The dynamics of *Gymnostoma* maquis on ultramafic soils in New Caledonia

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Declaration

The research presented in this thesis is my original and independent work. Specific contributions by others are referred to in the text and acknowledgments.

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Abstract

Ultramafics cover extensive areas of New Caledonia and present a variety of unique nutritional and metal toxicity problems for plant growth. The flora of these substrates is highly diverse and occurs as vegetation types ranging from a low sclerophyllous maquis (heath) to rainforest. These substrates have been the focus of intensive nickel mining over the last century and are often devoid of vegetation for several decades. This lack of plant establishment is a major environmental concern in New Caledonia and has been the focus of revegetation research. The genus *Gymnostoma* has received particular attention because of its nitrogen fixing association with *Frankia* and dominance in vegetation types which might be interpreted as a reflecting successional progression after fire. An understanding of the mechanisms surrounding these successional patterns might assist in solving practical issues of mine site revegetation with native species.

This thesis set out to firstly determine whether vegetation types containing *Gymnostoma* are successional communities, secondly to examine certain key processes which appear to be driving vegetation patterns, and thirdly, to identify the role of *Gymnostoma* in ultramafic vegetation. Key processes associated with vegetation were examined experimentally to determine their influence on plant growth on a range of ultramafic substrates.

Field surveys examining vegetation patterns and processes were carried out on three ultramafic soil types supporting *Gymnostoma* vegetation: iron crust oxisol, eroded oxisol and hypermagnesian soil. These three soil types have distinct chemical and physical properties which may affect plant growth. Floristic records from each soil type were firstly examined using MDS to determine floristic associations and subsequently with a successional index constructed from a PCA ordination of vegetation structure. The successional indices explained much of the variation on MDS axes which suggested that ultramafic vegetation patterns primarily reflects a post-fire succession. Fire records, annual growth rings of fire sensitive *Dacrydium araucarioides* and demographic trends in species composition also support a post-fire succession pattern. The succession pattern was found to be composed of an early successional group of maquis

species which either (i) decline or (ii) persist, and (iii) a late successional group of forest species. Another important pattern revealed in surveys is that early ultramafic successional stages progress more slowly than tropical vegetation on other soil types. More importantly, certain processes appear to be critical at early successional stages and predetermine later successional development.

Surveys of abandoned mine sites set out to determine what processes appear to be influencing plant establishment at early successional stages. The evidence implies that most species are dispersal limited and show an abrupt decline in abundance away from adjacent vegetation. Primary colonist establishment is more abundant on crevice sites which trap seed, and seedlings show higher rates of survival in such areas. The primary colonists eventually generate a micro-environment providing shade and litter which supports all of the subsequent colonisation of bare ground. Shade and litter levels were regarded as important factors driving succession on ultramafics and their effects at both the community and plant level were examined.

Measures of light regimes in successional vegetation indicated that light (PAR) declined with the development of vegetation cover over time. These changes in incident solar radiation effect the community composition depending on species light requirements for photosynthesis. Chlorophyll fluorescence measurements of plants in natural vegetation and in field experiments indicated that seedlings on bare ultramafic soil experienced chronic photoinhibitive stress from a combination of high light and substrate conditions. Seedlings under shade cloth and underneath tree canopies potentially received less light for photosynthesis but exhibited less stress indicative of photoinhibition. Therefore, shade may be crucial for seedling survival at early successional stages. Furthermore, plant species responded to high light conditions depending on their successional status. Maquis species generally overcame photoinhibitive effects of bare ground environments once they attained a certain age. In contrast, forest species continued to exhibit photoinhibitive stress on bare ground environments.

Measures of soil and litter nutrient content indicate that N, P, K and Ca content increased with successional progression. *Gymnostoma* plays a key role in the development of later successional phases by providing a major source of nitrogen through its *Frankia* association. This nitrogen is released along with other nutrients as an abundant litterfall that gradually

increases soil nutrient pools over time through slow decay. Glasshouse experiments indicated that leachates arising from slow cladode decay had no allelopathic effect on plant growth. However, litter build up in late maquis phases physically excluded large seeded species from establishing.

A fire susceptibility index was constructed from litter and vegetation properties of successional vegetation. It indicates that *Gymnostoma* may raise the susceptibility of maquis because its open canopy allows litter beds to remain dry and flammable. However, *Gymnostoma deplancheanum* and *G. chamaecyparis* are able to persist on their respective soil types even at high fire frequencies because rocky terrain reduces fire spread and protects patches of vegetation. In contrast, *G. intermedium* appears to have been excluded from early successional vegetation on eroded oxisol by a continuous cover of woody sedge maquis which is highly flammable. The eventual dominance of broad leafed vegetation at later succession forest stages decreases the fire susceptibility of these communities.

Results of field experiments indicate that slow maquis species growth is primarily due to the low nutrient status of ultramafic soils. Plants which received low doses of fertiliser and/or litter showed a significant positive response in terms of height and relative shoot growth. Fertiliser applications also raised the total *Frankia* nodule weight per plant, indicating that *Frankia* responds positively to slight increases in phosphorus. Contrary to expectation, lime applications had no effect on maquis species shoot growth. Lime additions resulted in fewer *Frankia* nodules and more extensive root systems in *Gymnostoma* seedlings by reducing the availability of other nutrients.

In summary, it is concluded that *Gymnostoma* dominated maquis represents a post-fire succession. Colonisation at early successional stages is dispersal limited and highly dependent upon the availability of crevices. Once pioneer plants have established, litter and shade levels become crucial factors in facilitating further succession. The relative abundance of *Gymnostoma* determines the rate and direction of this successional change.

Key words: *Gymnostoma*, New Caledonia, ultramafics, succession, colonisation, nickel mines, plant growth.

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Chapter 1

New Caledonia

1.1 Introduction

Ultramafic substrates present a variety of peculiar nutritional deficiencies and toxicity problems for plants which have received some attention (Proctor & Woodell, 1975; Jaffré, 1980; Brooks, 1987; Baker *et al*, 1992). However, the dynamics of vegetation on such extreme substrates are poorly known. In New Caledonia, these substrate properties virtually exclude agriculture, minimising human impact, but they provide rich sources of nickel, chromium and iron ores and have been a focus of mining activity (Jaffré *et al*, 1977; Bird *et al*; 1984; Jaffré *et al*, 1994 c; Pelletier & Esterle, 1995; Jaffré *et al*, 1997 b). Mine wastes dating back over a hundred years are still sparsely vegetated indicating the severity of these substrates for plant succession. It is estimated that 800 km^2 of New Caledonia (4% of land area, 14% of ultramafic area) is now covered by mine waste and severely eroded soils which result from associated activities, notably repeated burning of the vegetation.

Lightning induced fires have long been a factor affecting the vegetation (Hope & Pask, 1998). Maquis (heath) is widespread (4400 km^2, 80% of ultramafics) and considered to represent a post-fire succession (Jaffré, 1980). This gave me the notion that a study of successional patterns and processes might assist in solving practical issues of mine site revegetation with native species.

Seeking a native successional route to revegetation seems important as natives may be well adapted for establishment across the large areas of degraded land. More importantly, much of the area has long been long-abandoned and those mines are no longer generating revenue which can be allocated to more intensive revegetation projects. Currently (1998) it costs between A$ 50,000 to A$ 100,000 ha^{-1} to revegetate mine waste in New Caledonia - thus the cost of revegetation for the entire degraded area could be A$ 8,000,000,000. Evidently there are both economic and as well as scientific benefits to be made from understanding the dynamics of the ultramafic maquis. Accordingly, this thesis pursues two avenues of investigation (i) describing and analysing the successional processes in the ultramafic maquis and (ii) a parallel experimental study of mine site revegetation.

This chapter provides a general background introduction to the main components of this study: New Caledonian geology, climate and vegetation, *Gymnostoma* (Casuarinaceae) succession and revegetation. Much of the literature on New Caledonia is only available in French, so this chapter presents much material for the first time in English, assuming that the reader is not familiar with the island.

1.2 Location and geographic setting

New Caledonia is located in the south-west Pacific (latitude: 20-23° S longitude: 164-168° E). The main island Grand Terre, has an area of 16,750 km^2 and the mountain chain which extends along the entire island is largely composed of ultramafics, which constitutes 33% of the island (Jaffré, 1980). Figure 1.1 shows the distribution of ultramafic ranges on the island and the location of the Plaines des Lacs and Kouaoua study areas which are examined in this thesis.

1.3 Geological & climate history

During the mid to late Cretaceous (100-90 m.y. ago), eastern Gondwanaland was subject to northward movement and intense tectonic and magmatic activity which created a mountain chain along a narrow east coastal strip known as the Melanesian arc (Kroenke, 1996). This arc was separated from what became the east coast of Australia by sea-floor spreading 70 m.y. ago, forming the Tasman sea and arc fragments which became New Caledonia and New Zealand (Paris, 1981; Aitchison *et al*, 1995; Kroenke, 1996).

New Caledonia's continued north-east movement was interrupted by collision with the Pacific plate in the late Eocene (38 m.y. ago) (Paris, 1981; Latham, 1986; Kroenke, 1996). This resulted in the gradual upheaval of oceanic lithosphere over much of the island (fig. 1.2). Obduction of this 2000 m thick peridotite sheet coincided with tectonic alpine uplift of the central mountain chain and the intrusion of eruptive gabbro and granodiorite rocks in the Grand Massif du Sud during the Eocene/Oligocene (Paris, 1981).

