

Fire and succession in the ultramafic maquis of New Caledonia

S. McCoy^{1,2}, T. Jaffré¹, F. Rigault¹ and J. E. Ash³ ¹Laboratoire de Botanique et d'Ecologie, Centre ORSTOM, BP A5, 98848, Nouméa, New Caledonia, ²Department of Archaeology and Natural History, Research School of Pacific and Asian Studies, Australian National University, Canberra, Australia, 0200 and ³Division of Botany and Zoology, Faculties, Australian National University, Canberra, Australia, 0200

Abstract

Aim This study investigates the role of fire and post fire succession in determining the structure and composition of vegetation on ultramafic iron crust soils.

Location The study was conducted in the Plaines des Lacs region of southern New Caledonia.

Methods A survey was made of eighty-eight sites, recording floristic composition, trunk size-class distributions, regeneration after fire, growth ring counts of *Dacrydium araucarioides* (Podocarpaceae) and historical information on past fires. Floristic data was ordinated using multidimensional scaling and an index of succession based on structural and historical information. A transition matrix model was developed to predict the effect of fire frequency on vegetation composition.

Results The vegetation is undergoing postfire succession from maquis to forest, after about 75 years, and eventually to rainforest. *Gymnostoma deplancheanum* has a key role as an early colonist that produces shade, the bulk of the litter, and forms nitrogen fixing nodules with *Frankia* sp. However, the open canopy of *Gymnostoma* and slow litter decay creates flammable conditions. Though many species resprout from rootstocks, only thirty-nine persist through fires while 114 others colonize at later successional stages, as the litter layer and shade increase. Some early successional species are later excluded but these can persist locally in swamps and on rocky hill tops. Forest and rainforest are less flammable and the matrix model suggests that ignition frequency has a critical role in determining the abundance of maquis or forest.

Main conclusions The vegetation mosaic represents a post fire succession from open maquis to forest. Palynological and charcoal records from late Pleistocene sediments suggest that fire has been a major factor determining the development of maquis vegetation since before the arrival of humans. Recently, frequent fires have converted much of the vegetation to maquis, posing a threat to some forest species and largely eliminating rainforest from iron crust soils.

Keywords

Ultramafic vegetation, *Gymnostoma*, succession, fire, New Caledonia.

INTRODUCTION

Ultramafic rocks are rich in ferro-magnesian minerals, reflecting their plutonic origin. They outcrop as raised segments of ocean crust, and only constitute a very small proportion of the earth's land surface (Brooks, 1987). Soils formed on ultramafics possess several unusual characteristics: initially there are high concentrations of elements such as magnesium, manganese and

nickel which are later leached and may accumulate at depth in the profile. The remaining soil matrix is largely composed of relatively inert ferric and chromic oxides. These soils can present a number of problems for plant growth due to deficiencies in phosphorus, potassium, and nitrogen (Jaffré, 1980; Brooks, 1987). In addition, calcium deficiency and toxic levels of magnesium in these soils create an unfavourable Ca:Mg ratio which may lead to poor calcium assimilation (Jaffré,

1980). Plants native to ultramafics tend to be slow growing and of small stature (Proctor & Woodell, 1975; Baker & Brooks, 1989). Some ultramafic species accumulate heavy metals and have been the focus of ecophysiological studies into heavy metal tolerance (Jaffré *et al.*, 1976; Lee *et al.*, 1977; Brooks, 1987; Baker & Walker, 1990). However, mine revegetation research has suggested that nutrient deficiency is the critical limitation for plant growth by ultramafic tolerant species (Jaffré, 1976; Hill, 1977; Jaffré *et al.*, 1994c; Jaffré *et al.*, 1997).

Vegetation on ultramafics tends to have a distinct species composition which is rich in local endemics and lacks species from adjacent substrates (Proctor & Woodell, 1975; Brooks, 1987). In many parts of the world the ultramafic flora is poor in species (Brooks, 1987) but on the subtropical Pacific island of New Caledonia it is species rich and the vegetation ranges from stunted maquis (low sclerophyllous shrubland) (Viro, 1956; Jaffré, 1980) to structurally complex rainforest (Jaffré, 1980; Jaffré & Veillon, 1990; Jaffré *et al.*, 1994a). New Caledonia was separated from Eastern Gondwanaland by ocean-floor spreading in the late-Cretaceous (Paris, 1981; Kroenke, 1996), and the early Tertiary flora and vegetation was probably similar to that described in tropical Australia (Walker & Singh, 1981; Cristophel, 1994; Hill, 1994; MacPhail *et al.*, 1994). The ultramafic flora evolved following the placement of an extensive peridotite sheet in the Eocene (Paris, 1981). Ultramafic massifs, which cover 5500 km² of the main island (Jaffré, 1980), were subject to extensive uplifting and faulting which has generated a variety of climates and soils at altitudes from sea level to 1618 m a.s.l. This varied habitat supported infra-generic radiation in families such as Araucariaceae, Myrtaceae, Epacridaceae, Cunoniaceae and Sapotaceae, while other families, e.g. Poaceae, are virtually excluded from ultramafics (Morat *et al.*, 1986; Jaffré *et al.*, 1987).

Ultramafic maquis vegetation found in lowland regions of New Caledonia (< 250 m a.s.l.) is often associated with ferritic soil (Latham *et al.*, 1978). This soil type is characterized by a 1–5 m deep blocky iron crust surface (cuirasse), Fig. 1, composed of porous conglomerates of ironstone and gravel which contains >70% ferro-chromic oxides (Guillon & Trescases, 1972; Latham *et al.*, 1978). These soils were formed through prolonged solution weathering in broad valleys, and have created a series of rocky undulating plateaus of 20–50 m relief with pseudo-karst sink holes forming swamps and shallow lake basins. (Guillon & Trescases, 1972; Guillon, 1975; Latham, 1986; Bourdon & Podwojewski, 1988). Iron crust soils cover ≈70 km² of the southern massif of New Caledonia

Iron crust vegetation ranges from an open maquis of scattered small shrubs to continuous tall maquis (maquis paraforestier) (Fig. 2) and forest. *Gymnostoma deplancheanum* (Miquel) L. Johnson (Casuarinaceae) is a characteristic component of the maquis. Patches of *Arillastrum gummiferum* Pancher ex Baillon (Myrtaceae) forest occur on rocky mounds, along valley foot slopes, and as an abundant emergent tree, together with *Nothofagus* spp. (Read *et al.*, 1995; Read & Hope, 1996), in rainforest patches found in adjoining valleys (Jaffré, 1980; Papineau, 1989). Swamplands and surrounding peridotite hill slopes typically support sedge dominated

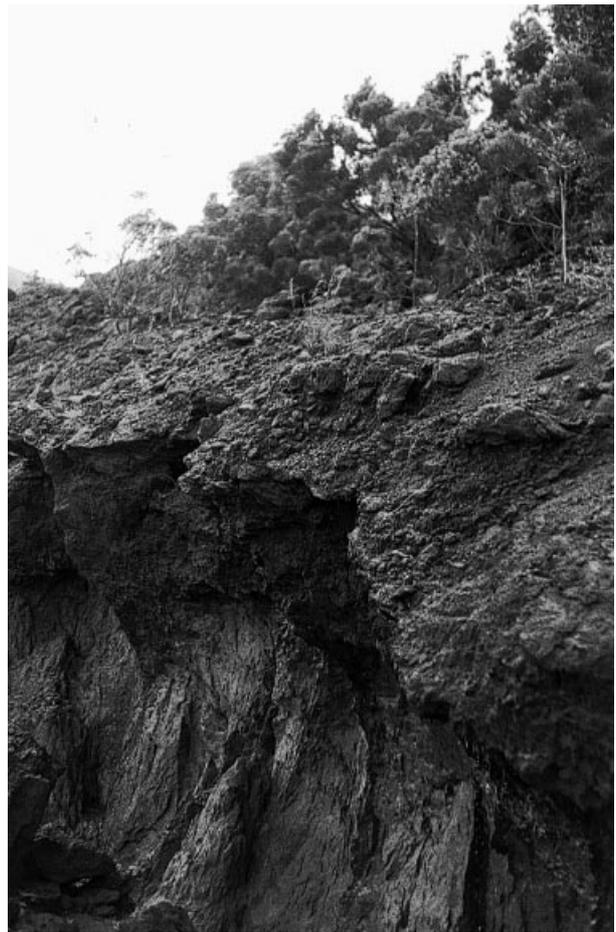


Figure 1 View of a ferritic soil profile at Goro Plateau showing a 3-m deep iron crust overlying a deep clay horizon. The vegetation is open maquis.

