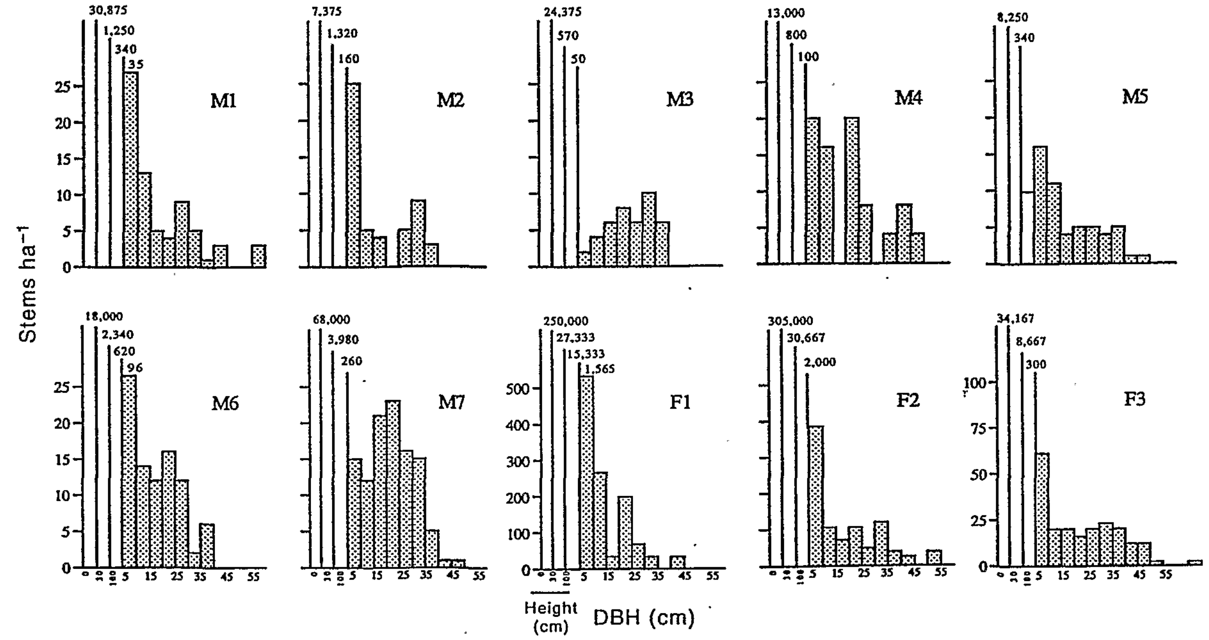

Fig. 3. Size–class diagrams for *Araucaria laubenfelsii*, Mont Do, New Caledonia. Frequencies based on data collected within permanent maquis and forest plots (M1–M7, F1–F3).

viduals progressively decreased as size increased (Fig. 3). M5 differed from the other maquis stands as it had a recruitment gap in the second sapling category (Fig. 3).

The shape of the size–class distribution for individuals ≥5 cm d.b.h. ranged from 'reverse J' (or all-sized) in M1, M5 and M6, to multimodal in M2, M3, M4 and M7. There were a number of 'gaps' in M4 and in M2, with no recorded individuals in one or more size class (Fig. 4). Among the maquis plots, M3 was significantly different from M1 and M2 in the distribution of individuals among the size classes (Komolgrov–Smirnov two sample test, $P = 0.05$). The significant differences found between the three plots result from the low number of individuals in the 5–10 cm d.b.h. size class in M3. Compared with the other maquis plots, M7 had a greater number of individuals in the larger size classes, and fewer individuals in the smaller size classes (Fig. 3), resulting in a significant difference ($P < 0.01$) in stand structure between M7 and both M2 and M6.