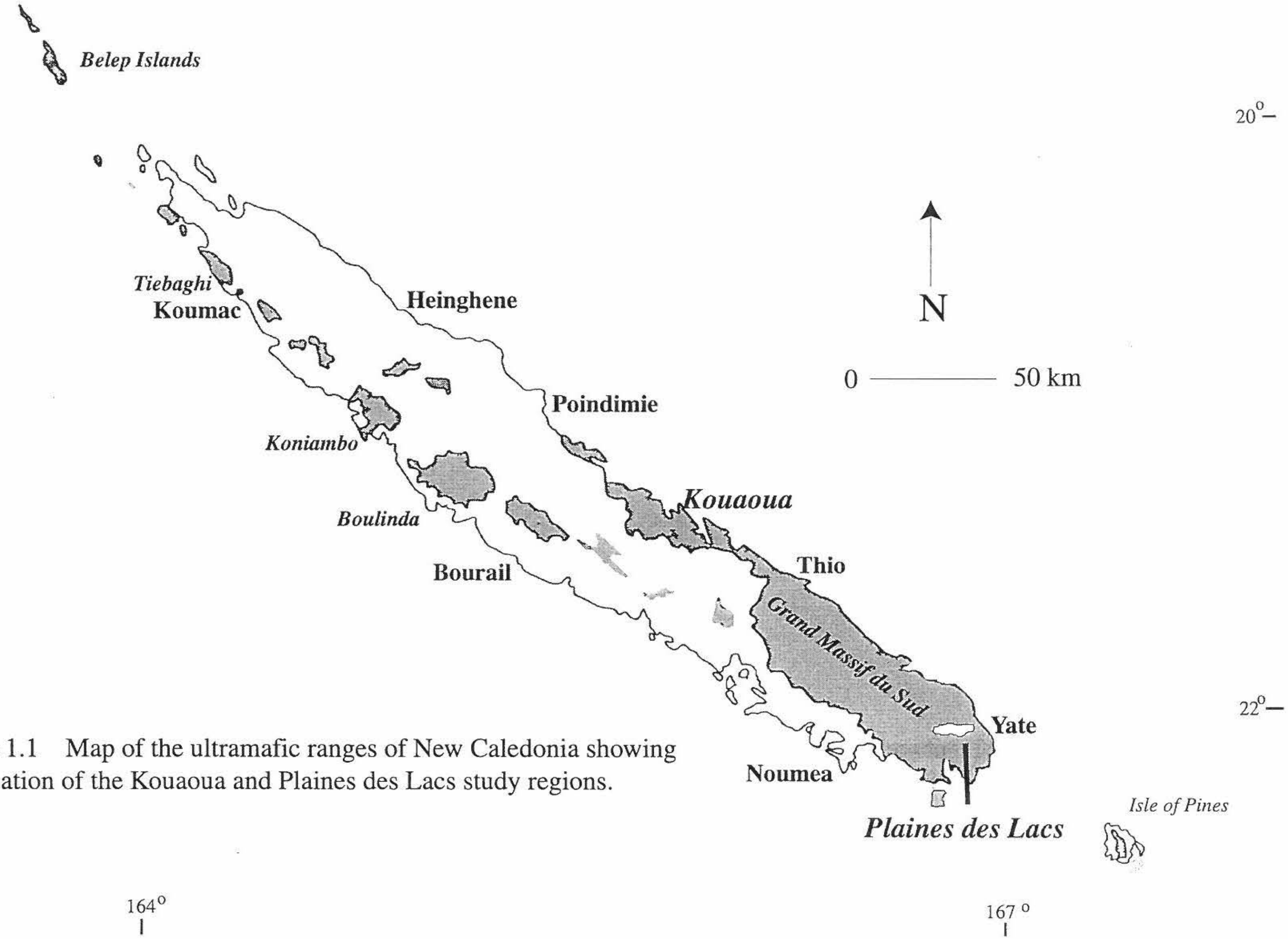
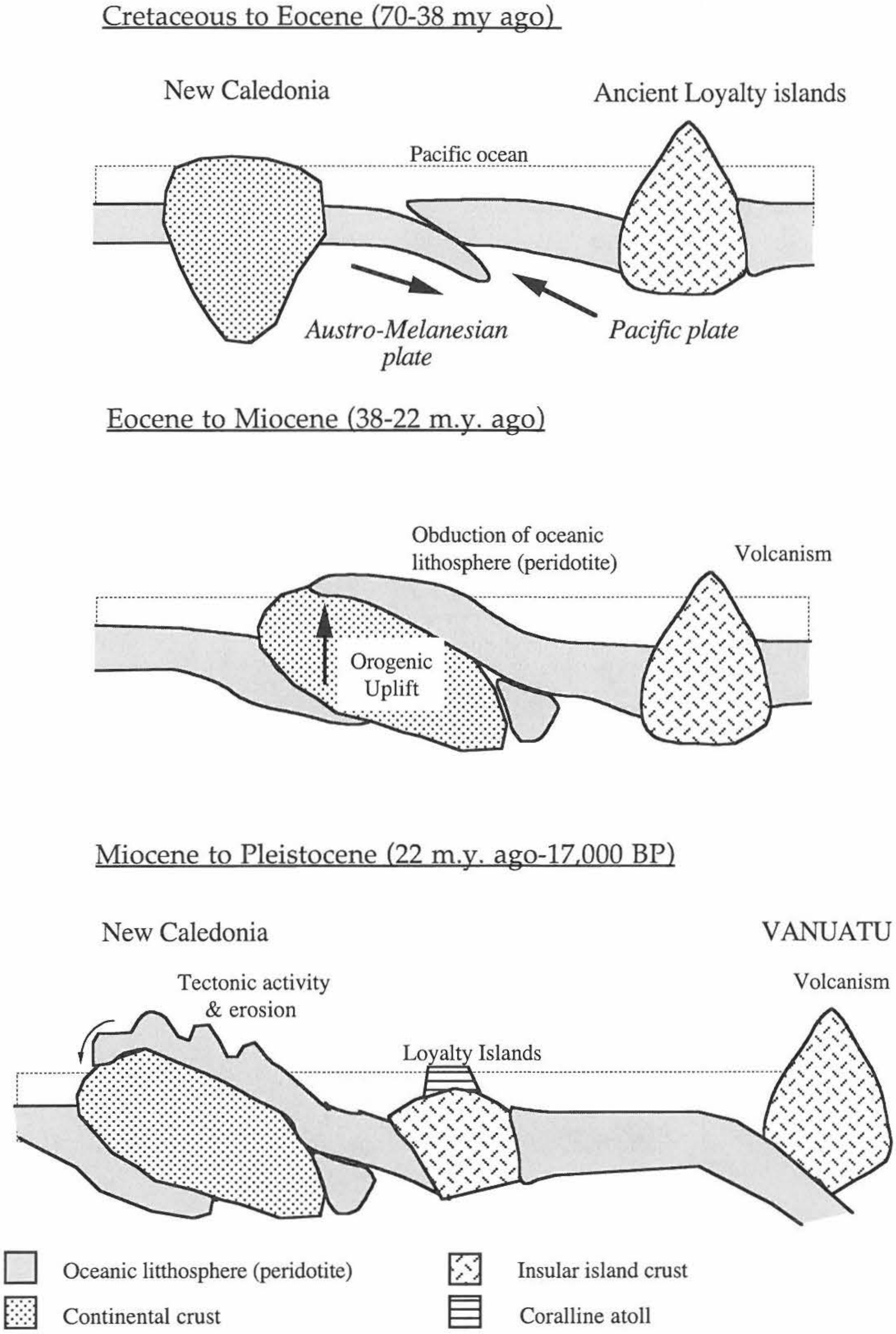


Figure 1.1 Map of the ultramafic ranges of New Caledonia showing the location of the Kouaoua and Plaines des Lacs study regions.



Cretaceous to Eocene (70-38 my ago)

Eocene to Miocene (38-22 m.y. ago)

Miocene to Pleistocene (22 m.y. ago-17,000 BP)

Figure 1.2 Schematic representation of the general geological history of ultramafic ranges in New Caledonia (adapted from Dupont, 1989).

Peridotites at the base of the sheet were transformed into serpentinite by intense metamorphism (Latham, 1986). After the Miocene, there was an episode of peneplanation alternating with orogenic thrusts (Paris, 1981; Aitchison *et al*, 1995).

No direct evidence exists for pre-Quaternary climates in New Caledonia. However, palaeo-ocean temperature estimates from the Lord Howe Island Rise (Murphy & Kennet, 1983) and north-eastern Australia (Feary *et al*, 1991), suggest that the climate of the south-west Pacific since the Eocene oscillated between temperate and sub-tropical conditions, reflecting the northward movement of Gondwanan landmasses and changing ocean currents (Feary *et al*, 1991). A cooler oceanic phase during the Oligocene was associated with the reorganisation of Southern Ocean currents and the onset of the deep Circum-Antarctic Current (Murphy & Kennet, 1983). Oceanic temperatures in the SW Pacific gradually became warmer in the late Oligocene reflecting the northward movement of Gondwanan landmasses (Feary *et al*, 1991).

During the Miocene-Pleistocene period, increasingly hot and humid conditions in the south west Pacific (Feary *et al*, 1991) are believed to have caused erosion of the ultramafic sheet into a series of mountain ranges, the development of deep iron crust profiles on ultramafic plateau areas and the accumulation of nickel deposits at depth (Trescases, 1975; Trescases & Guillon, 1977; Paris, 1981; Latham, 1986). Extensive faulting which occurred throughout the ultramafic ranges during this period accelerated erosion to create deep incised valleys within the ranges and expose serpentinite bands along thrust zones at the base of many of these ranges (Trescases, 1969, 1975; Trescases & Guillon, 1977; Latham, 1986). This increased tectonic activity and accelerated erosion is believed to have also generated much of the landscape within the Plaines des Lacs and Kouaoua study regions (Guillon & Trescases, 1972; Trescases, 1975; Trescases & Guillon, 1977; Guy *et al*, 1979). Fluvio-colluvial iron crust (cuirasse) in the form of boulders, cobbles and gravel were eroded from unstable slopes and deposited in lower reaches creating piedmont formations (Bird *et al*, 1984), and filling sections of valley basins (Trescases, 1975; Trescases, & Guillon, 1977). Latham (1986) suggests that iron crust continued to form in valley depressions from slope material.

The Quaternary was characterised by increasing climate instability (Fontes *et al*, 1976; Coudray, 1976, 1977). A sea level fall of 126 m between 30,000-17,000 BP resulted in the expansion of Grand Terre surface to its present day barrier reef (Coudray, 1977; Cabioch *et al*, 1989). The formation of gypsum and calcium carbonate deposits on the coastal plain and magnesite nodules in valleys neighbouring serpentinite outcrops from 26,900 BP (Podwojewski, 1995) to 17,690 BP (Latham, 1986) suggests increasing aridity during this glacial phase.

Sea level rises in the Holocene peaked at approximately 1.5 m above the present level at 5,500 BP and dropped to its present level by 3,000 to 4,000 BP (Cabioch *et al*, 1989). Rainfall was more abundant during this period in north eastern Australia and New Caledonia (Kershaw, 1975; Bowler *et al*, 1976). According to Podwojewski (1995), increased rainfall and floods of magnesium rich waters from ultramafics led to hydromorphic conditions in the coastal plains which reworked gypsum and calcium carbonate resulting in dolomite deposits 5000 BP.

1.4 Climate

1.4.1 Synoptic patterns in New Caledonia

New Caledonia has a sub-tropical oceanic climate that is influenced by seasonal variation in latitude of the South Pacific Convergence Zone (SPCZ) to the north and the sub-tropical anticyclonic belt in the south (Revell, & Goulter, 1986). The wettest and hottest period of the year occurs between late December and March when the SPCZ is in its most southerly location. Tropical storms and cyclones often occur during this summer period (Hastings, 1990). The northerly return of the SPCZ from April to November allows greater influence of stable anticyclonic conditions and results in a decrease in precipitation. This anticyclonic regime is occasionally interrupted in June-July by storms originating from polar regions which bring intermittent rainfall and cooler conditions. Dry soil conditions are frequent from August to early December, arising from low rainfall and greater evaporation due to the increasing duration of solar radiation (fig. 1.3).

Extended dry periods correlate with the Southern Oscillation/ El Nino phenomena, although the duration and severity of these events is modified by local effects of topography and the influence of south-east trade winds (Morlière & Rebert, 1986). During recent El Nino events (eg: 1972-73, 1991-1993), the precipitation on the west coast was as low as 250-300 mm pa (Morlière & Rebert, 1986; Bouchet *et al*, 1995).

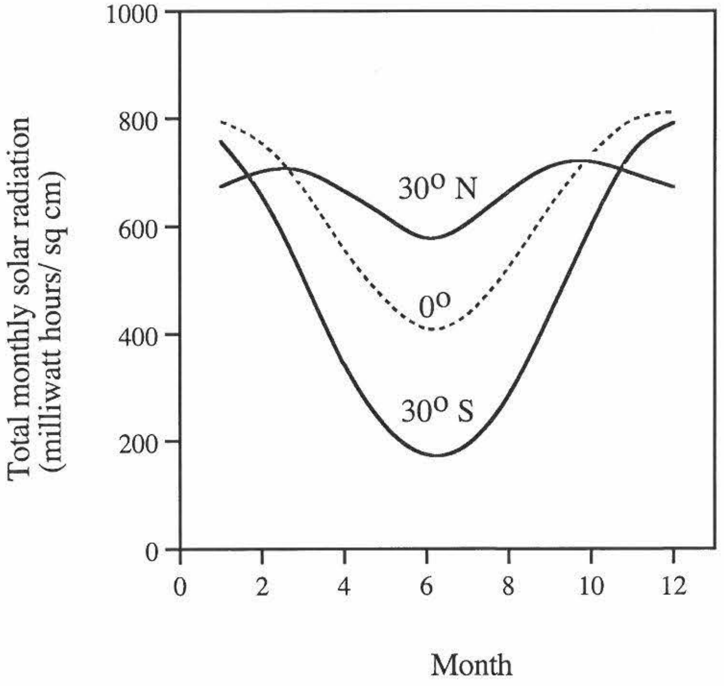


Figure 1.3 Total monthly solar radiation estimated for flat surfaces and 30° slopes on north and south facing aspects at Plaines des Lacs. (200 m a.s.l) using CLOUDY (refer to Fleming, 1986). CLOUDY estimates solar radiation recieved on landforms according to geographic location and slope. Atmospheric dust is qualitatively estimated based on the extent of bare ground sources of dust.