shrublands (Jaffré, 1980; Jaffré *et al.*, 1994a). Jaffré (1980) suggested that vegetation on iron crust substrates represents a postfire succession from open low maquis to tall closed maquis and forest, leading eventually to rainforest.

This paper examines the floristics and structure of vegetation found on iron crust substrates and the effects of fires. Firstly, does the vegetation primarily represent succession following fire rather than a response to local substrate or climate variation? Secondly, what processes are controlling vegetation development after fire: species persistence, dispersal or vegetation induced environmental change? Thirdly, are the species fire tolerant, suggesting a long association and adaptations to cope with fire? Fourthly, are maquis species intolerant of closed canopy rainforest conditions which might exclude them in the prolonged absence of fire? Lastly, how does the frequency of fire affect the overall composition of the vegetation?

STUDY AREA AND METHODS

This paper focuses on vegetation occurring on iron crust soils at low altitudes in southern New Caledonia (Long,



Figure 2 View of 25-year-old open maquis on iron crust dominated by *Gymnostoma deplancheanum* at Creek Pernod.

165°4′–167°0′ E; Lat. 22°10′–22°20′ S), Fig. 3. The climate is oceanic with air temperatures fluctuating by only about 6 °C seasonally and 6 °C daily, around an annual average of 25 °C. However, iron crust surface temperatures often exceed 50 °C under full sunshine. Annual rainfall in the region varies from 2000 mm in the south-west to 3500 mm on mountains in the north-east, with a relatively dry season from August to November (Danloux, 1987). Seasonal variation is sufficient to induce regular fluctuations in plant growth, such as growth rings, and permit fires during the dry season.

Eighty-eight study sites were selected at accessible localities in five regions (Yaté Lake, Creek Pernod, Goro Plateau, Port Boisé and Prony) across the study area so as to sample the range of vegetation. All sites were located on low relief iron crust or gravel substrates, avoiding swamps and water courses. Certain forest types have a restricted geographical distribution (Jaffré *et al.*, 1987) so it was not possible to impose a survey design in which all the types were sampled in all regions. Preliminary sampling revealed that variability in composition and species diversity varied with the vegetation type, so the number of sites and their area was varied as follows: thirty-five sites of 100 m² in open maquis, twenty-three sites of 196 m² in tall maquis and thirty sites of 256 m² in forest. Due to the absence of large rainforest patches on iron crust, six sites of 500 m² in rainforest were sampled in neighbouring valleys on eroded ferritic soil. An additional three rainforest sites described by Jaffré & Veillon (1990) and Read *et al.* (1995) are included. Records were made at each site of: altitude (m), slope (degrees), soil type (cover of surface iron crust *v.* gravel, %), annual rainfall (mm), vegetation cover (%), canopy height (m), canopy cover (%), litter cover (%), average litter depth (mean of five observations), years since last fire (from historical records, see below). The Braun-Blanquet cover classification (Kent & Coker,

1992) was used to record the abundance of each species. Species were identified at the ORSTOM herbarium (Nouméa).

The fire history of sites was assessed from various sources, notably C. Attiti and M. Boulet (pers. comm.), Heckel (1892, 1913), Chevalier (1996) and contemporary newspaper reports. However, the exact boundaries of past fires are rarely known. More precise but sporadic fire histories are available from air photographs and tree growth rings. Growth rings were examined in finely sanded trunk sections of *Dacrydium araucarioides* Brongniart (Podocarpaceae) from various sites, and were sufficiently well defined and regular to suggest that they were of annual frequency (Fig. 4). Annual rings are apparent in most conifers at similar latitudes and with seasonal climates elsewhere in the S. W. Pacific (Ash, 1985, 1986). Since *Dacrydium araucarioides* is generally killed by fire, growth ring counts indicate the minimum time since a fire, excluding the time for establishment and early growth to the height at which trunks were cut (30–50 cm). Growth rings (characterized by abundant large vessels) were examined in several *Arillastrum*, some of which possessed fire scars.

Statistical analysis focused on maquis and forest, and the rainforest sites are examined independently to determine whether maquis species are present. Species found in less than three sites were eliminated, as rare species unduly modify similarity coefficients (Belbin, 1989). The Bray-Curtis dissimilarity measure was calculated from species abundance, between sites which was then ordinated by hybrid multidimensional scaling (MDS), using the PATN program (Belbin, 1989). Environmental and vegetation parameters were correlated with MDS scores using multiple linear regression. A second ordination was made using principal components analysis (PCA) of correlation coefficients between estimated time since the last fire, vegetation cover, canopy height and litter