Although the number of seedlings ha^{-1} in the forest plots is much greater than in the maquis, the ratio of saplings (first category) to seedlings is comparable. The size–class distributions for all three forest plots can be described as reverse-J, with large numbers of individuals in the seedling, sapling and the 5–10 cm d.b.h. size classes, and fewer in the larger size classes (Fig. 3). F3 exhibited a flat structure for trees >10 cm d.b.h., as did F2 and while these were not significantly different from each other, they were different from F1 ($P = 0.05$). The distribution of individuals among the size classes in F1 was significantly different from those in all other plots except M6 ($P < 0.01$).

The stand structure for *A. laubenfelsii* in F4 has a reverse-J shape and is comparable with that in F1 and F2, while F3a has no clear structure, with only two size classes containing individuals. The other species in these forests all show a clear reverse-J structure, with individuals in the smaller size classes well represented (Fig. 4). *Nothofagus codonandra* showed fewer individuals in the smallest size class than in the next four

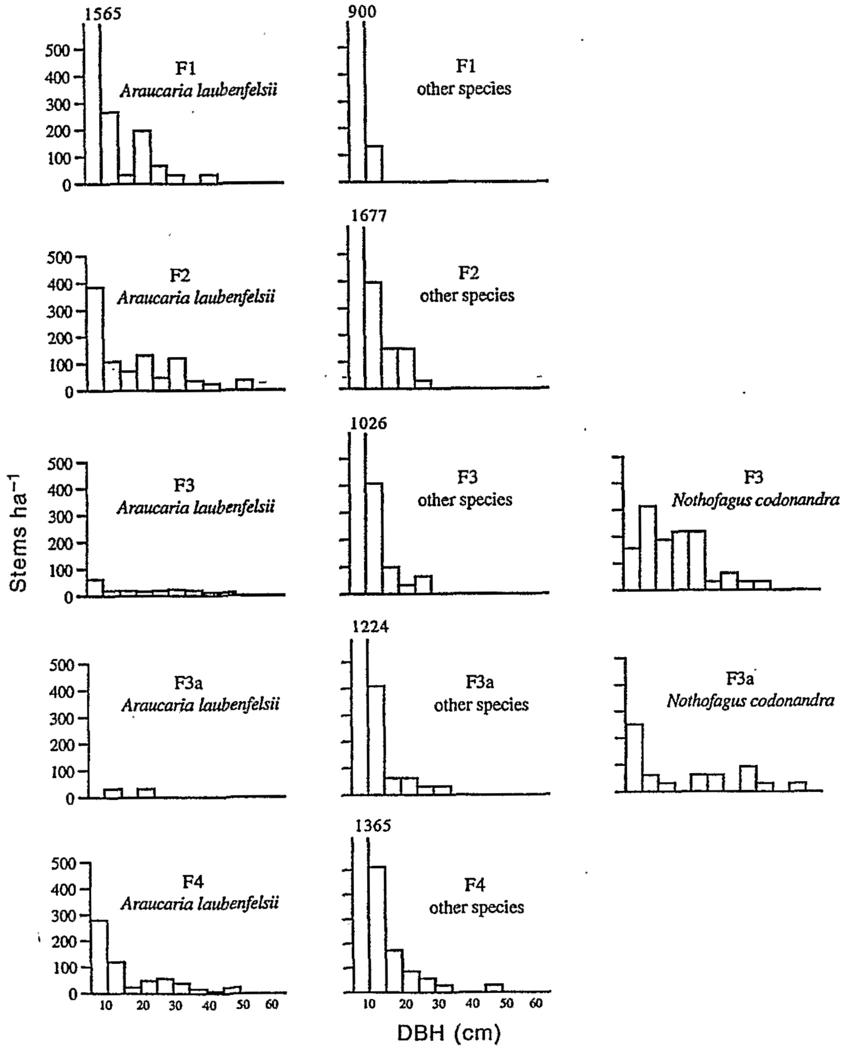

Fig. 4. Size class diagrams (trees ≥5 cm d.b.h.) for *Araucaria laubenfelsii*, 'other species', and *Nothofagus codonandra*, in forest plots, Mont Do, New Caledonia. Frequencies based on data collected from forest surveys using the point-centred-quarter method.