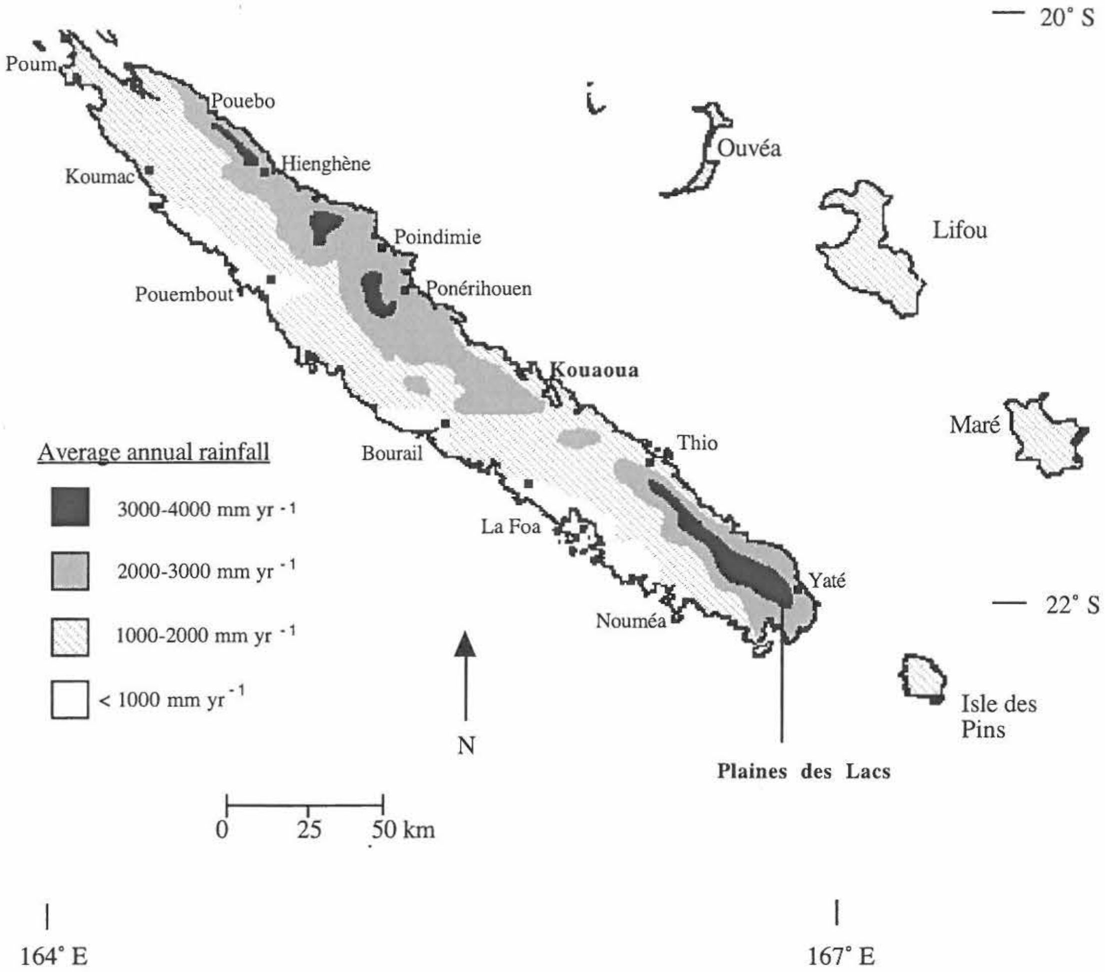


Figure 1.4 Average annual rainfall in New Caledonia (adapted from Renson, 1989).

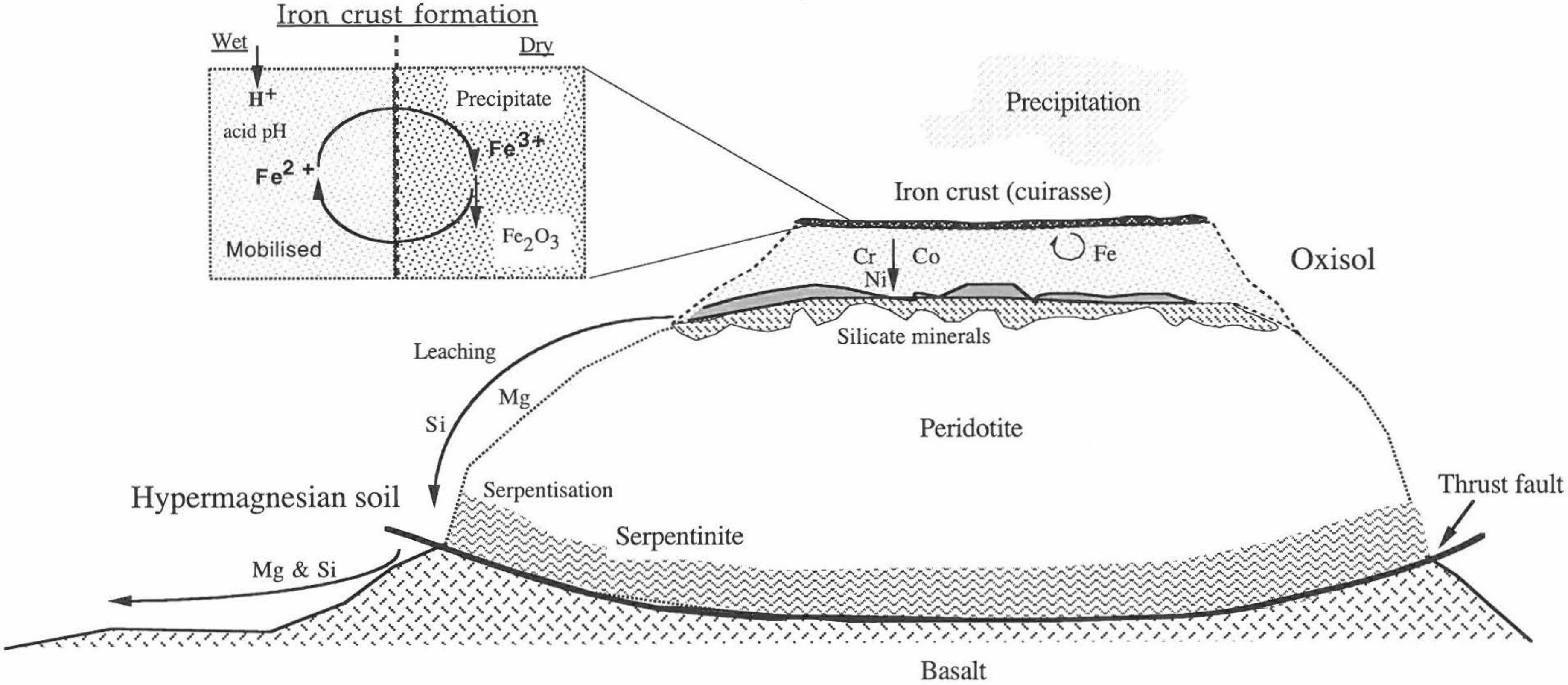


Figure 1.5 Schematic representation of geochemical processes involved in the formation of oxisol and hypermagnesian soil on New Caledonian ultramafic ranges (adapted from Coleman, 1977).

1.4.2 Topographic variations in climate

Climatic patterns in New Caledonia are influenced by the central mountain chain which rises to 1628 m a.s.l. Sea-level air temperatures typically range from 15°C to 32°C (Morlière & Rebert, 1986) and decrease by about 0.57°C for every 100 m increase in elevation (Trescases, 1975). Minimum temperatures of less than 0°C are often recorded above 1000 m a.s.l (Jaffré & Latham, 1974).

Much of the moisture carried by the south-east trade winds is intercepted by the central mountain range which may receive up to 4000 mm yr^{-1} in elevated areas. Cloud and fog are common above 700 m a.s.l. These mountains exert a strong rain shadow effect on west coast regions which often receive less than 1000 mm yr^{-1} (fig. 1.4). The narrow east coast plain receives higher rainfall (2000-3000 mm yr^{-1}) (Danloux, 1987; Renson, 1989).

1.5 Ultramafic soils of New Caledonia

The ultramafic substrates of New Caledonia are represented by two broad soil groups, oxisols (sol ferralitique ferritique) and brown hypermagnesian soils (sol brun hypermagnèsien) (Latham *et al*, 1978). These soil groups are very different in their physical and chemical composition.

1.5.1 Oxisols

On the summits and slopes of mountain ranges, humid weathering processes have led to the development of oxisols through solutional weathering of peridotite (Trescases, 1975; Latham *et al*, 1978; Latham, 1986; fig. 1.5). Magnesium and heavy metal silicates are leached and accumulate as ferrous clays at depths depending on the position of the soil in the landscape (Latham *et al*, 1978; Schwertmann & Latham, 1986; Latham, 1986; Bourdon *et al*, 1997). Surface horizons of the oxisols are largely composed of free draining inert iron oxides (50-75% Fe_2O_3), chromium oxide (3-8% Cr_2O_3) and trace amounts of silica (0.5-1.7% SiO_2)(Schwertmann & Latham, 1986, Latham, 1986). Oxisols tend to be acidic and possess poor exchange capacities, which decrease in lower clayey horizons because of iron smectites (Jaffré, 1980).

In areas of low relief such as the Plaines des Lacs and the summit plateaus of ultramafic mountain ranges, solutional weathering is very advanced and oxisols may attain 20-30 m in depth. Iron rich goethite, hematite and chromite found at deeper parts of the profile may experience abrupt water table changes and become cemented by hydroxides and organic material to form pisolite gravels (Trescases, 1975; Trescases & Guillon, 1977; Latham, 1986). Such conditions over long periods of time lead to the formation of iron crusts which may be several metres deep (Trescases, 1975; Latham; 1986; Bourdon & Podwojewski, 1988). Trescases (1969 a, 1975) suggests that these pedological formations developed under higher rainfall fluctuating environments of the Miocene. Such environments still exist on the summits of ranges and in the Plaines des Lacs swamplands, but the extent of iron crust development in swamps is minor compared to deposits created by erosion events in the past (Trescases, 1975; Guy *et al*, 1979; Bourdon & Podwojewski, 1988).

Eroded oxisol (sol ferralitique ferritique erodé; Latham *et al*, 1978) on mountain slopes are typically shallow and may contain peridotite which has either been exposed through erosion or deposited as erosion debris (Latham *et al*, 1978; Jaffré, 1980). Gravel A horizons are often very shallow or absent, and the underlying soil surface is composed of B and C horizon ferrous clay containing higher levels of heavy metals such as nickel, cobalt and manganese (Jaffré, 1980; Latham, 1986; Bourdon *et al*, 1997; Becquer *et al*, 1995).

1.5.2 Brown hypermagnesian soil

Brown hypermagnesian soils on serpentinite or serpentinized peridotite are often found along the thrust zone, or fault lines occurring at the base of mountain ranges. Soluble magnesium silicates which are leached from the upper reaches of the peridotite range, precipitate under dry conditions and form magnesium and iron rich smectite clay minerals such as magnesium carbonate; gioberitite (Trescases, 1975, Jaffré, 1980). Under wet conditions magnesium continues its movement into valleys leaving silica accumulations along ruptures (veins, sills) in the parent rock (Latham, 1986). This active solutional movement of elements causes serpentinite to be very friable and on steep slopes, brown hypermagnesian soil is often very shallow and interrupted by weathered serpentine outcrops (Latham, 1986). Deeper soils (< 50 cm) at the base of foot slopes possess better moisture retention properties due to the accumulation of altered clay minerals such as montmorillonite (Latham *et al*, 1978, Jaffré, 1980). The cation exchange capacity of these soils is very high due to the abundance of magnesium, and they tend also to possess a higher pH than oxisols (Jaffré, 1980).

1.6 Vegetation in New Caledonia

1.6.1 Floristic diversity

New Caledonia is renowned for its highly diverse and endemic flora. This arises from New Caledonias' isolation, varied ultramafic geology and topography which have generated a range of climates and substrates suitable for speciation (Virot; 1956; Jaffré, 1980; Jaffré *et al*, 1987; Morat, 1993; Morat *et al*, 1994; Jaffré *et al* 1997 a).

The native phanerogamic flora of the archipelago has 3,088 species belonging to 788 genera and 165 families. This native flora is highly endemic at the species level (79%), but less so at the generic level 14% and family level 2.6% (Morat, 1993; Morat *et al*, 1994) (table 1.1). Much of the species endemism results from radiation within New Caledonia rather than simple divergence from species known elsewhere. Such radiation is particularly evident in the Myrtaceae, Cunoniaceae, Proteaceae, Pittosporaceae, Rubiaceae, Euphorbiaceae, Dilleniaceae and Araucariaceae (Morat *et al*, 1986 a; Jaffré *et al*, 1987; Morat *et al*, 1994). Despite covering only 33% of New Caledonia, ultramafics support 60% of the total native flora of the island archipelago (Jaffré, 1996).