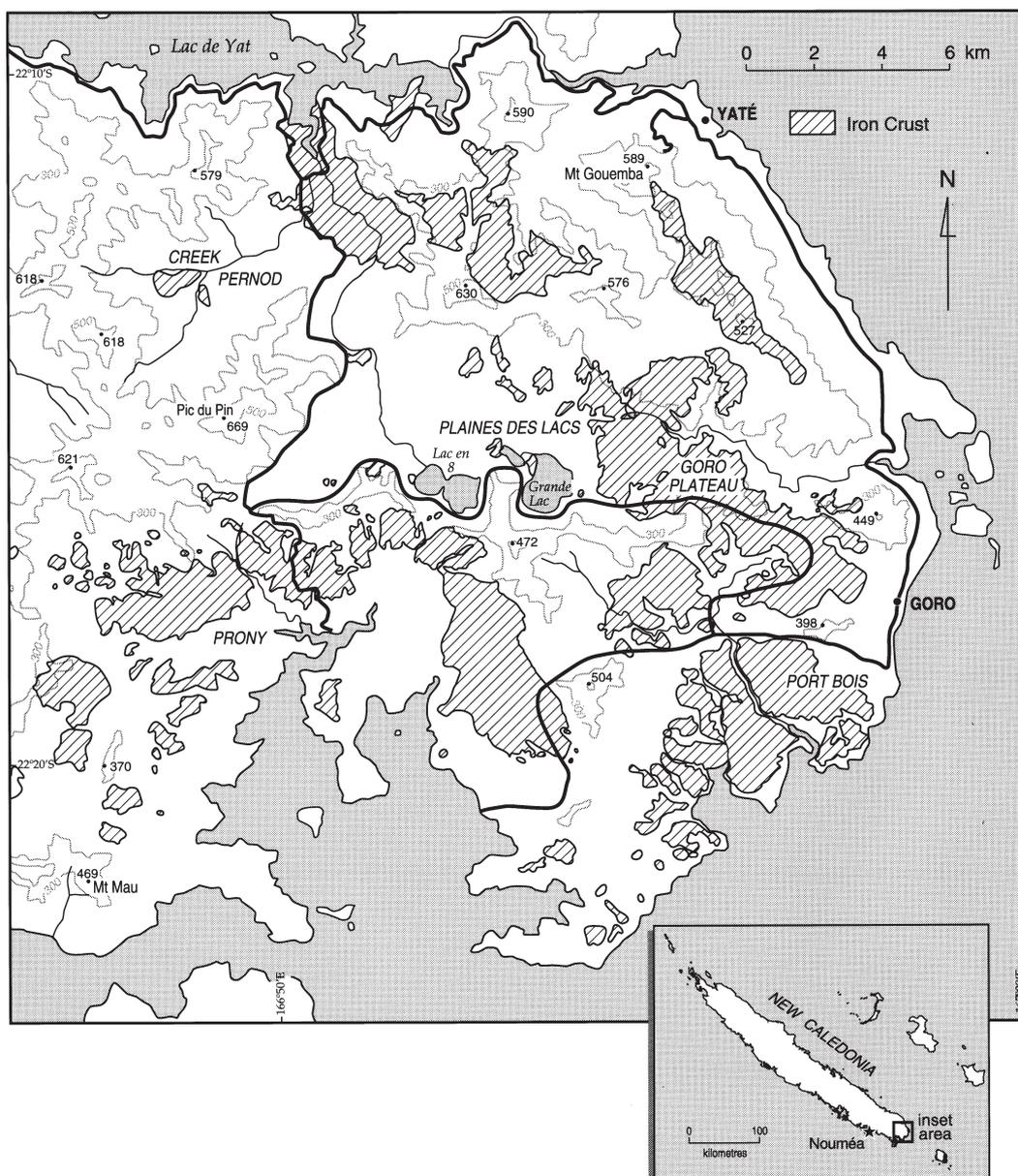


Figure 3 (i) Inset map shows the location of the study area. (ii) Main map shows the distribution of iron crust soils (adapted from Trescases & Guillon, 1977) and the survey regions.

cover. This ordination yielded a first eigenvector accounting for 80.3% of the total variation, and the vector showed a high correlation with the estimated time since the last fire ($r^2 = 0.80$). This suggests that the vegetation structure is reflecting successional change, and the PCA site scores on axis 1 were interpreted as succession index. The index was preferred to using the estimated time since the last fire since age estimates were not always considered reliable, and the index also included information on the development of the vegetation. A constant (3.63) was added to the succession index such that it ranged up from a minimum of one. Species were then ordinated according to a species index (I) calculated as the mean of the

product of their abundance and the succession index (SI) at each site where they were present. A low species index (I) value indicates that species are most abundant early in the successional sequence, a high value indicates the opposite, while intermediate values indicate an intermediate or a uniform pattern. Multiple linear regression was used to examine the effect of environmental factors on the succession index.

The size class structure of woody plant stems (> 2 cm d.b.h.) was measured in selected plots in what appeared to be typical stands. Greater size suggests an older population, and when accompanied by a paucity in small size classes suggests a decline in regeneration. Such patterns can suggest that succession is

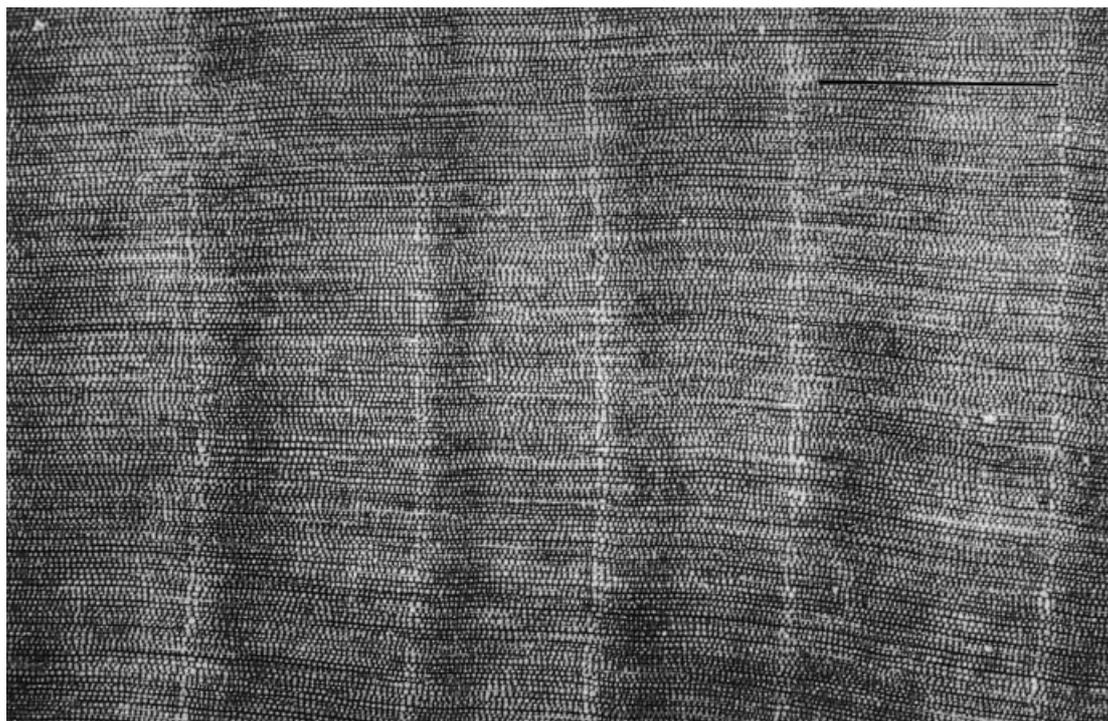


Figure 4 Transverse section of *Dacrydium araucarioides* wood showing growth rings. Scale bar is 1 mm.

occurring. Plots were located on iron crust soils in open maquis and tall maquis near Creek Pernod, and forest on the Goro Plateau. Sub-plots were used for recording smaller trunks: 20 × 25 m for 2–4.9 cm d.b.h., 25 × 30 m for 5–9.9 cm d.b.h., and 25 × 50 m for larger trees. Multiple-stems were recorded individually. Two 50 × 50 m plots were located in a footslope rainforest near the Goro Plateau.

Fire tolerance was assessed in two ways, firstly by noting which species regenerated following recent fires, and secondly by noting the presence of certain traits which can confer fire tolerance. These traits were: resprouting from rootstock, thick trunk bark, protected epicormic buds, seed held in woody capsules or cones which open after fire (bradyspory: Gill, 1981; Lamont *et al.*, 1991).

At each site an index of the susceptibility of the vegetation to fire, F_s , was calculated, based on parameters identified in Cheney (1981) as,

$$F_s = a L_d C e^{-b m}$$

where a and b are constants ($a \approx 50$, $b \approx 22$);

L_d = mean litter depth, cm;

C = connectance of fuel,

$$= 2.77 L_c^2 \text{ if } L_c < 0.6 \text{ and } 1.0 \text{ if } L_c > 0.6;$$

L_c = litter cover as a proportion of ground cover;

m = wet weight of litter as a proportion of dry weight.

Litter moisture was recorded 7–10 days after the last rain.

Light intensity was measured with a PAR quantum sensor, and midday 20 minute dark adapted photoinhibition (Fv/Fm) of selected plants with a Plant Efficiency Analyser (Hansatech, Kings Lynn) at a number of sites.

RESULTS

Figure 5 shows the structural characteristics of the vegetation plotted against the succession index. Tree canopy cover, canopy height, litter cover and litter depth all increase, with a transition from bare to fully covered sites. Shading increased across this sequence with midday understorey PAR light levels declining to about 10–25% of unshaded values in the tall maquis and 5–10% in the forest, and 2–8% in rainforest. Severe photoinhibition was noted in many seedlings (< 50 cm height) growing on unshaded iron crust, with midday dark adapted Fv/Fm of 0.4–0.7. In contrast, seedlings of shaded sites were generally not strongly affected (Fv/Fm > 0.7).