Table 5. Fire scarred trees (>5 cm d.b.h.) and trees killed by blow-down in the seven maquis plots and three forest plots on Mont Do, New Caledonia

	Trees/plot	Scarred trees/plot	% Scarred trees/plot	Trees blown down	Date of cyclone
M1	59	10	17.0		
M2	57	15	26.3	1	Jan/97
M3	21	8	38.1		
M4	20	4	20.0		
M5	34	12	35.3	1	Jan/97
M6	79	3	3.8		
M7	83	50	60.2	3	Mar/96 (1) and Jan/97 (2)
F1	66	0	0		
F2	45	2	4.4		
F3	26	2	7.7		

classes in F3. There was a greater number of individuals in the first size class than in any other size class in F3a, but a number of size classes had no trees. In every case 'other species' showed a clear reverse-J size structure.

Fire scars and blow-downs

Within the maquis the proportion of trees with fire scars ranged from 17 to 60%, with M6 an exception at 3.8% (Table 5). The forest plots had a much lower proportion of trees with fire scars, with no fire scars recorded in F1 and 4.4 and 7.7% in F2 and F3, respectively.

Several tree falls were attributable to winds associated with tropical cyclones in the summers of 1996 (Cyclone Betsie, 27 March 1996) and 1997 (Cyclone Drena, 8 January 1997) (Table 5). In 2 years of observations a total of five trees within the study plots (all of which had previous fire scars) were felled during cyclones. Three of the tree falls occurred within M3, which also had the highest proportion of trees with fire scars (Table 5). The other two tree falls occurred within M2 and M5, respectively. While treefalls were noted within F1 and F2, no tagged trees within the study plots fell.

Tree ring analysis

Regression analysis showed that growth ring counts and d.b.h. of trees in maquis and forest (Fig. 5) were significantly correlated ($P < 0.001$). Using the slope of the line from the linear regression analysis, the average width per growth ring was determined, with forest trees ($n = 25$) having narrower rings ($n = 25$, $= 0.07$ cm ring^{-1}), than maquis trees ($n = 67$, $\bar{x} = 0.10$ cm ring^{-1}). Homogeneity of slope tests (comparing the slopes from the linear regression analysis) revealed a significant difference in the ring width/tree radius relationship between maquis and forest trees ($P < 0.001$). If *A. laubenfelsii* lays down annual rings, then trees in the forest are the slower growing.

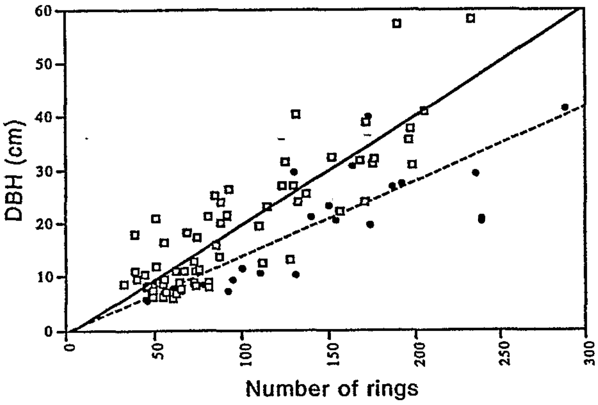

Fig. 5. Relationship between the number of rings and diameter at breast height (d.b.h.) of trees cored in (□) maquis and (●) forest. Lines are line of best fit for maquis trees (—) and forest trees (----).

Based on the regression equations, a tree 60 cm d.b.h. in maquis would have an estimated age of 300 years, while in forest a tree with the same d.b.h. would be 440 years old. Given the maximum d.b.h. of maquis and forest trees of 58.3 cm and 68.8 cm, respectively, the oldest trees in the maquis may be approximately 300 years of age and in the forest approximately 500 years. Ring count analysis of harvested saplings was inconclusive due to poor ring definition and small sample size and it is difficult to say (at this stage) whether saplings in the forest are younger or older than individuals of the same height in the maquis.