1.6.2 Origins of the flora

According to Morat *et al* (1986 a, b), 70% of non-endemic genera in New Caledonia are also found in either Australia or New Guinea. This reflects New Caledonia's ancestral association with eastern Gondwanaland. Many New Caledonian genera were present in Cretaceous Gondwanaland and have been recorded as fossils in Australia (Macphail *et al*, 1994; Cristophel, 1994). New Caledonia's late Cretaceous isolation may explain the absence of characteristic Australian taxa such as phyllodinous *Acacia*, *Banksia* and *Eucalyptus* (Morat *et al*, 1986 b) which are believed to have arisen later in the Tertiary (Walker & Singh, 1981).

The emplacement of ultramafics over New Caledonia during the Eocene is believed to have been gradual and resulted in forest taxa

Table 1.1: The number of native and endemic species found in vegetation types of New Caledonia, and the approximate surface area (km^2) occupied by each vegetation type. Values are based on Morat (1993) and Morat *et al* (1994).

Vegetation type	Native species	%	Endemic species	%	Area (km^2)
Total	3090		2370	76	
Rainforest	2010	58	1660	82	4000
Sclerophyll dry forest	410	13	230	56	350
Maquis	1140	35	1020	89	4400
Melaleuca savanna	130	4	.	.	6000
Mangrove	20	0.6	.	.	200

extinctions (Morat *et al,* 1986 b). Jaffré *et al,* (1987) suggests that newly developed ultramafic substrates favoured the colonisation of many Eocene forest taxa which were preadapted to low nutrient conditions. Low nutrient demanding taxa belonging to families such as Podocarpaceae, Cupressaceae, Araucariaceae, Myrtaceae, Sapotaceae and Proteaceae experienced intense speciation on ultramafics (Jaffré *et al,* 1987). These taxa presumably colonised more metalliferous substrates by developing adaptations to high levels of magnesium and nickel. Continued transformation of the peridotite sheet into a disjunct series of ranges has spatially isolated habitats containing subsets of flora that have undergone further speciation. The distance between suitable habitats on neighbouring ranges effectively isolated taxa and led to high geographic endemism within mountains of genera such as *Phyllanthus, Psychotria, Pittosporum, Alyxia* and *Eugenia* (Jaffré, 1980). This spatial isolation of habitats has also resulted in the disjunct distribution of relictual species, in particular gymnosperms (Jaffré *et al,* 1987, Jaffré, 1995).

1.6.3 Vegetation types of New Caledonia

New Caledonia contains a broad range of habitats in terms of combinations of substrate, topography and climate. These support terrestrial vegetation communities such as rainforest, maquis, sclerophyll dry forest and savanna that vary in floristic composition and structure, and form patterns which might be interpreted as zonational or successional.

1.6.3.1 Rainforest

Rainforests are generally defined as closed canopy broad-leafed formations exceeding 15 m in height with trees > 1 m d.b.h. Rainforest represents the most diverse vegetation formation in New Caledonia and contain about 2,011 vascular plant species belonging to 484 genera and 132 families, of which 1659 species are endemic (Jaffré *et al,* 1994 a; Jaffré *et al,* 1997 a). Much of the present day distribution of rainforest on non-ultramafic (2,750 km^2) and ultramafic (600 km^2) substrates is restricted to mountainous regions above 300 m a.s.l which receive a mean annual rainfall > 1,500 mm. Rainforest is also found at lower elevations in locations under the continual influence of moist south-east trade winds (Jaffré, 1993, Jaffré, 1995). Mid to high altitude rainforests (from 300-1000m a.s.l and 1,500-3,500 mm pa rainfall) are typically composed of a closed canopy 20-25 m in height of trees up to 1 m in trunk diametre. Mountain plateaus and summits (> 1000 m a.s.l and >3,500 mm pa) are often covered in a montane rainforest of low stature (3-8 m high) with many epiphytic mosses and less woody species than rainforest at lower altitudes (Jaffré *et al*, 1994 a; Jaffré, 1995).

Ultramafic rainforests have a lower and denser canopy than rainforest on schist soils and contain gregarious species such as *Nothofagus*, *Arillastrum*, *Gymnostoma* (Jaffré & Veillon, 1991; Jaffré & Veillon, 1995; Jaffré, 1995; Jaffré *et al*, 1997 a). The floristic diversity of ultramafic forests is generally equivalent to those on schist. However more rainforest families are found in schist than on ultramafics which are dominated by Myrtaceae and Rubiaceae (Jaffré & Veillon, 1995). According to Morat *et al* (1986 a), the floristic under-representation in ultramafic rainforests is an artefact of post-Eocene extinctions which have offset speciation in many families.

1.6.3.2 Maquis

Maquis is the most widespread ultramafic vegetation in New Caledonia and is found at all altitudes and covers an area of 4,500 km^2 (Jaffré, 1980). It is a low heath-like formation which is generally dominated by evergreen, sclerophyllous species which exhibits a preference for high light environments on slopes, ridgelines and open valleys, and often replaces montane rainforest on the summits of mountains (Jaffré, 1980; Jaffré, 1995). Maquis has a highly diverse vascular flora of 1,142 species of which 1,019 are endemic (Jaffré *et al*, 1994 a). Jaffré (1980) has classified maquis into three physiognomically and floristically distinct groups found in different parts of the landscape.

(i) Shrubby maquis (maquis arbustif), found on brown hypermagnesian soils, is composed of a sparse sedge ground cover and medium sized nanophyll and microphyll shrubs < 3 m in height. The species composition of this formation is often specific to a particular region due to the disjunct distribution of this substrate on ultramafic ranges.

(ii) Woody maquis (maquis buissonnant), often forms dense thickets of low branching shrubs < 3 m in height on oxisols with an iron crust. This includes much of the open basin vegetation surrounding swamplands in the Plaines de Lacs region.

(iii) Woody-sedge maquis (maquis ligno-herbacé) is found on mountain slopes and valley basins at all altitudes and represents the most common form of ultramafic vegetation on eroded oxisols. It is characterised by a continuous sedgeland containing isolated woody shrubs < 2 m in height.

These three types of maquis may develop into a tall maquis (maquis paraforestier) that is generally characterised by an open tree canopy < 8 m in height composed of a few species (*Gymnostoma, Tristaniopsis, Acacia*) that rarely exceed 20 cm d.b.h (Jaffré, 1980). The understorey is composed of shrubs and sedges are generally absent. Certain broad leafed rainforest taxa may also occur as isolated individuals.

Much of the flora found in these maquis types is specific to ultramafic soils and often has a sharp boundary with non-ultramafics such as the transition to *Melaleuca quinquenervia* savanna grassland at the base of ultramafic ranges (Jaffré, 1980, 1996).

1.6.3.3 Forest

Ultramafic forest is generally characterised by a tall closed tree canopy < 17 m in height dominated by a few species (*Gymnostoma, Arillastrum*) that occur as large diametre trees < 1 m d.b.h (Jaffré, 1980). The understorey is composed of a mixture of broad leafed rainforest taxa and maquis shrubs and trees. Forest contains fewer palm and pandanus species than rainforest and epiphytes are generally absent (Jaffré, 1980).

1.7 Disturbance & plant succession in New Caledonia

1.7.1 Natural disturbance

Plant communities in New Caledonia have evolved under various regimes of disturbance which operate at different spatial scales from the regional landscape level (fire, flood, cyclone, drought) to small patches (tree-fall, land slips). Natural disturbance of vegetation in New Caledonia arises mostly from cyclones and lightning induced fires. These disturbances are irregular both in frequency and intensity, with most cyclone activity confined to the wet season from December to March (Renson, 1989; Hastings, 1990) and fires from August to November (Dugain, 1952). Cyclones cause flooding tree fall, and erosion (Bird *et al*, 1984). Fires resulting from lightning often only burn small patches due to the rain which often accompanies thunderstorms (Papineau, 1989). Disturbed patches in rainforest are often colonised by genera such as *Nothofagus, Alphitonia, Pancheria* and *Gymnostoma* (Read *et al*, 1995, Jaffré *et al*, 1994 b;

Jaffré & Veillon, 1995). Hope & Pask (1998) recorded charcoal in lake sediments dated to 26,000 BP which suggests that fire has been a factor affecting vegetation before human arrival.

1.7.2 Human Disturbance

1.7.2.1 Fire

Humans settlement about 3000 BP (Sand, 1993) had a profound impact on the vegetation of New Caledonia by increasing the frequency of fire. This favoured the expansion of fire tolerant *Melaleuca quinquenervia* grassland savanna into dry sclerophyll forest and rainforest on non-ultramafic soils (Jaffré *et al*, 1994 a; Bouchet *et al*, 1995; Jaffré *et al*, 1998 b). Fires also favoured the expansion of fire tolerant maquis into rainforest on ultramafics (Jaffré, 1980; Morat *et al*, 1986 b; Papineau, 1989; Jaffré *et al*, 1998 a).

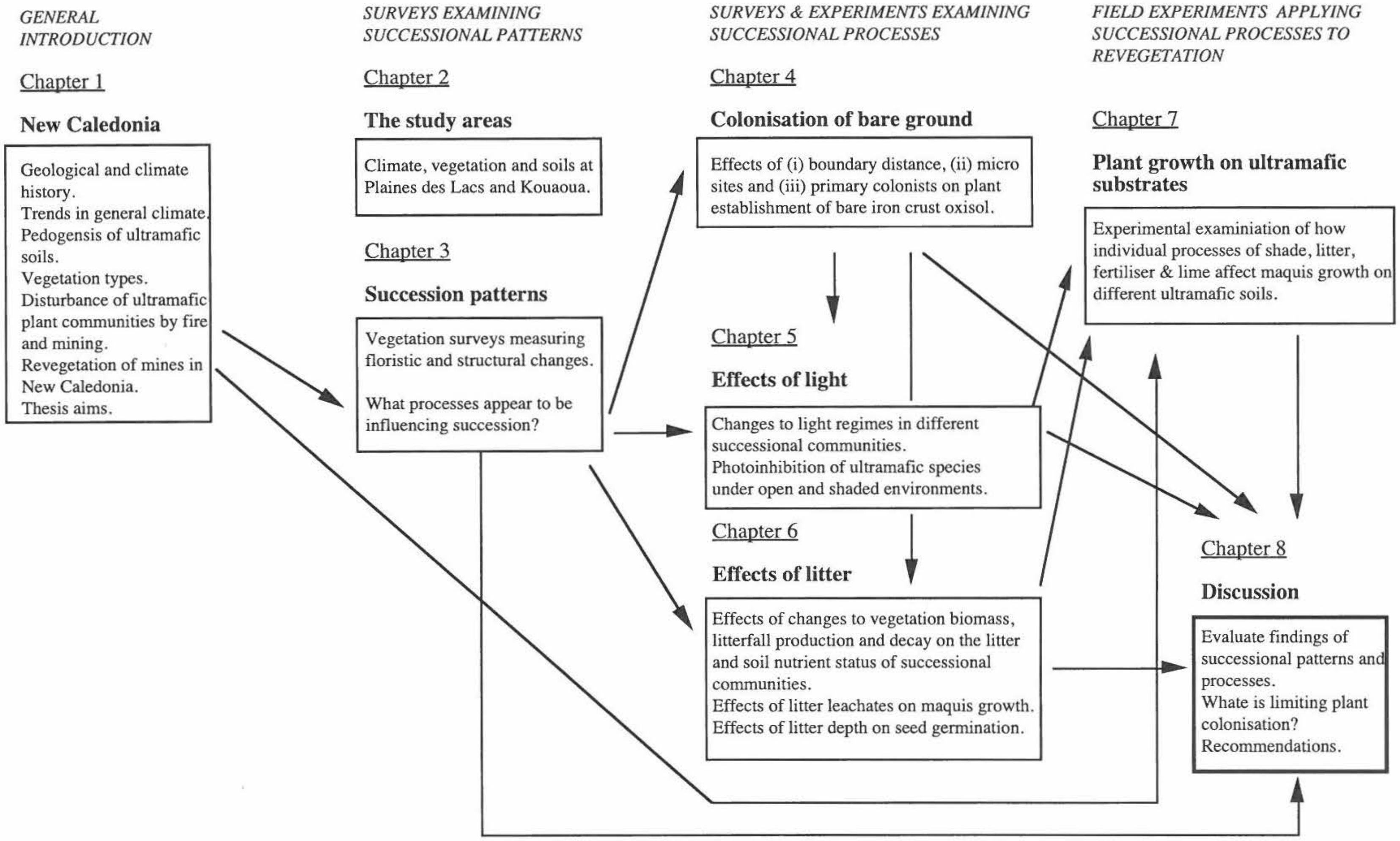
Vegetation clearance by Melanesians and more recent European settlers (since 1840) for agriculture was restricted to non-ultramafic areas due to the poor quality of ultramafic substrates for cultivation (Avias, 1953; Barrau, 1956). Even though ultramafics were not settled, increases in ignition frequency associated with mining and fires from surrounding agricultural land and *Melaleuca* savanna presumably shifted the vegetation towards its current dominance by maquis. Many forest communities have been subject to repeated fires from surrounding *Melaleuca* savanna and have been reduced to pockets in valleys (Virot, 1956, Jaffré, 1980, Papineau, 1989, Jaffré *et al*, 1993; Jaffré *et al*, 1994 a; Jaffré *et al*, 1998 a). Since the 1870s, vegetation in southern New Caledonia has been affected by frequent fires and disturbance associated with prospecting, mining and logging of rainforest trees (principally *Agathis lanceolata* and *Arillastrum gummiferum*) (Heckel, 1892, 1913; Dugain, 1952; Jaffré, 1980; Chevalier, 1996; fig. 1.6). Fire frequencies probably reached a peak between 1910 and 1960 when wood burning steam trains were in use in the region (Chevalier, 1996). There were extensive fires in 1914 and 1971 (J-M, Veillon, pers. comm).