The floristic survey of iron crust sites recorded 269 species of which 100 were excluded from further analysis because they occurred on less than three sites. A further fifty species only occurred in the rainforest sites. Ordination of species abundance using MDS required four dimensions to reach a Kruskal stress value of 0.19, the minimum considered adequate to summarise the pattern. Multiple linear regression of each environmental factor (as dependent variable) simultaneously on the four MDS axis scores revealed significant strong correlations with the succession index ($r^2=0.80$), and weaker relationships with altitude ($r^2=0.19$), rainfall ($r^2=0.14$), and slope ($r^2=0.07$) (Table 1). A MANOVA test for the effect of regions on MDS axis scores was significant, largely due to differences in the Goro Plateau sites on MDS axis 4 (Hotelling-Lawley test, $F_{12,239} = 4.95$, $P < 0.0001$). Multiple linear regression analysis of the succession index showed a significant effect of region ($F =$

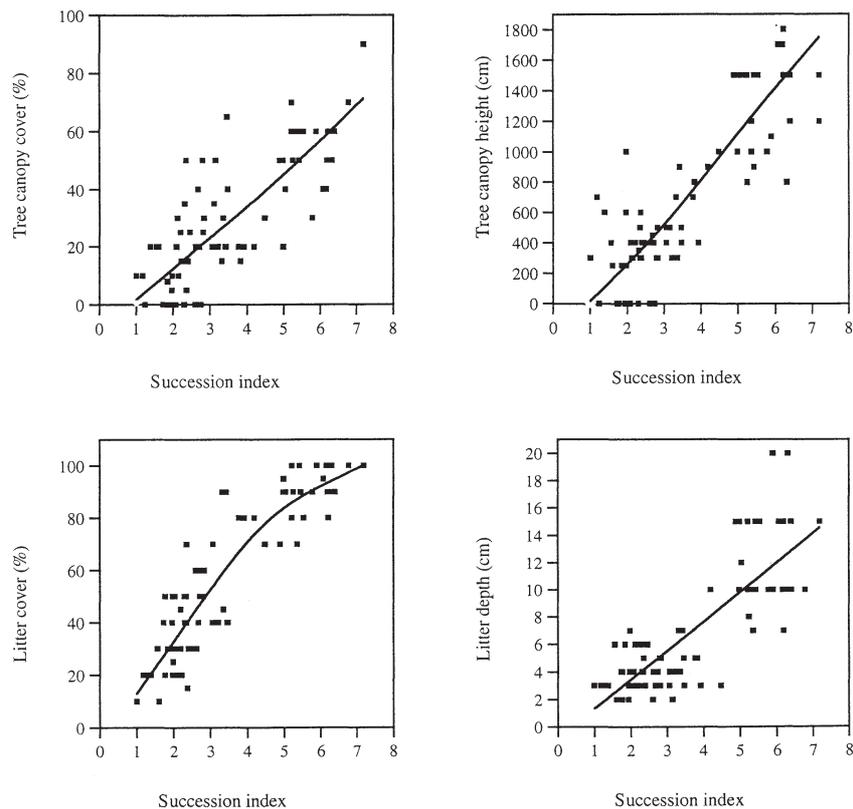


Figure 5 Tree canopy cover, tree height, litter cover and litter depth in the eighty-eight sites plotted against the succession index. Trends are shown by fitted spline curves.

Table 1 Multiple linear regression analysis of environmental factors in relation to the four MDS axis scores, fitted simultaneously, showing r^2 and F ratios.

Environmental factors	r^2	MDS 1	MDS 2	MDS 3	MDS 4
Succession index	0.80	8.45**	26.78***	0.09 ns	222.17***
Vegetation cover	0.48	0.53 ns	11.94**	0.097 ns	49.15***
Canopy height	0.55	7.3**	15.0***	0.60 ns	52.53***
Litter depth	0.62	7.32**	3.97*	0.62 ns	102.9***
Litter cover	0.71	6.2*	10.74*	0.26 ns	148.08***
Altitude	0.19	1.18 ns	1.34 ns	11.8**	10.91*
Annual rainfall	0.14	3.9 ns	1.76 ns	10.41*	2.20 ns
Slope	0.07	6.97**	0.003 ns	0.001 ns	2.50 ns

Significance is indicated, $P > 0.05$ = ns; $P < 0.05$ = *; $P < 0.01$ = **; $P < 0.001$ = ***.

6.45, $P < 0.0001$) and slope ($F = 6.47$, $P = 0.01$), however, the slope effect was dependent on two unusually steep sites with forest. The strong relationship between MDS scores and the succession index suggests that most of the variation in species composition is due to succession, though there are confounding effects of region and slope, while the remaining 20% of the variation is partly due to region, rainfall and altitude.

Figure 6 shows the successional ranking of sites (by SI) and species (by I). It is apparent that species presence shows considerable variation between successive sites but overall most species show clear trends in occurrence, and may be grouped into four categories (Fig. 6). Figure 7 shows the total number of species in each category in relation to rank order of sites by

the succession index. There is an early successional group of 26 species which are initially abundant but absent later. A second group of twenty-nine persistent species are present from start to finish while the third and fourth groups of fifty-nine and fifty-six species are only present from the middle and late stages.

Stem size class distributions for each vegetation type are shown in Fig. 8 and distribution for selected species are shown in Fig. 9. Overall, there is an increase in the maximum size of trunks from open maquis to rainforest. Species in the early succession group show an increase in size coupled with a decline in the frequency of smaller classes suggesting a decline in regeneration in the forest stages. Multi-stemmed open maquis