DISCUSSION

Recruitment of *Araucaria laubenfelsii* in maquis

Seedling and sapling densities in maquis plots suggest that *A. laubenfelsii* is able to establish within the maquis environment. Certain areas (e.g., bottom of M3) were void of adult trees or saplings, but seedlings were still evident, even if in low densities. Seeds, although winged, are heavy and do not usually fall far from the parent, but can be washed downslope in rainstorms and this movement of seed can account for the establishment of seedlings in areas devoid of adults where seed sources occur directly up slope. Maquis plot M7 located on a ridge had the highest seedling and sapling densities of any of the maquis plots. The ratios of seedlings and saplings to small trees suggests that at present *A. laubenfelsii* is regenerating successfully in maquis sites.

The stand structure of the maquis hints that in some areas, given a lack of disturbance by fire, *A. laubenfelsii* is able to regenerate continuously in open areas. The ratio of small trees to saplings in the maquis plots suggests that *A. laubenfelsii* is successfully regenerating in all plots, with M5 as an exception with limited evidence of recruitment of saplings >1 m (Fig. 3). This low sapling count in M5 may reflect a localized disturbance such as a fire that destroyed a large proportion of several seedling cohorts. Similarly the low frequency of stems in the small size classes in M3 may be the result of a fire which killed smaller stems, but left larger stems alive. The plots located along ridge lines (M6 and M7) did not exhibit any regeneration gaps, but the stand structures were multimodal, perhaps reflecting varying degrees of regeneration success in the past (Fig. 3).

Community composition of maquis

The occurrence of *A. laubenfelsii* in maquis may be restricted to certain areas within the study site due to compositional or environmental circumstances. This hypothesis would require *A. laubenfelsii* to occur in areas with a certain species composition, while being excluded from areas with differing species composition or environmental conditions. Distinct maquis vegetation communities do not occur within the study area, and *A. laubenfelsii* was found in association with all the species recorded. In areas dominated by ferns and sedges maquis development may be slowed, including the development of the emergent tree layer. Where ferns and sedges occur there is less bare ground evident and this may promote the spread of fire, also helping to slow maquis species establishment and growth, and successful recruitment of *A. laubenfelsii* to a size where it can survive fire.

The correlation between the ordination axis scores, topographic position and total basal area in the sample plots, suggests that community composition may not be the dominant control over the presence or absence of the emergent tree layer. Rather, ridge top positions within the maquis may be somewhat protected from fire and therefore able to sustain the emergent layer of *A. laubenfelsii.*

Characteristics of forest stand structure

Seedling and sapling densities in the forests (F1 and F2) greatly exceeded those found in the maquis, but the ratios of sapling to seedlings and small trees to saplings, indicate that the increased densities are probably required in these forest stands to maintain the present tree densities. The ratio of height to d.b.h. of saplings in the forest plots compared with those in the maquis suggests that forest saplings are responding to lower light levels in the forest environment by concentrating more of their growth on height increase.

Forest F1, which is located in a small valley-bottom drainage area surrounded by maquis vegetation, is interpreted to be an immature stand. In this forest *A. laubenfelsii* is the dominant canopy species and other tree species present are a combination of rainforest and maquis species, all of small d.b.h., with no *N. codonandra* present. More mature forest fragments, F2 and F4, also occur in drainages but are more extensive and have a greater number of larger individuals across all species groups (Fig. 4). The size frequency diagrams for 'other species' in these forests suggest that there is also adequate regeneration and establishment of many of these species.

In the two forest plots containing *N. codonandra* (F3 and F3a), *A. laubenfelsii* is not a major component of the forest, either in terms of basal area or density. Read *et al.* (1995) have studied the population structure of *N. codonandra* at a similar elevation on Mt Dzumac, New Caledonia. They suggest that *N. codonandra* probably established as a dense cohort following a severe disturbance (e.g., fire), but continues to regenerate in large treefall gaps. Current recruitment of *N. codonandra* on Mont Do is (apparently) greater than that of *A. laubenfelsii*, where they co-occur, although in forest F3, there were stems of *A. laubenfelsii* in all size classes up to 50 cm d.b.h. (Fig. 4). *Nothofagus codonandra* shows a regeneration gap in F3 with fewer individuals in the smallest size class than in the next four size classes, suggesting that species other than either *N. codonandra* or *A. laubenfelsii* may eventually dominate this forest in the continued absence of disturbance.