1.7.2.2 Mining

Since the discovery of nickel ores by Garnier in 1864, mining has focussed on the plateau regions of steep sided ultramafic ranges, which contain nickel, cobalt and chrome ores at depths of 10-30 m below the

Figure 1.6 *Arillastrum gummiferum* tree at Prony showing large fire scar at base.

Figure 1.7 Nitrogen fixing *Frankia* nodule on a 20 yr old *Gymnostoma deplancheanum* tree at Plaines des Lacs.


GENERAL INTRODUCTION

Chapter 1

New Caledonia

Geological and climate history.
Trends in general climate.
Pedogensis of ultramafic soils.
Vegetation types.
Disturbance of ultramafic plant communities by fire and mining.
Revegetation of mines in New Caledonia.
Thesis aims.

SURVEYS EXAMINING SUCCESSIONAL PATTERNS

Chapter 2

The study areas

Climate, vegetation and soils at Plaines des Lacs and Kouaoua.

Chapter 3

Succession patterns

Vegetation surveys measuring floristic and structural changes.

What processes appear to be influencing succession?

SURVEYS & EXPERIMENTS EXAMINING SUCCESSIONAL PROCESSES

Chapter 4

Colonisation of bare ground

Effects of (i) boundary distance, (ii) micro sites and (iii) primary colonists on plant establishment of bare iron crust oxisol.

Chapter 5

Effects of light

Changes to light regimes in different successional communities.
Photoinhibition of ultramafic species under open and shaded environments.

Chapter 6

Effects of litter

Effects of changes to vegetation biomass, litterfall production and decay on the litter and soil nutrient status of successional communities.
Effects of litter leachates on maquis growth.
Effects of litter depth on seed germination.

FIELD EXPERIMENTS APPLYING SUCCESSIONAL PROCESSES TO REVEGETATION

Chapter 7

Plant growth on ultramafic substrates

Experimental examiniation of how individual processes of shade, litter, fertiliser & lime affect maquis growth on different ultramafic soils.

Chapter 8

Discussion

Evaluate findings of successional patterns and processes.
Whate is limiting plant colonisation?
Recommendations.

Figure 1.8 Schematic diagram of the structure the thesis. Arrows indicate the direction of focus of different chapters.

lateritic oxisol (Jaffré *et al*, 1994 c; Pelletier & Esterle, 1995). Prospecting and open-cut mining for these minerals involves the removal of vegetation from prospecting roads and the mine site, and fires associated with these activities often degrade the surrounding vegetation and expand the area of exposed oxisol (Jaffré *et al*, 1977; Jaffré *et al*, 1994 c). Iron and chrome mining operations from the 1930 to the 1960s' in southern New Caledonia resulted in extensive surface stripping of large areas of iron crust and leaving exposed gravelly substrates (Valette, 1996; Chevalier, 1996). These gravelly oxisols are easily eroded by extreme cyclonic rainfall to expose sub-surface clays.

Much of the direct disturbance associated with mining is a product of the extraction processes used. To obtain the 3-4 x 10^6 tonnes yr^{-1} of nickel ore extracted in New Caledonia, 10 x 10^6 tonnes of overburden surface material must also be removed (Jaffré *et al*, 1994 c; Pelletier & Esterle, 1995). Overburden includes nutrient poor A horizons and heavy clay B/C horizons which contain high concentrations of nickel, magnesium and manganese (Jaffré *et al*, 1977; Jaffré *et al*, 1994 c; Pelletier & Esterle, 1995). Prior to the 1970s, this overburden was dumped onto surrounding valleys leading to massive sediment accumulation in coastal rivers (Bird *et al*, 1984). Since 1970, mining operations have focussed on compacting overburden in terraces and revegetating these surfaces (Pelletier & Esterle, 1995).

1.8 Revegetation in New Caledonia

Revegetation work on mine sites in New Caledonia has aimed at stabilising overburden waste with a vegetation cover that would eventually provide an environment suitable for colonisation from surrounding vegetation (Jaffré & Latham, 1973; Cherrier, 1990; Jaffré & Rigault, 1991; Jaffré *et al*, 1994 c; Jaffré *et al*, 1997 b; Lucon *et al*, 1997). Early trials in the 1970 s focussed on fast growing exotic *Pinus carribaea, P. elliotti* and native *Casuarina collina, Acacia spirorbis* (CTFT, 1971; Cherrier, 1990). According to Cherrier (1990), using fast growing species would rapidly provide conditions for plants colonising from surrounding vegetation by raising the nutrient content of mine substrates through litterfall or nitrogen fixation (*Casuarina collina*). However in most cases, these species required large initial doses of fertiliser to alleviate nutrient deficiencies and metal toxicity problems and suffered high rates of mortality at high altitudes sites where most mines occur (Cherrier, 1990; Jaffré *et al*, 1994 c; Sarrailh, 1997). Furthermore, plantations of *Acacia spirorbis* and *Casuarina collina* were often devoid of plant colonisation from vegetation surrounding the mine (Jaffré *et al*, 1994 c), possibly either because conditions provided by trees or the environment of mine substrates were unsuitable for the colonisation and growth of maquis species (Jaffré *et al*, 1994 b).

During the 1990s', revegetation work has focussed on endemic ultramafic species from vegetation surrounding mines at different altitudes (Jaffré & Rigault, 1991; Jaffré *et al*, 1994 c; Jaffré *et al*, 1997 b). Many of the maquis species naturally occur in a narrow range of ultramafic habitats ranging from maquis to forest, and often grew slowly on mine sites. Emphasis was placed on the genus *Gymnostoma* as potential nurse species because of (i) its association with nitrogen fixing *Frankia* bacteria (fig. 1.7), (ii) the wide range of niches occupied by this genus, (iii) on a variety of ultramafic substrates containing different degrees of nutrient deficiency and metal toxicity (Jaffré *et al*, 1994 b). Furthermore, *Gymnostoma* species are common in disturbed habitats surrounding mines (Jaffré *et al*, 1994 b). The ecology of Casuarinaceae in general, and *Gymnostoma* in particular, are therefore a focus of this thesis.

1.9 Casuarinaceae & *Gymnostoma*

Pollen and macrofossils indicate that Casuarinaceae were widespread in the Southern Hemisphere during the Tertiary (Dilicher*et al*, 1990; Cristophel *et al*, 1995) presumably reflecting a Cretaceous Gondwanan origin. *Gymnostoma* is the oldest and most broadly distributed genus in the macrofossil record (Dilicher *et al*, 1990). It has been recorded from the Palaeocene and Eocene in Australia, as well as the Miocene in New Zealand and South America (Hill, 1994; Scriven & Hill, 1995). *Gymnostoma* no longer naturally occurs in New Zealand and South America, and its current distribution is restricted to northern Australia and the island archipelagos of Indonesia, Malaysia, Philippines, New Guinea, New Caledonia and Fiji (Johnson, 1980, 1982). The species of *Gymnostoma* are either trees or tall shrubs which occur in moist tropical regions, often in open forest formations on substrates ranging from old dune sands to ultramafic soils (Barlow, 1981). Ultramafic habitats containing *Gymnostoma* range from diverse rainforests in Sulawesi (Van Balgooy & Tantra, 1986) and New Caledonia (Jaffré *et al*, 1991, Jaffré *et al*, 1994 b) to tall shrublands in the Philippines, Solomon islands, New Guinea and New Caledonia (Whitmore, 1969; Whitmore, 1975; Paijmans, 1976, Jaffré *et al*, 1994 b; Proctor, 1992; Proctor *et al*, 1997). The diversity of this genus in most of these ultramafic communities is restricted to a single species (Proctor, 1992), however in New Caledonia, *Gymnostoma* has undergone considerable speciation and is represented by seven ultramafic species and one non-ultramafic species (Jaffré *et al*, 1994 b).

Much work has been done on the use of the closely related genus *Casuarina* for revegetating adverse sites because of their particular adaptations to withstand severe substrate conditions (high salinity, low nutrients, low rainfall, high metal concentrations, low soil moisture) and often exposed windy conditions (Midgely *et al*, 1981; NRC, 1984; Diem & Dommergues, 1990; El-Lakany, 1996). Casuarinaceae can develop an association with nitrogen fixing bacteria (*Frankia*), which may improve growth on substrates deficient in this element (Reddell, 1990; El-Lakaney, 1996). Casuarinaceae have xeromorphic needle-like segmented branchlets termed cladodes (Barlow, 1981). The cylindrical shape of cladodes, with stomata in sunken grooves and a thick waxy cuticle, minimise water loss and provide a high water use efficiency (Barlow, 1981).

1.10 General aims and organisation of the thesis

Several accounts of vegetation patterns in New Caledonia have suggested that maquis may be successional (Virot, 1956; Jaffré, 1980; Papineau, 1989) however no study has focussed on changes to the vegetation after disturbance and factors influencing plant colonisation of disturbed areas.

The general aims of this thesis are to firstly examine vegetation patterns on a range of ultramafic substrates to document the proposed successional trends. Secondly, to examine certain processes which are driving succession. Thirdly, to test how processes influence plant growth on a range of substrates, including mine waste.

An overview of the chapter lay out of the thesis is presented in figure 1.8. Each chapter addresses one or more specific aims.

Chapter 2 outlines the choice of substrates (iron crust oxisol, eroded oxisol, hypermagnesian soil) and locations of study sites. It describes the substrates, climate and vegetation of each study region.

Chapter 3 examines the floristic and structural patterns of vegetation at the three study sites on different substrates. Post-fire successional models are developed which seem to adequately describe the vegetation variation within each substrate type.

Chapter 4 examines patterns and processes affecting colonisation of bare ground on mine sites. This highlights the role of micro-topography and the influence of pioneers through their shade and litter upon colonist establishment.

Chapter 5 examines the light regime across the successional vegetation and focuses on measurement of photoinhibition.

Chapter 6 examines the effects of litter on succession. This chapter includes estimates of nutrient dynamics, especially N-fixing role of the *Gymnostoma-Frankia* symbiosis. It also examines various physical and chemical effects of litter.

Chapter 7 present an experimental investigation of the roles of litter, shade, fertiliser and calcium on the growth of a range of maquis species across the study soils.

Chapter 8 presents a synthesis of the findings and places them in a comparative framework against other tropical and ultramafic regions. The discussion focuses on general issues about the role of nutrient availability, metal toxicity and fire in determining the evolution and ecological characters of the New Caledonian ultramafic ranges. These conclusions are then applied to the practices of mine revegetation in New Caledonia.

Chapter 2

Study regions

2.1 Introduction

2.1.1 Site selection

The general aims outlined in chapter 1 can be restated in more practical terms as an investigation of vegetation successional patterns and processes on a range of ultramafic substrates and how processes might apply to revegetation of adjacent mines.