Figure 6 caption on following page

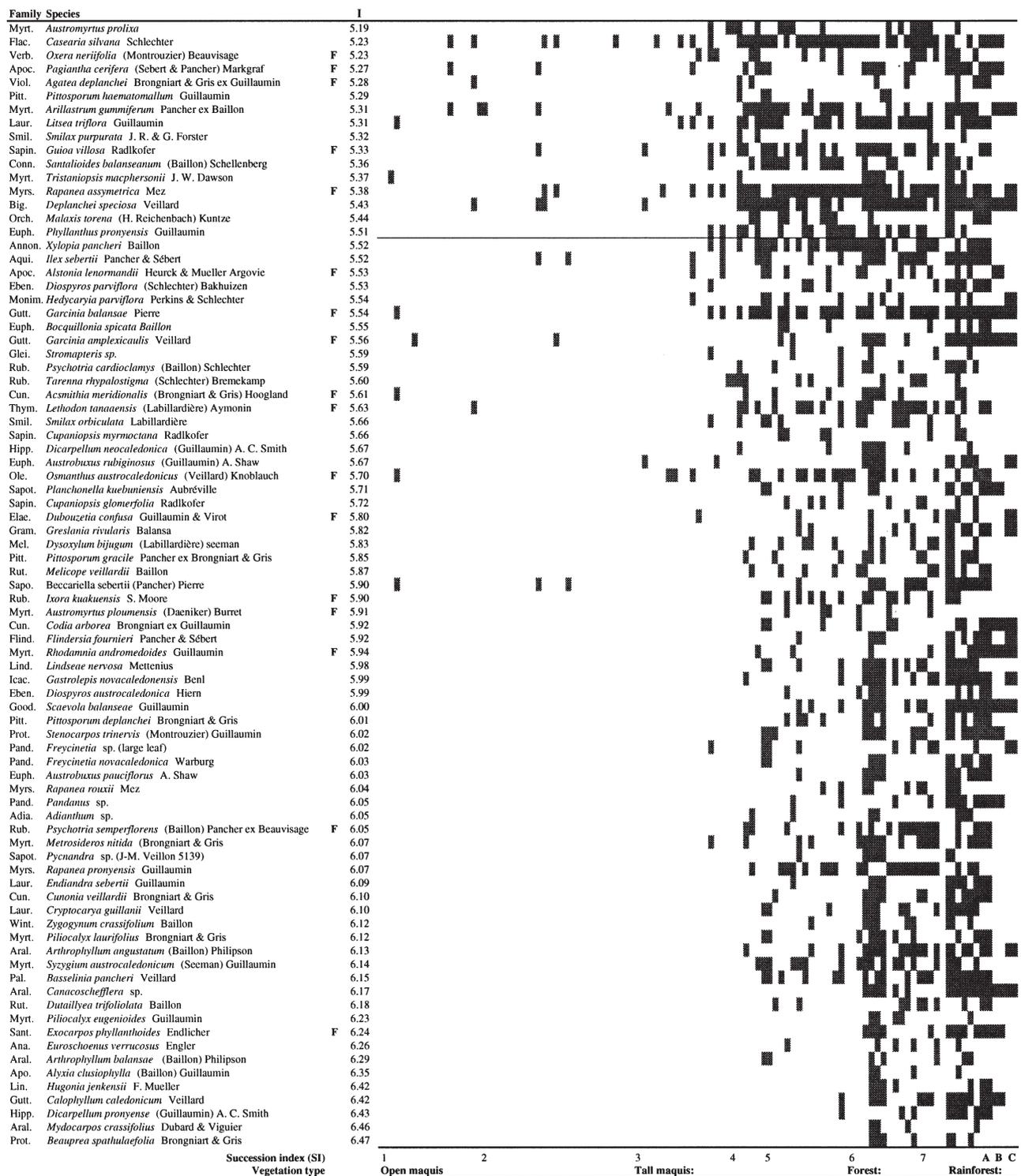


Figure 6 Presence of species (shaded) in the eighty-eight sites ranked by the succession index (SI). Species are ranked by the species index (I). Horizontal lines indicate the boundaries between early, persistent, mid-late and late successional groups of species. F indicates vegetative resprouters from rootstocks. Rainforest sites are placed last and include sites at (A) Pic du Pin (0.75 ha) and (B) Col de Yaté (0.9 ha) (Read *et al.*, 1995), and (C) at Rivière Bleue on slopes (2.79 ha) (Jaffré & Veillon, 1990).

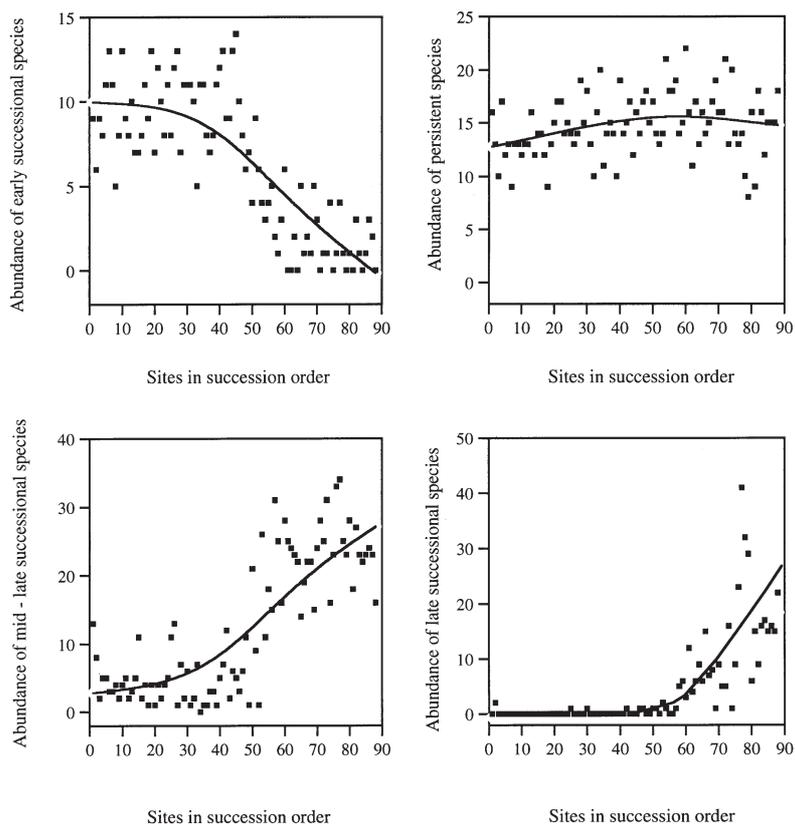


Figure 7 The number of early successional, persistent, mid-late succession and late successional species in relation to rank order of sites by the succession index. Trends are shown by fitted spline curves.

species such as *Montrouziera sphaeroidea*, *Tristaniopsis guillainii* var. *balansae* and *T. callobuxus* exhibit a notable decline in regeneration. This decline coincides with increases in *Gymnostoma* trunk diameter and stem density from open maquis (1000 stems ha⁻¹) to tall maquis (2800 stems ha⁻¹). Under this continuous canopy, species such as *Ilex sebertii*, *Myodocarpus fraxinifolius*, *Garcinia neglecta*, *Xylopia pancheri*, *Styphelia* sp. *cymbulae* first appear as small diameter class trees and then increase in abundance and in trunk size in forest. *Gymnostoma* is rare in rainforest and is replaced as the dominant species by emergent *Arillastrum gummiferum*.

Growth rings in *Dacrydium araucarioides* sections collected from a site which was completely cleared of vegetation in 1970 (C. Tessarolo, personal communication), had seventeen to twenty-one growth rings by 1996 suggesting that there is a delay of 5–9 years before a tree might be used to indicate the age of the site. Samples from the survey sites suggest that it takes about 55 years to reach the tall maquis phase and 75 years to reach the forest stage. These ages for maquis stands are consistent with reports of extensive fires early this century. Growth rings in *Arillastrum gummiferum* typically had a width of 3–6 mm suggesting that a tree takes 30–50 years to reach the canopy, and perhaps 100–170 years to reach 1 m d.b.h.

Seventy percent of species present at the early succession stage have the ability to resprout from rootstocks after fire,

while only 45% of mid and late successional species resprout, and this does not appear to confer fire tolerance. Some later successional trees, such as *Arillastrum* had one or more fire scars suggesting some tolerance of fire, however, there are many locations where forests have been killed by fire (Fig. 10). Isolated stands of mature *Arillastrum* in forest and tall maquis suggests that the species may have been more widespread (Papineau, 1989), apparently an increase in the fire frequency has restricted it to fire protected valleys.

Dispersal of most (66%) early successional species is by wind. Many of these species (e.g. *Gymnostoma*, *Codia*, *Grevillea* and *Tristaniopsis*) produce abundant seed during the wet season, and are often the first to colonize burnt maquis after dry season ground fires. Most (59%) later successional species rely more on vertebrate (primarily bird and bat, and perhaps geckkonid lizards: Bauer & Sadlier, in press) dispersal, and the vectors may not visit early successional vegetation. However, some common forest and rainforest species are wind dispersed (e.g. *Alstonia*, *Nothofagus*, *Metrosideros*, *Arillastrum*) and may have limited dispersal distances.