The high density of seedlings and saplings in immature forest stands (e.g., F1) may reflect the ability of *A. laubenfelsii* to recruit quickly in forests disturbed by fire, due to seed input from surviving trees. The low levels of recruitment in more mature forests, at site F3, of both *A. laubenfelsii* and *N. codonandra*, suggests that shading probably inhibits successful regeneration of both species. Individual tree deaths have been observed from cyclone blow-down. In the forests, tree-fall gaps may increase light levels, providing occasional recruitment sites in stands where shading may otherwise preclude regeneration. In a possible analogue, Veblen (1982) found that *Araucaria araucana* and *Nothofagus* spp. were regenerating in forest gaps in Chilean forest sites that had not been severely disturbed for several hundred years.

Continuous regeneration is typical of shade-tolerant species within closed forest in the absence of disturbance (Veblen & Stewart 1980; Veblen 1992; Ogden & Stewart 1995). Seedlings and saplings of species which are shade-tolerant establish continuously resulting in the eventual replacement of dying canopy trees. On Mont Do, immature, open-canopy forests show evidence of continuous recruitment of *A. laubenfelsii*. In more mature forests with greater shading (F3) continuous regeneration is not occurring, suggesting a successional gradient of sites which are dominated by *Araucaria* through to those dominated by *Nothofagus* and (ultimately) mixed angiosperm species.

The role of fire

The size structure of trees in the study plots, within both maquis and rainforest, suggests a mosaic of developmental stages reflecting a varied disturbance history, including fire and blow-down. Due to the rocky substrate (cuirasse), vegetation cover in the maquis is not continuous and bare ground comprised 25% of the ground surface. As a result, the spread of fire is likely to be patchy, and the intensity of any burn highly variable. Enright and Goldblum (1998) suggest that the association of *Agathis ovata* in New Caledonia with rocky sites, and the presence of fire scars reflect the importance of fire disturbance on the stand structure and persistence of *A. ovata* within maquis.

In this study, the 'gaps' in some of the size classes in maquis plots, suggest that intermittent fires may kill seedlings, saplings and small trees, but that these fires are patchy and not always stand-devastating. A closely related species to *A. laubenfelsii*, *Araucaria montana*, was observed 6 months post-fire and all seedlings and most saplings were destroyed, but the larger of the tree-sized individuals (more than approximately 10 cm d.b.h.) survived.

On Mont Do, maquis plots along ridges had high basal areas and densities of *A. laubenfelsii* relative to other maquis plots, probably as a result of protection from frequent fire due in part to topographic position combined with the rocky substrate. The low proportion of fire scars found on trees in M6 indicates that this plot, located on a flat ridge-top, has been protected from recent fire. Maquis plot M7, with the highest proportion of trees with fire scars, must have been subjected to recent fire, but of a low intensity since there was a high density of stems, including saplings, living.

Many authors caution the use of size–class data without corresponding age–class data (Stewart & Rose 1990; Read *et al.* 1995). In many temperate regions, conifers lay down annual growth rings (Veblen 1986), but in tropical zones the relationship between ring counts and age is difficult to determine (Ash 1983, 1985, 1986). Further study of the growth rings in *A. laubenfelsii* is required before the results from size class analysis can be confirmed with age class data.

Tree ring counts for *A. laubenfelsii* so far, indicate that the maximum age for forest trees may be about 500 years, while in the maquis the maximum age may be approximately 300 years. This, combined with the difference in the proportion of fire scars between the two communities, shows that fire is more prevalent in the maquis than in the forest. Many of the forest patches are in gullies and are protected from fire by a break in slope. Field observations suggest that some areas of Mont Do have been regularly burned and there are entire slopes void of *A. laubenfelsii*. The ridge crests adjacent to these areas have a well developed maquis with high densities of emergent *A. laubenfelsii*.