To achieve these aims it was decided that the study should focus on three major substrate types: iron crust oxisol, eroded oxisol and hypermagnesian soil. Each of these substrates occur in particular parts of the landscape and have undergone different degrees of weathering to produce distinct soils that contain different conditions for plant growth (fig. 2.1). Iron crust oxisol is a deep highly weathered substrate that is widespread at the Plaines des Lacs. Eroded oxisol and hypermagnesian soil are shallow poorly weathered substrates that occupy particular altitudinal parts of the landscape at Kouaoua typical of ultramafic ranges in New Caledonia. On each substrate it was considered desirable (i) to be able to study both (i) the natural vegetation and (ii) cleared and/or mine sites through surveys and experimentation.

Logistic considerations dictated that these sites should be as close together as practical to minimise travel. It was not practical to replicate the study on each substrate at more than one region, instead replication is made within each region. However it can be argued that these three separate studies constitute independent replicates of New Caledonian ultramafic substrates and vegetation.

This chapter presents background information concerning the geographic setting, climate, soils and vegetation of study areas at Plaines des Lacs and Kouaoua. Soil profiles were examined to give a general overview of the edaphic conditions of these oxisols and hypermagnesian soils.

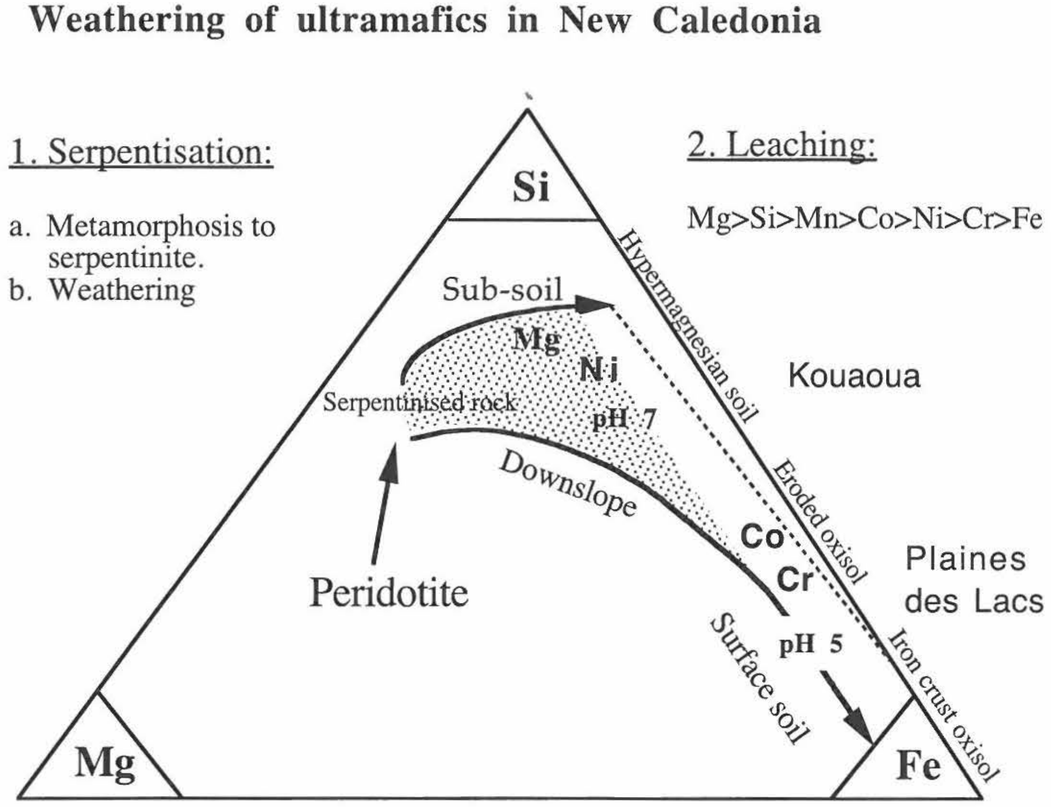


Figure 2.1 Schematic representation of ultramafic weathering in New Caledonia and soil types (hypermagnesian soil, eroded oxisol and iron crust oxisol) focussed in this thesis. Axes indicate the proportion of Mg, Si and Fe at various stages of ultramafic weathering.

2.2 Plaines des Lacs

2.2.1 Geographic setting

The Plaines des Lacs region (fig. 2.2) (Lat. 22°15'-22°20' S, Long. 166°50'-167° E) consists of a series of gently sloping drainage basins at 200-300 m a.s.l which are separated by steep low peridotite ranges (< 400 m a.s.l). Undulating iron crust plateaus, 20 to 50 m in relief, occupy most of the lower landscape of these basins and often surround swamplands and lakes (Guillon & Trescases, 1972; Trescases & Guillon, 1977) (fig. 2.3). Pseudo-karst sink holes are common on iron crust plateaus along zones of subterranean drainage and often create deposits of colluvial iron crust in adjoining valleys. (Guillon *et al*, 1972; Guillon, 1975; Guillon & Trescases 1977; Latham, 1986; Podwojewski & Bourdon, 1988).

2.2.2 Climate

Mean monthly rainfall, evaporation and temperature for Plaines des Lacs are given in figure 2.4. The Plaines des Lacs has a seasonal climate. Mean temperatures reflect maritime influences and only vary by about 7°C daily and 7°C seasonally about a mean of 22°C. The region receives 2,000 to 3,000 mm yr^{-1} rainfall and is often covered in low lying cloud and fog. Rainfall varies seasonally between about 70 mm in September and 450 mm in March. Evaporation often exceeds rainfall between August and November. Plants may experience water deficits during this period and open vegetation become dry enough to sustain extensive fires. Plant stress may become severe from November to December because of a combination of low rainfall and high temperatures.

2.2.3 Iron crust oxisols

Twenty iron crust oxisols profiles located along roads found at Plaines des Lacs were described using guidelines outlined by McDonald *et al* (1990). A summary of the morphological characteristics of these profiles is given in table 2.1. Measures of soil structure, hydraulic conductivity and chemical composition were carried out on flat bare iron crust oxisol gravel pockets using techniques (table 2.2) given in Appendix 1 and Appendix 2.

Iron crust oxisols (sol ferralitique ferritique gravillionaire ou cuirassé) (Latham *et al*, 1978) at Plaines des Lacs are nutrient poor and have a surface

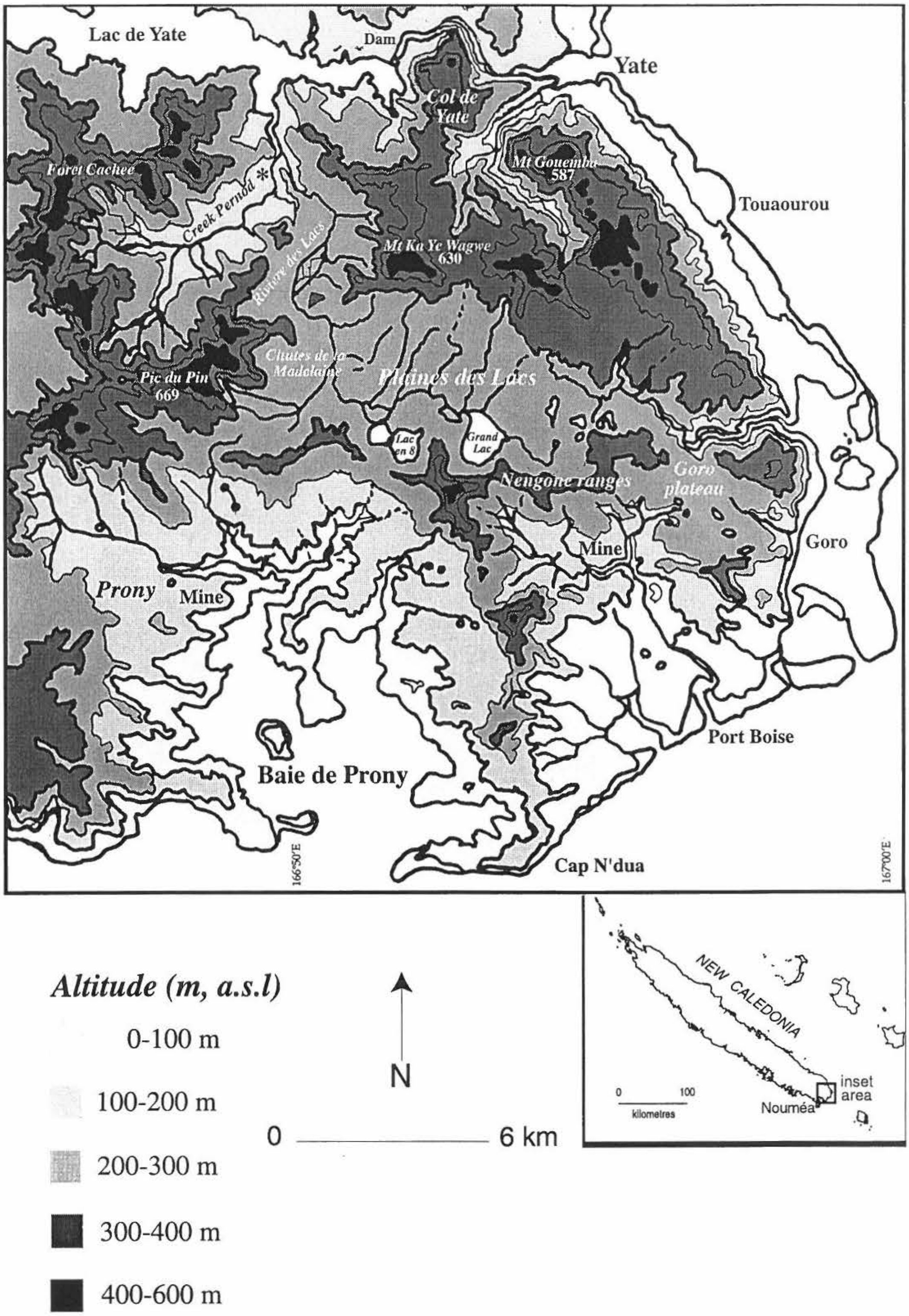


Figure 2.2 (i) Inset map shows the location of the study area. (ii) The main map shows the general topography of the Plaines des Lacs region. The asterisk indicates the field experiment site at Creek Pernod (chapter 7). Mines sites surveyed at Prony and on the Goro plateau (chapter 4) are indicated as - Mine.

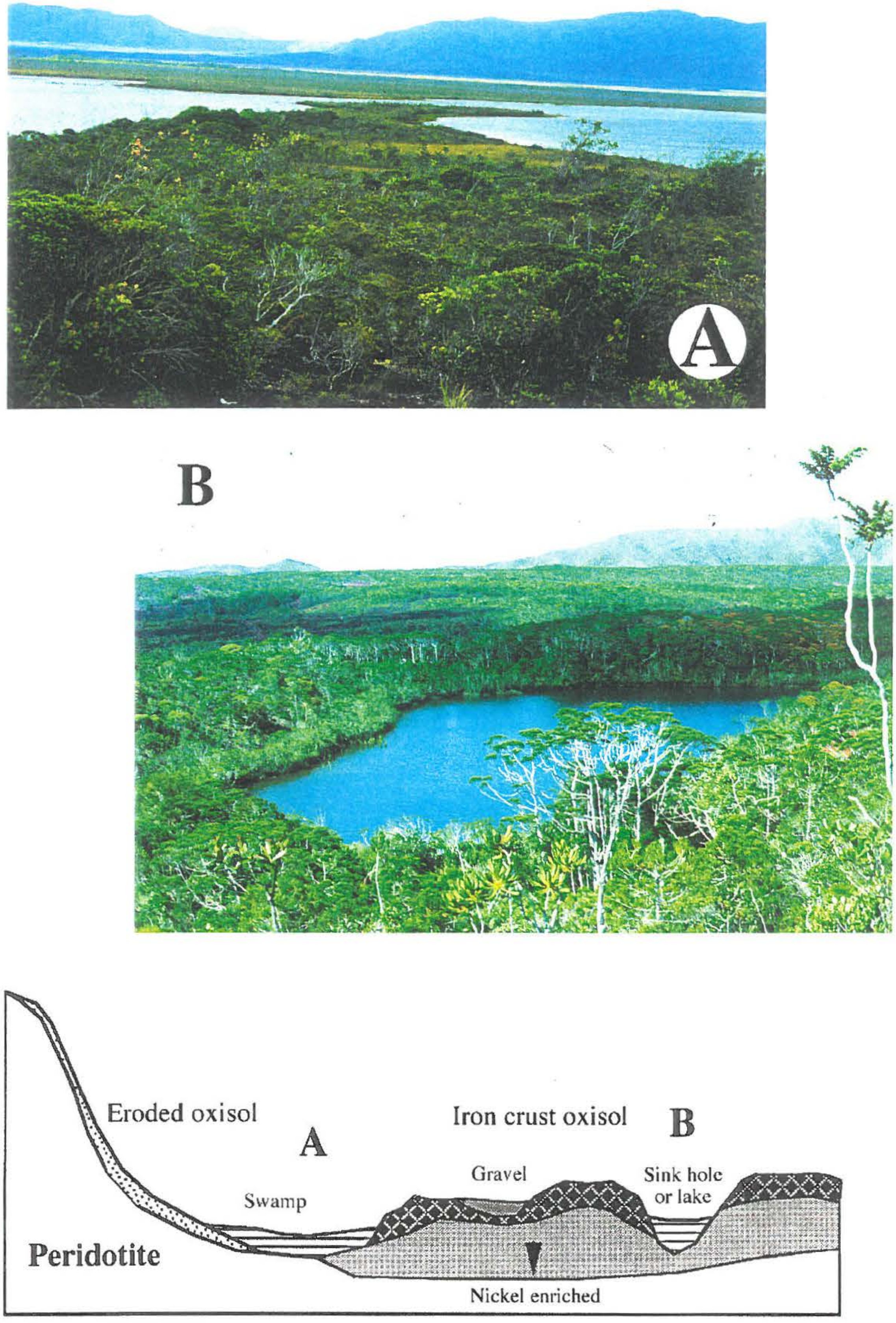


Figure 2.3 Landscapes of the Plaines des Lacs region showing extensive swamplands at Lac en Huit (A) and sinkholes which form localized swamps on iron crust plateaus (B). A diagrammatic profile shows geology, geomorphology and soils of the Plaines des Lacs region. Note the diagram is not drawn to scale, in particular soil depths and slopes are exaggerated.