The fire susceptibility index, *F_s* (Fig. 11) is highly variable in early successional sites (25–40-year-old), reflecting the variability in litter cover combined with low moisture content, whereas the index declined in late successional forest sites which had a continuous but moister litter layer. This suggests

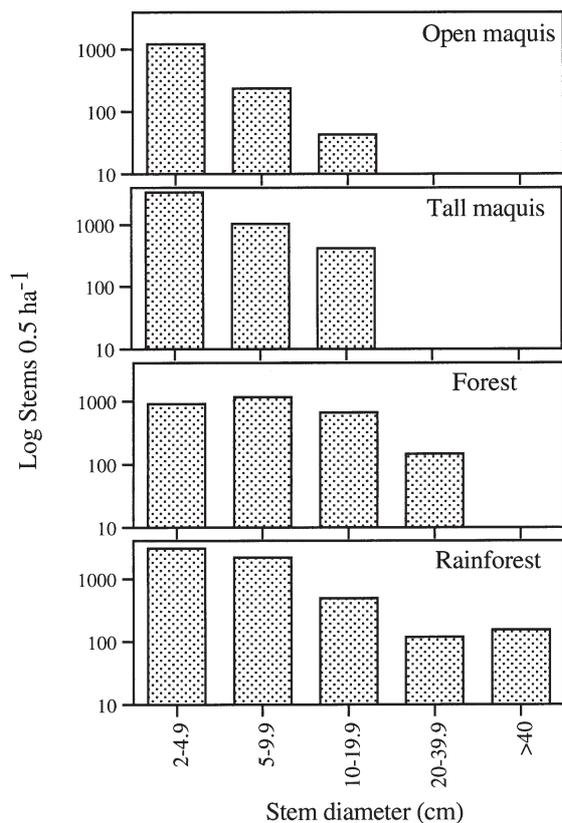


Figure 8 Size class distribution (d.b.h.) for all stems in open maquis, tall maquis, forest and rainforest.

that early mid successional vegetation is more flammable but fire spread is likely to be limited by bare ground. At later stages, fires may be more extensive but limited to drier periods.

Based on the pattern of fire susceptibility index estimates for maquis (20–70-year-old) and forest (70–120-year-old), Fig. 11, and the lower flammability noted for earlier successional and forest sites, a flammability index was constructed to indicate the probability that vegetation of various successional stages would burn if ignited (Fig. 12). Decadal transition matrices were then derived from the product of the flammability index and a selected decadal probability of ignition. Starting from burned vegetation, the frequency of successional stages was calculated after 1000 years under each ignition regime, when the distribution was reaching a stable state. Figure 13 was derived by grouping the resulting age classes as maquis (0–70 years), forest (71–250 years) and rainforest (> 250 years). At a low probability of ignition rainforest dominates, but this proportion declines until at a probability > 0.6 (i.e. a fire expected every 17 years) virtually all forest is replaced by maquis.

DISCUSSION

Successional patterns and processes

Both the structural and floristic results suggest that much variation in the vegetation on iron crust substrates is in response

to past fires. The transition from low open maquis to tall closed maquis and forest appears to be successional, in accordance with Jaffré (1980). This conclusion is supported by several lines of evidence, the reported age of the vegetation since the last fire, ages inferred from growth rings of *D. araucarioides*, the demographic trends in population structures and the changing floristic composition of sites.

The MDS ordination of floristic data was strongly related to the derived succession index, and only about 20% of the variation was unexplained. Some of this unexplained variation was correlated with environmental factors, notably rainfall, though this was confounded with regional variation. The Yaté Lake region was dominated by early successional vegetation, while the Goro Plateau was dominated by forest. The association of some forest stands with rocky knolls is thought to result from reduced flammability. Since rainforest was not recorded on the iron crust substrate it cannot be definitely placed as a late stage of the succession though this seems possible given enough time without fire.

From floristic records, suites of species can be identified as (i) early resprouters which either (a) persist or (b) die out of later forest stages; and (ii) species only present from closed maquis, forest, or rainforest stages. Trunk size-class distributions of common species indicate that the floristic changes are associated with population changes indicative of succession. Based on historical sources and tree growth rings, the time scale for these changes appears to be about 40–75 years to reach the closed maquis phase, 75–100 years to reach the forest stage, and, possibly, > 250 years to reach a rainforest stage (assuming 100 years for rainforest colonists to invade a forest and reach canopy height).

The succession appears to be facilitative (Connell & Slatyer, 1977; Noble & Slatyer, 1981) with primary colonization of the bare iron crust surface by a restricted suite of species. Iron crust is a harsh environment with extreme temperatures and very little penetrable soil, except in crevices. Seedlings which do establish often show signs of severe photoinhibition until they exceed a height of about 0.5 m. Sources of early successional maquis species include both resprouters (from prior maquis) and some soil seed bank species which might persist in rock crevices (e.g. *Alphitonia*).

Gymnostoma is generally the most abundant of the early colonist species and appears to have a dominant influence on the succession, possibly due to its nitrogen fixing *Frankia* association (Jaffré *et al.*, 1994b) which may contribute to its relatively rapid establishment such that it forms a nearly pure but open canopy 2–5 m in height after 40–70 years. *Gymnostoma* cladodes produces a persistent litter which decays slowly to form an organic soil horizon. Most colonization by later successional species is restricted to litter. The *Gymnostoma* canopy permits about 10–25% light penetration which may facilitate the establishment of a variety of late successional species, possibly by shielding them from deleterious photoinhibitory processes.

Eventually broad-leaved forest trees such as *Arillastrum* may colonize and, when these reach the canopy, reduce light levels to about 2–10% in the understorey. This apparently suppresses regeneration by most of the primary colonists including

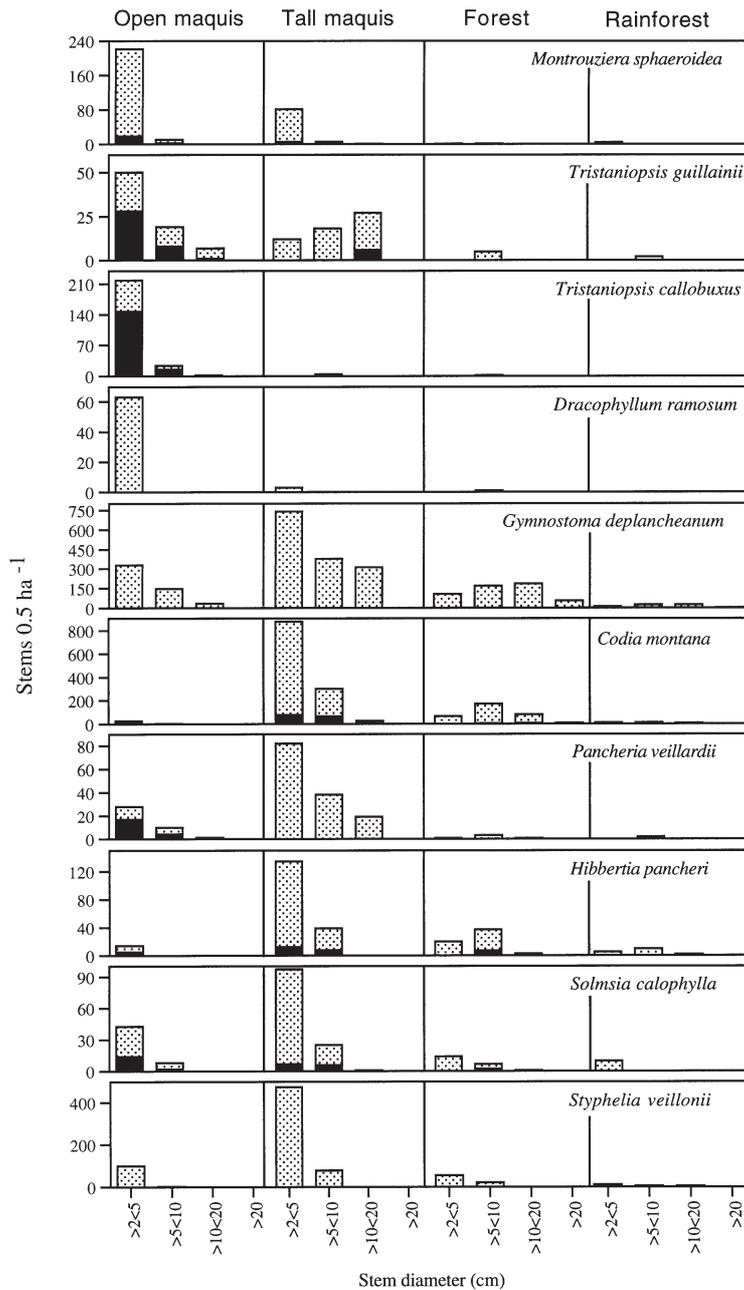


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Gymnostoma. These forest stands are invaded by rainforest species, though no stands which had reached a rainforest dominated canopy were observed on the iron crust. Sources of later successional species are limited to the localized forest and rainforest stands and this may be constraining succession. Rainforest stands are typically several kilometres from the iron crust forest sites.