CONCLUSION

Araucaria laubenfelsii exists as an emergent tree in both maquis and forest communities on Mont Do, New Caledonia. The evidence so far from Mont Do suggests that *A. laubenfelsii* regenerates continuously in both the maquis and immature forest communities, but that maquis communities are more prone to fire. The ability of *A. laubenfelsii* to regenerate continuously in the maquis during periods of no disturbance is clear from the reverse-J shape of the size–class distributions from many of the plots. This continuous regeneration is interrupted by occasional low intensity fires. Forest stands on Mont Do represent a successional gradient from immature sites dominated by *Araucaria*, to more mature sites where *A. laubenfelsii* is less abundant and *N. codonandra* or mixed species dominate.

The establishment, growth, survival and reproduction of approximately 2500 individuals is currently being traced in permanent plots which were established in 1995. Future research will focus on the processes which create and maintain the structure of the maquis–conifer community and the stand dynamics of these conifers within closed forest.

ACKNOWLEDGEMENTS

We gratefully acknowledge the assistance of M. Boulet (Head of the Department of the Environment, Parks and Reserves for the Province Sud, New Caledonia), who provided valuable information on the study site, logistical support and permission to work in the Mont Do Botanical Reserve, J-M. Veillon (ORSTOM) for species identification, J. Danloux (ORSTOM) for precipitation data from Mont Do, ORSTOM for providing logistical support and accommodation, and L. Blaze and METEO-France for providing precipitation and temperature data for several sites in New Caledonia. We would also like to thank David Goldblum and

Bruce Burns for assistance in the field. This study was supported by a Melbourne University Postgraduate Scholarship and a PhD Fieldwork Grant from the Faculty of Arts, University of Melbourne to LSR, and an Australian Research Council grant to NJE.

REFERENCES

Ash J. (1983) Growth rings in *Agathis robusta* and *Araucaria cunninghamii* from Tropical Australia. *Aust. J. Bot.* **31**, 269–75.

Ash J. (1985) Growth rings and longevity of *Agathis vitiensis* (Seemann) Benth. & Hook. f. ex Drake in Fiji. *Aust. J. Bot.* **33**, 81–8.

Ash J. (1986) Growth rings, age and taxonomy of *Dacrydium* (Podocarpaceae) in Fiji. *Aust. J. Bot.* **34**, 197–204.

Bond W. J. (1989) The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biol. J. Linnean Soc.* **36**, 227–49.

Brooks R. R. (1987) *Serpentine and its Vegetation.* Croom Helm, London.

Burns B. R. (1993) Fire-induced dynamics of *Araucaria araucana–Nothofagus antarctica* forest in the southern Andes. *J. Biogeog.* **20**, 669–85.

Ekern P. C. (1964) Direct interception of cloud water on Lanaihale, Hawaii. *Proc. Soil Sci. Soc. Am.* **28**, 419–21.

Enright N. J. (1982) The Araucaria forests of New Guinea. *Monographiae Biologicae.* **42**, 381–99.

Enright N. J. & Goldblum D. (1998) Stand structure of the emergent conifer *Agathis ovata* in forest and maquis, Province Sud, New Caledonia. *J. Biogeography* **25**, 641–8.

Enright N. J. & Odgen J. (1995) The southern conifers—A Synthesis. In: *Ecology of the Southern Conifers* (eds N. J. Enright & R. S. Hill), pp. 271–287. Melbourne University Press, Melbourne.

Farjon A., Page C. N. & Schellevis N. (1993) A preliminary world list of threatened conifer taxa. *Biodiversity Conserv.* **2**, 304–26.

Gauch H. G. J. (1982) *Multivariate Analysis in Community Ecology.* Cambridge University Press, Cambridge.

Jaffré T. (1980) *Étude Écologique du Peuplement Végétal des Sols Dérivés De Roches Ultrabasiques En Nouvelle Calédonie.* Travaux et Documents De L'ORSTOM, N°124. ORSTOM, Paris.