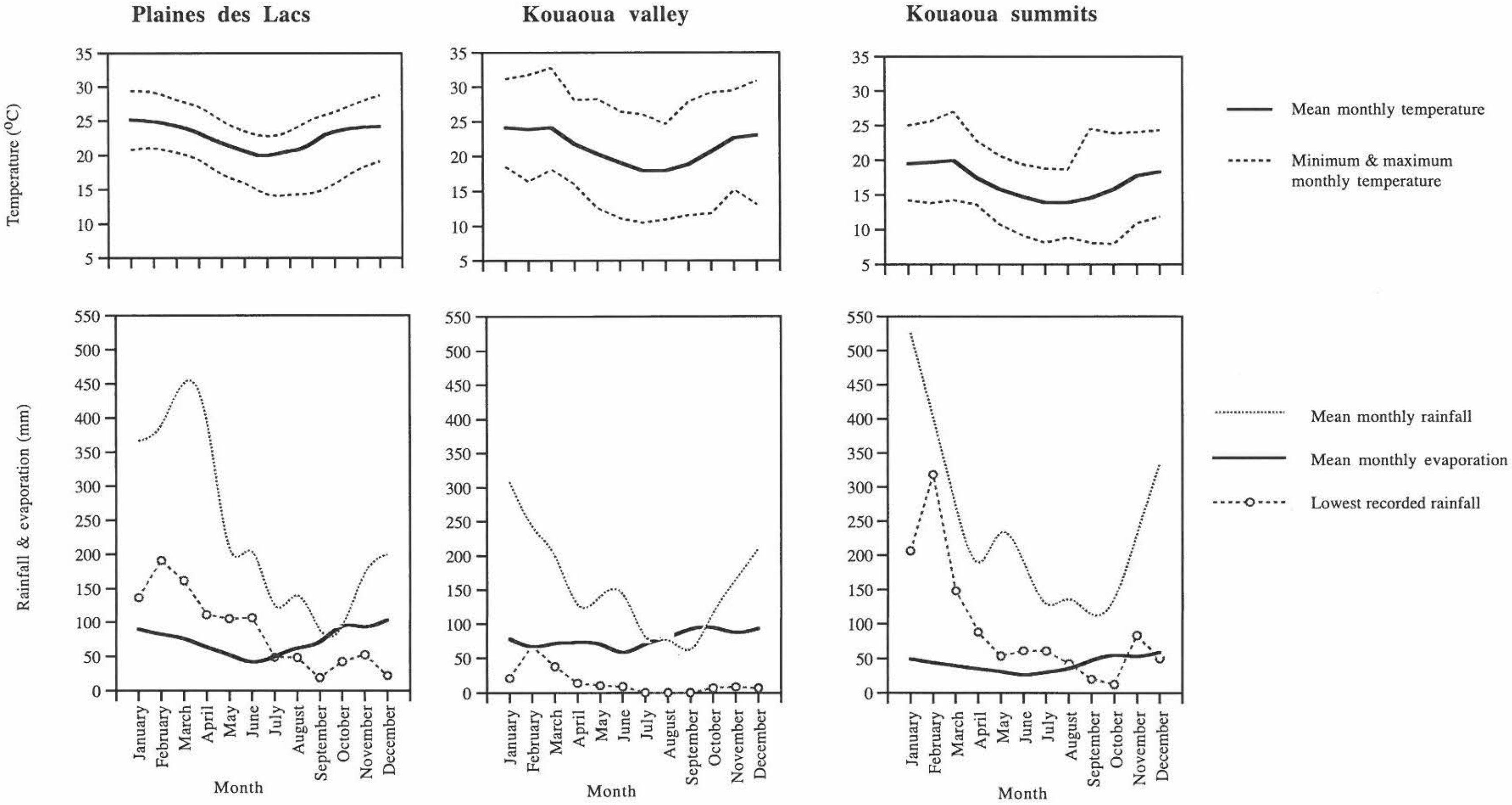


Figure 2.4 Mean, minimum and maximum monthly temperatures for the Plaines des Lacs region (Ouenarou, Jan 1983 - Dec 1992; 170m a.s.l), the Kouaoua valley (Kou 1, Jan 1993 - March 1995; 200m a.s.l; Rigault *et al*, 1996) and high altitude parts of the Kouaoua range (Kou 2, Jan 1993 - March 1995; 800m a.s.l; Rigault *et al*, 1996). Mean monthly rainfall and lowest recorded rainfall for the Plaines des Lacs (Chutes de la Madelaine; Jan 1960 - Dec 1995; 260m a.s.l), the Kouaoua valley (Kouaoua village; Jan 1983 - Dec 1992; 2m a.s.l) and summits of the Kouaoua range range (Mea mine, Jan 1986 - December 1994; 765m a.s.l). Mean monthly pan evaporation at Plaines des Lacs are from Ouenarou (1983-1992), from Ponerihoen (1983-1992) for the Kouaoua valley and from Col d'Amieu (1961-1980) for high altitude parts of the Kouaoua range.

Table 2.1: Generalised iron crust oxisol soil profiles at Plaines des Lacs for plateau (11 profiles), plateau slopes (6 profiles), and piedmont footslopes (3 profiles) at Creek Pernod, Goro Plateau, Port Boise, Prony and Chute de la Madelaine. All soil profile surveys were conducted in 1994 using guidelines given in Macdonald *et al* (1990).

		Plateau	Plateau slopes	Piedmont
A 1 Horizon Morphology				
Depth	Upper (cm)	0	0	0
	Lower (cm)	40 to 60	30 to 40	25 to 60
Colour	Field	Dark red - brown	Dark red - brown	Dark red - brown
	Munsell	3/3 10 R	3/4 2.5 R	4/4 5 YR
Field texture		course gravelly	sandy gravel	sandy loam
Coarse fragments	Abundance (%)	>90	50 to 90	50 to 90
	Type	Gravel - boulders	Gravel - stones	Gravel - cobbles
	Distribution	Dispersed	Dispersed	Dispersed
	Size (mm)	2 to 2000	2 to 600	2 to 200
	Shape	sub - angular sub - rounded	sub - angular sub - rounded	sub - angular sub - rounded
Structure	Pedality & fabric	massive & sandy	massive & sandy	massive & sandy
	Cutans	absent	absent	absent
Voids (cracks)	Type	very coarse	coarse	medium
	Size (mm)	20 to 50	10 to 20	5 to 10
Macropore abundance	Fine (mm^2)	> 5/100	1 - 5/100	< 1/100
	Medium - Coarse (m^2)	1 - 5/0.01	< 1/0.01	< 1/0.01
Horizon boundary		Gradual & irregular (50 - 100 mm)	Gradual & irregular (50 - 100 mm)	Diffuse & wavy (> 100 mm)
B 1 Horizon morphology				
Depth	Upper (cm)	40 to 60	30 to 40	25 to 60
	Lower (cm)	90 to 120	65 to 100	80 to 120
Colour	Field	Dark orangy red	Dark orangy red	Red brown
	Munsell	3/6 - 4/6 10 R	3/6 10 R	3/4 2.5 YR
Field texture		Medium clay	Sandy clay loam	Clayey sand
Coarse fragments	Abundance (%)	10 to 20	20 to 50	20 to 50
	Type	Gravel - cobbles	Fine - coarse gravel	Fine - coarse gravel Laminar iron crust
	Distribution	dispersed	dispersed	dispersed
	Size (mm)	2 to 200	2 to 60	2 to 60
	Shape	Sub - rounded, sub - angular	Sub - rounded, sub - angular	Sub - rounded, sub - angular
Structure	Pedality	Weak - moderate	Weak	Weak
	Type	Polyhedral	Polyhedral	Polyhedral
	Ped diameter (mm)	10 to 20	5 to 20	2 to 5
	Cutans (mangans)	Faint & few	Distinct & few	Faint & few
Voids (cracks)	Size (mm)	Fine < 5	Fine < 5	Fine < 5
Macropore abundance	Fine (mm^2)	1 - 5/100	< 2/100	< 2/100
	Medium - Coarse (m^2)	< 1/0.01	< 1/0.01	< 1/0.01
Depth to parent rock		10 to 30 m	10 to 30 m	10 to 30 m
Root distribution		Soil depth (cm)	Soil depth (cm)	Soil depth (cm)
Fine roots < 2 mm	Abundant > 200/0.01 m^2	0 to 30	0 to 30	0 to 20
	Few 1 - 10/0.01 m^2	30 to 40	30 to 40	20 to 80
	Absent	> 40	> 40	> 80
Coarse roots > 2 mm	Common >2 - 5/0.01 m^2	0 to 60	0 to 60	0 to 60
	Few 1 - 2/0.01 m^2	60 to 90	60 to 90	60 to 100
	Absent	>90	>90	>100

Table 2.2: The physical and chemical properties of ultramafic soils at Plaines des Lacs and Kouaoua. Techniques used to measure the physical and chemical properties of iron crust oxisols, hypermagnesian soil, eroded oxisol and mine overburden are given in Appendix 1 and Appendix 2.