Vegetation flammability and fire frequency

In addition to its facilitative effects on succession, *Gymnostoma* has a major impact on flammability. Firstly, the persistent litter

forms a deep fuel bed and, secondly, the open canopy allows this fuel to dry relatively rapidly during rain-free periods. Connectance between patches of litter around individual trees is critical for fire spread at early successional stages. It may take several decades for some rocky sites to be colonized and support fires due to the patchiness of the fuel. Fires are most likely to spread at the mid-successional tall maquis stages where fuel is abundant, continuous and relatively dry. Conversely, a fire is likely to be suppressed beneath stands of broadleaved forest trees casting deep shade and maintaining higher fuel moisture.

The observed frequency of maquis (95%) and forest (5%),

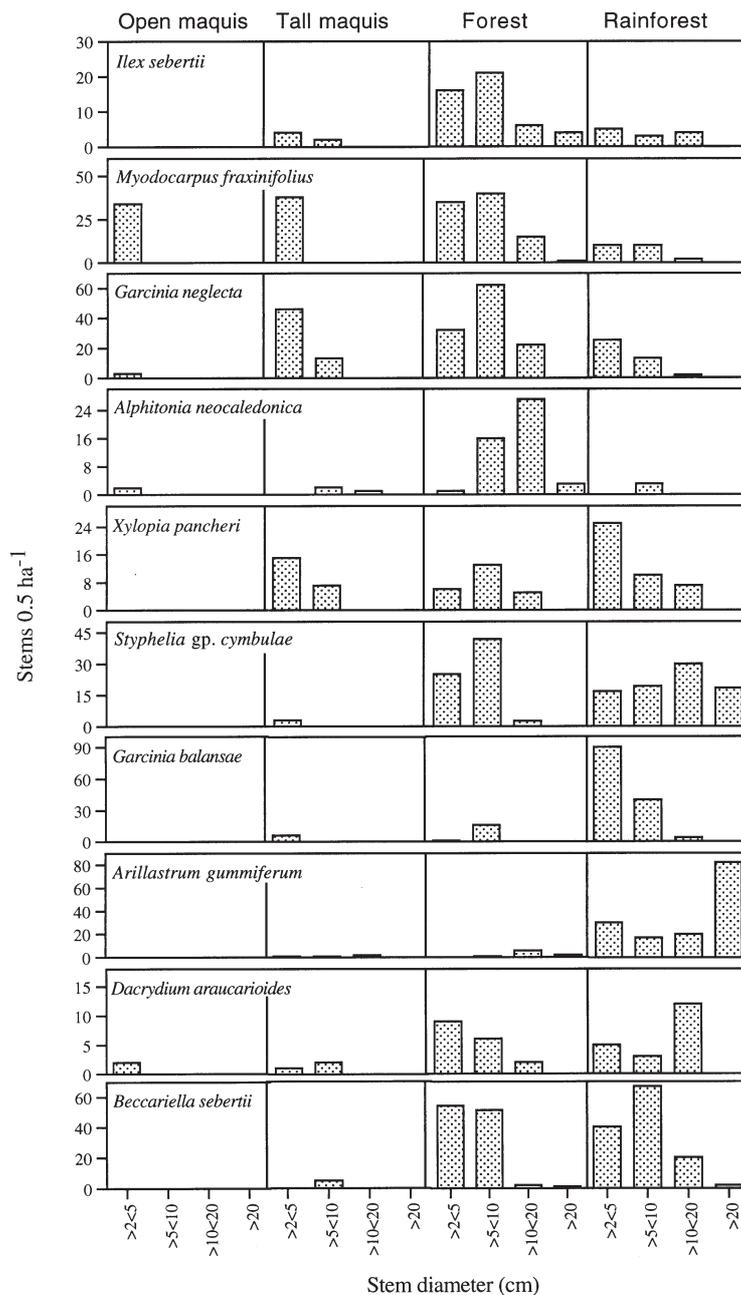


Figure 9 Size class distributions (d.b.h.) for stems of select species in open maquis, tall maquis, forest, and rainforest. Black bars represent total number of stems treating multistems as single stems.

and the absence of rainforest on iron crust sites, may be compared with the values predicted from the transition matrix model (Fig. 13). The model suggests that with a ignition probability of 0.5, the vegetation would be about 95% maquis, 3% forest and 2% rainforest. The forest component may be underestimated, and rainforest over-estimated if there was an underestimate of the time for rainforest to develop or the flammability of rainforest was underestimated. While the model may be imprecise in detail, the overall implications are robust.

(i) Ignition probabilities of $<0.1 \text{ decade}^{-1}$ could maintain a maquis component in predominantly rainforest vegetation. (ii) A shift of ignition probability from about 0.1–0.4 would radically change the vegetation composition from predominantly rainforest to predominantly maquis. (iii) At a high fire frequency (prob. $>0.6 \text{ decade}^{-1}$) all forest is likely to be excluded. The composition of iron crust vegetation is likely to be critically dependent on ignition frequency and is likely to shift disproportionately as the frequency changes. Stands of



Figure 10 View of maquis on the Goro Plateau showing dead emergent *Arillastrum gummiferum* killed by fire.

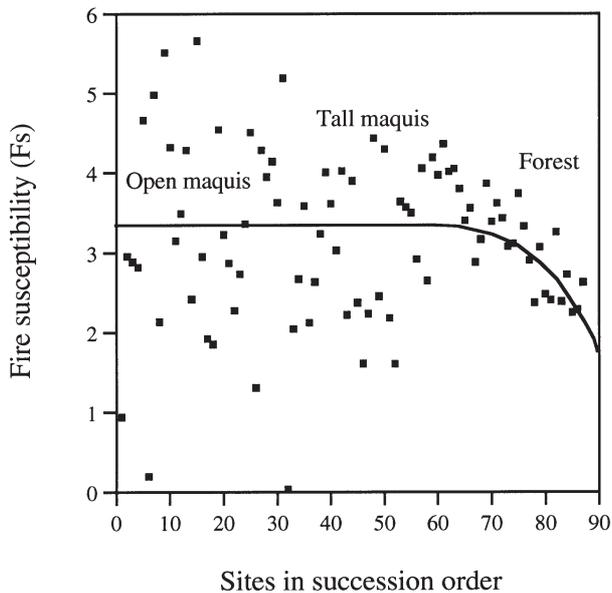


Figure 11 Fire susceptibility of sites in rank order of the succession index. Vegetation types are indicated and the trend is shown. Note that the youngest sites were burned about 25 years previously and that variation in susceptibility decreases as succession proceeds.