Jaffré T. (1995) Distribution and ecology of the conifers of New Caledonia. In: *Ecology of the Southern Conifers* (eds N. J. Enright & R. S. Hill), pp. 171–196. Melbourne University Press, Melbourne.

Jaffré T., Morat P., Veillon J-M. & MacKee H. S. (1987) Changements dans la végétation de la Nouvelle-Calédonie au cours du Tertiaire: la végétation et la flore des roches ultrabasiques. *Bull. Natural History Museum Paris* **4**, 365–91.

Jaffré T. & Pelletier B. (1992) *Plantes de Nouvelle Calédonie permettant de revegetaliser des sites miniers.* Société Métallurgique le Nickel – SLN, Doniambo.

Kent M. & Coker P. (1992) *Vegetation Description and Analysis: A Practical Approach.* John Wiley & Sons Ltd., Chichester.

Latham M., Quantin P. & Aubert G. (1978) *Études des sols de la Nouvelle-Calédonie.* Office de la Recherche Scientifique et Technique Outre-Mer, Paris.

METEO-France (1994) Climat de Nouvelle Calédonie. METEO-France en Nouvelle Calédonie, Nouméa.

Minchin P. R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**, 89–107.

Minchin P. R. (1991) *DECODA, Database for Ecological COmmunity DAta,* Version 2.04. Australian National University, Canberra.

Mueller-Dombois D. & Ellenberg H. (1974) The Count-Plot Method and Plotless Sampling Techniques. In: *Aims and Methods of Vegetation Ecology* (eds D. Mueller-Dombois & H. Ellenberg), pp. 93–138. John Wiley & Sons, Toronto.

Ogden J. & Stewart G. H. (1995) Community Dynamics of the New Zealand Conifers. In: *Ecology of the Southern Conifers* (eds N. J. Enright & R. S. Hill), pp. 81–119. Melbourne University Press, Melbourne.

Peet R. K., Knox R. G., Case J. S. & Allen R. B. (1988) Putting things in order: the advantages of detrended correspondence analysis. *Am. Nat.* **131**, 924–34.

Read J., Hallam P. & Cherrier J-F. (1995) The anomaly of monodominant tropical rainforests: some preliminary observations in the *Nothofagus*-dominated rainforests of New Caledonia. *J. Trop. Ecol.* **11**, 359–89.

Siegel S. (1956) The Kolmogorov-Smirnov two-sample test. In: *Nonparametric Statistics for the Behavioral Sciences* (ed. S. Siegel), pp. 127–136. McGraw-Hill Kogakusha, Tokyo.

Stewart G. H. & Rose A. B. (1990) The significance of life history strategies in the development history of mixed beech (Nothofagus) forests, New Zealand. *Vegetatio* **87**, 101–14.

Veblen T. T. (1982) Regeneration patterns in *Araucaria araucana* forest in Chile. *J. Biogeog.* **9**, 11–28.

Veblen T. T. (1986) Age and size structure of subalpine forest in the Colorado Front Range. *Bull. Torrey Bot. Club.* **113**, 225–40.

Veblen T. T. (1992) Regeneration dynamics. In: *Plant Succession: Theory and Prediction.* (eds D. C. Glenn-Lewin, R. K. Peet & T. T. Veblen), pp. 152–187. Chapman & Hall, London.

Veblen T. T., Donoso C. Z., Schlegel F. M. & Escobar B. R. (1981) Forest dynamics in south-central Chile. *J. Biogeog.* **8**, 211–47.

Veblen T. T. & Stewart G. H. (1980) Comparison of forest structure and regeneration on Bench and Stewart Islands, New Zealand. *NZ J. Ecol.* **3**, 50–68.

Wartenberg D., Ferson S. & Rohlf F. J. (1987) Putting things in order: a critique of detrended correspondence analysis. *Am. Naturalist* **129**, 434–48.

Zar J. H. (1984) *Biostatistical Analysis.* Prentice-Hall, Englewood Cliffs, NJ.