large fire scarred or killed, *Arillastrum* within live *Gymnostoma* dominated maquis suggests that *Gymnostoma* may have recently spread following destruction of forest by fire (Jaffré, 1980; Papineau, 1989). There are no equivalent areas of tall

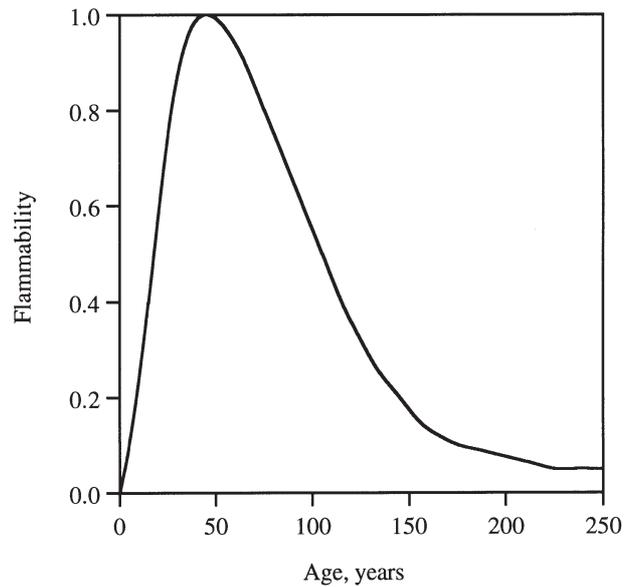


Figure 12 The relative flammability of different successional ages of vegetation used in the transition matrix models.

maquis progressing to this forest stage, and live forest stands are infrequent. Thus, the current vegetation appears to reflect an increased ignition frequency and much is maquis entering the phase of maximum flammability. These results are relevant to an understanding of both vegetation history and future management.

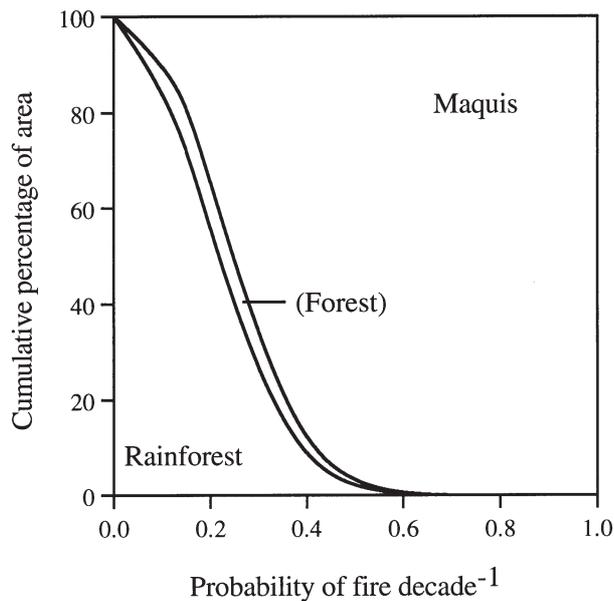


Figure 13 Composition of vegetation in relation to decadal ignition probability predicted using a transition matrix model over a 1000-year period starting from burned sites.

Vegetation history and adaptation to fire

Several swamps and lakes in the region have yielded records of fossil pollen and charcoal from which vegetation history has been reconstructed for the Late Pleistocene (20,000–40,000 BP: Hope, 1996; Hope & Paske, 1998). These suggest that there were alternating episodes of *Gymnostoma* dominated maquis, associated with charcoal, and rainforest dominated by *Nothofagus*. Such episodes may reflect shifts in the frequency of dry periods and ignition by lightning. These records do not indicate to what extent either fire tolerant maquis species or rainforest species were ever excluded from the area. They do suggest, however, that given a prolonged absence of fire, rainforest can develop on the iron crust soils.

Fire has evidently been a factor shaping the vegetation before human arrival and may have influenced the evolution of the flora. The maquis flora contains many species (70%) which regenerate from rootstocks, a common attribute in fire adapted shrubs but one which is not exclusive to fire tolerance. A number of species (5%) with similar rootstocks were only recorded from mid-late successional stages, and may not be fire tolerant. Resprouting of these forest species may occur in response to damage, such as from cyclones. Other fire adaptations, such as thick bark and epicormic regrowth (Gill, 1981) were not recorded. However, several species possess woody fruits which may protect seed from fire (e.g. *Grevillea*, *Tristaniopsis*), though the protection may not be sufficient for these to be classified as bradysporous. Some early successional fire tolerant genera, e.g. *Baeckea*, *Grevillea*, *Hibbertia*, *Lepidosperma* and *Lomandra* are also found in Australian heathlands (Fox & Fox, 1986; Whelan, 1995), suggesting that fire tolerance may be ancestral and reflect conditions in Late Cretaceous Gondwanaland. Alternatively, fire tolerance may be

an outcome of adaptations to low nutrient soils independently generating an open flammable vegetation in both Australian heaths and New Caledonian maquis (Morat *et al.*, 1986; Jaffré *et al.*, 1987). In comparison with the many highly fire adapted heath species in Australia (Fox & Fox, 1986), the New Caledonian maquis has few examples of strong fire adaptation, though, the maquis contains a core of fire tolerant species (Morat *et al.*, 1986).

The palynological record suggests that rainforest dominated for some periods which raises questions about the persistence of early successional species. Fifty maquis species were not recorded in the rainforest sites. Some early colonists such as *Pteridium*, *Montrouzieria*, *Xanthostemon*, *Homalium* and *Grevillea* also occur in swamps (Jaffré, 1980) where they might persist during fire free periods. Thus, it may not be necessary to invoke a fires to explain the maintenance of early successional species.

Vegetation clearance for cultivation by Late-Holocene Melanesian settlers was restricted to nonultramafic areas due to the poor quality of ultramafic substrates for cultivation (Avias, 1953; Barrau, 1956). Even though ultramafics were not settled, increases in ignition frequency presumably shifted the vegetation towards its current dominance by maquis. Since the 1870s, vegetation in southern New Caledonia has been affected by frequent fires and disturbance associated with prospecting, mining and logging of forest trees (principally *Agathis lanceolata* Lindley ex. Warb and *Arillastrum gummiiferum*) (Heckel, 1892, 1913; Dugain, 1952; Jaffré, 1980; Chevalier, 1996). Fire frequencies probably reached a peak between 1910 and 1960 when wood burning steam trains were in use in the region (Chevalier, 1996), and there were extensive fires in 1914 and 1971 (J-M, Veillon, pers. comm.).

Fire management and conservation

Fire management is evidently a central issue for controlling the structure and floristic composition of the maquis and forest types. In particular, a high fire frequency is likely to prevent the development of later forest stages and threaten the survival of riverbank vegetation which now supports a large proportion of the fire sensitive species. Several rare endemic gymnosperms such as *Dacrydium guillauminii* J. Buchholz (Podocarpaceae), *Neocallitropsis pancheri* (Carrière) Laubenfels (Cupressaceae) and *Retrophyllum minor* Carrière (Podocarpaceae) are restricted to a few fire protected sites (Jaffré, 1995).

Though the iron crust soils are too rocky and infertile to be of interest for agriculture, they provided sources of iron ore (and were mined for this in the 1950s), and currently, more valuable sources of cobalt and nickel beneath the iron crust. Much of the region has been prospected and parts are the focus of open-cut mining. Revegetation of the mine waste and the iron crust overburden, may proceed along a successional path as outlined in this paper, however, attention must also focus on fire management or the succession may be curtailed at the early maquis stage. In particular, fire breaks in appropriate locations may allow stands to pass through the highly flammable maquis phase. Without such care, the unique endemic flora and fauna may be threatened.

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