	Iron crust oxisol		Hypermagnesian soil		Eroded oxisol		Laterite overburden	
Locality	Creek Pernod		Kouaoua		Kouaoua		Kouaoua	
Altitude	220 m a.s.l		180 m a.s.l		700 m a.s.l		700 m a.s.l	
Sample depth (cm)	0 - 7.5		0 - 6		0 - 9		0 - 9	
Soil physical properties	Mean	St.dev	Mean	St.dev	Mean	St.dev	Mean	St.dev
Number of samples	8		8		8		8	
Soil texture, %								
Coarse material > 2 mm	81.2	9.3	79.8	2.8	26.5	9.9	1.4	1.5
Bulk density, g cm^{-3}								
Auger hole method	2.1	0.3	2.5	0.2	3.0	0.6	1.7	0.2
Sand replacement method	1.3	0.1	1.5	0.2	1.6	0.2	0.9	
Soil - water content, %	3.8	0.8	13.0	2.3	9.4	3.3	29.2	5.2
Total porosity, % by volume	69.0	2.8	60.0	3.2	72.0	6.5	46.0	6.2
Hydraulic conductivity, mm/hr								
0 hPa	1013.8	558.7	200.4	21.1	341.7	52.5	90.8	40.6
0.5 hPa	439.6	359.6	-	-	-	-	-	-
5 hPa	25.1	15.5	-	-	-	-	-	-
15 hPa	15.8	7.5	-	-	-	-	-	-
Pore size, mm	2.9	2.1	-	-	1.6	0.9	0.3	0.3
Soil chemical properties	Mean	St.dev	Mean	St.dev	Mean	St.dev	Mean	St.dev
Number of samples	8		8		8		8	
pH (H_2O)	4.8	0.7	6.7	0.2	5.2	0.8	5.7	0.3
Total, %								
Loss on ignition	12.1	3.3	14.2		17.2		12.9	
Residue	6.0	2.1	8.1		5.2		6.1	
N (Kjeldahl)	< 0.01	< 0.01	0.27	0.08	0.26	0.11	0.06	0.06
P (Olsen)	0.02	< 0.01	0.01	< 0.01	0.02	< 0.01	0.02	0.01
K	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Na	< 0.01	< 0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Mn	0.27	0.22	0.43	0.17	0.55	0.15	0.68	0.30
Ni	0.26	0.17	0.60	0.08	0.61	0.08	1.34	0.43
Cr	1.54	0.36	0.35	0.10	2.20	0.28	1.25	0.14
Fe	43.02	4.76	18.70	3.24	49.06	3.36	53.50	4.70
Ca	0.03	0.04	0.11	0.07	0.01	0.03	< 0.01	< 0.01
Mg	1.02	0.06	6.91	2.09	1.69	0.13	3.17	1.03
Exchangeable bases, meq/100g								
Na^+	0.10	0.03	0.26	0.01	0.18	0.01	0.08	0.03
K^+	0.13	0.07	0.28	0.07	0.19	0.00	0.02	0.01
Ca^{2+}	0.69	0.55	1.59	2.16	0.34	0.95	0.05	0.14
Mg^{2+}	0.86	1.18	54.09	8.16	0.81	0.53	0.44	0.66
Extractable Nitrogen and phosphorous, mg/g								
N - NH_4^- (KCl)	1.4	1.1	1.7	0.9	0.4	0.2	0.0	0.0
N - NO_3^- (KCl)	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0
P - PO_4^- (Olsen)	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0

of iron crust (cuirasse) composed of boulders, stones, cobbles and gravel aggregates that may be up to 7 metres deep (Trescases & Guillon, 1977; Jaffré, 1980; Papineau, 1989) (fig. 2.5). On higher parts of plateaus, the surface is characterised by large cemented blocks of iron crust. Such surfaces contain pockets of breccia iron crust colluvial material along drainage lines. Iron crust on piedmont slopes surrounding lakes is often composed of large boulders, cobbles and cemented breccia iron crust which have eroded from peridotite slopes to form a shallow surface deposit less than 1 m deep (Bourdon & Podwojewski, 1988).

Iron crust gravel pockets have an A horizon (0 to 30 cm) largely composed of a coarse gravel (81% of sample weight) containing large pore spaces (average pore size 2.9 mm) between aggregates. Such gravel aggregates may contribute up to 69% of the total porosity. Hydraulic conductivity (K) measured using a disc permeametre (Vauclin & Chopart, 1993) show that gravel pockets are highly permeable ($K > 1000$ mm hr^{-1}) and retain very little moisture (3.8% by volume) due to the lack fine particles, which have been transported to depths ranging from 0.3 to 20 m to form ferrous clay B and C horizons. Roots < 2 mm in diametre are abundant in the A horizon to a depth of 30 cm and become scarce on contact with the B horizon. According to Bourdon *et al* (1997), the scarcity of roots in the B horizon arises from the compacted structure of ferrous clays which contain few voids necessary for root development. Plants establishing on bare iron crust oxisols may experience periodic water stress despite the high rainfall because of the porous nature of the surface iron crust horizon.

The chemical properties of iron crust oxisols are largely a product of the very porous nature of surface horizons and the abundance of negatively charged iron oxides. In surface horizons, iron oxides are continually saturated by free hydrogen resulting in acidic conditions and very low exchange capacities for base elements (Jaffré, 1980). Extractable nitrogen and phosphorus levels in surface horizons are also very low because of intense leaching (Jaffré, 1980; Bourdon & Podwojewski, 1988; Bourdon *et al*, 1997). Heavy metals such as manganese and nickel are also leached from surface horizons (Bourdon & Podwojewski, 1988; Bourdon *et al*, 1997) and are therefore unlikely to exert toxic effects on overlying vegetation (Rigault *et al*, 1997).

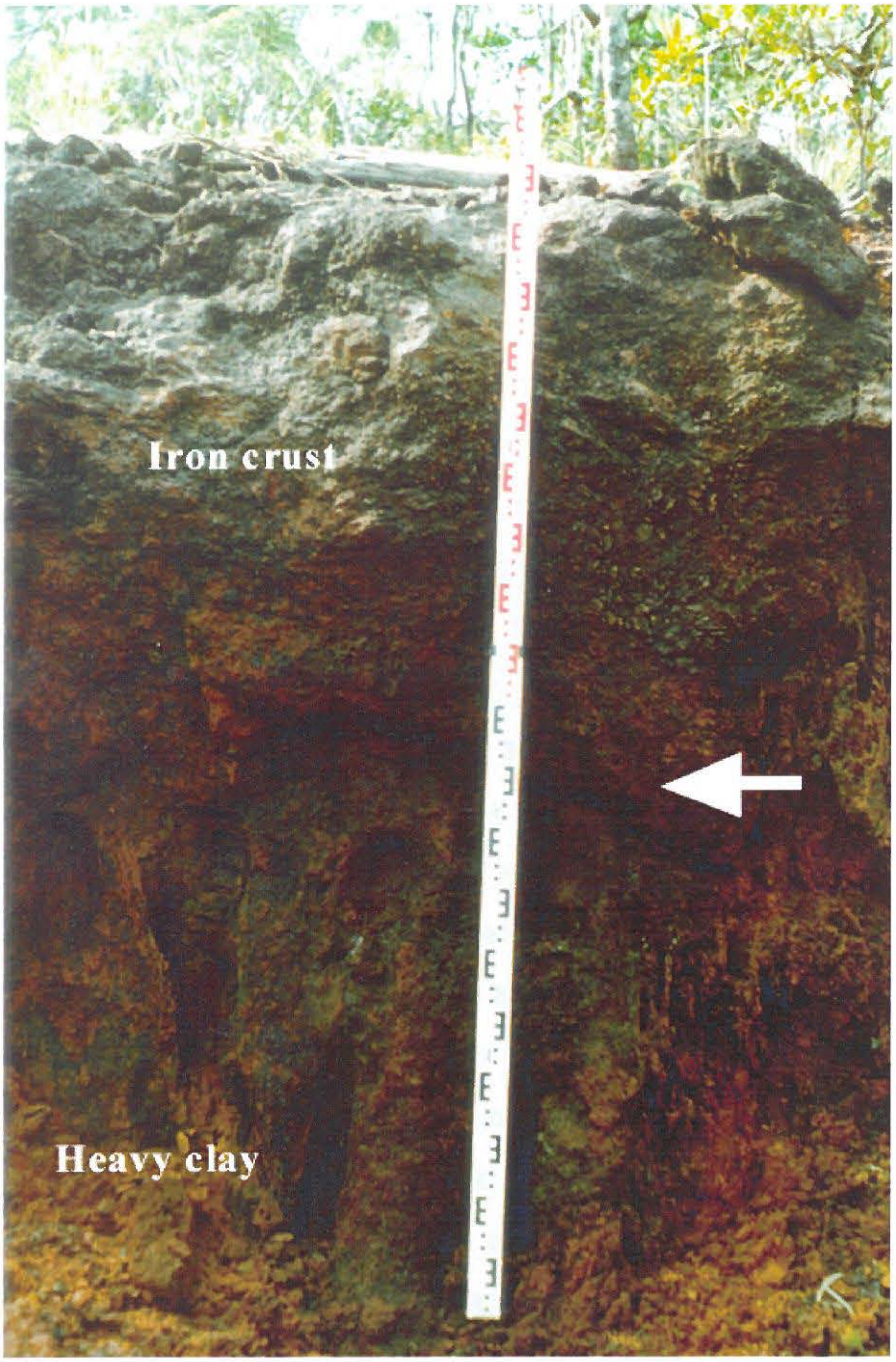


Figure 2.5 An iron crust oxisol profile on a road cutting at the Goro plateau in the Plaines des Lacs region. The transition between A horizon iron crust and B horizon heavy clay is indicated by an arrow. Gravel occurs as a poorly defined layer below the iron crust. Red and black scales are each 1 m and graded at 2 cm intervals.

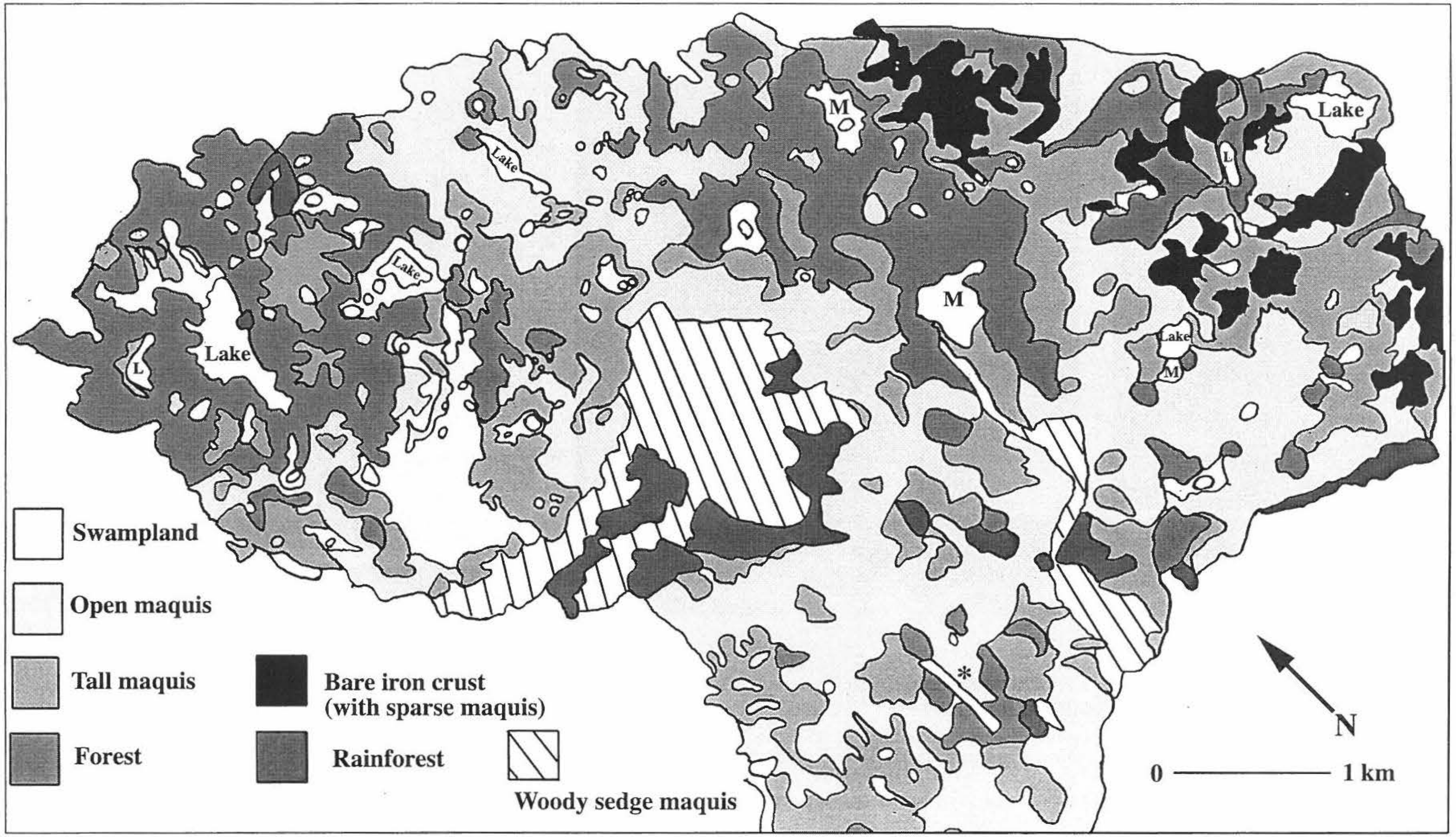


Figure 2.6 Vegetation patterns on the Goro plateau in the Plaines des Lacs region. Patterns are based on a false colour infrared photograph taken in 1988. Areas in white indicate lakes or sinkholes in the iron crust. The asterisk indicates a vegetation colonisation survey area in chapter 4.

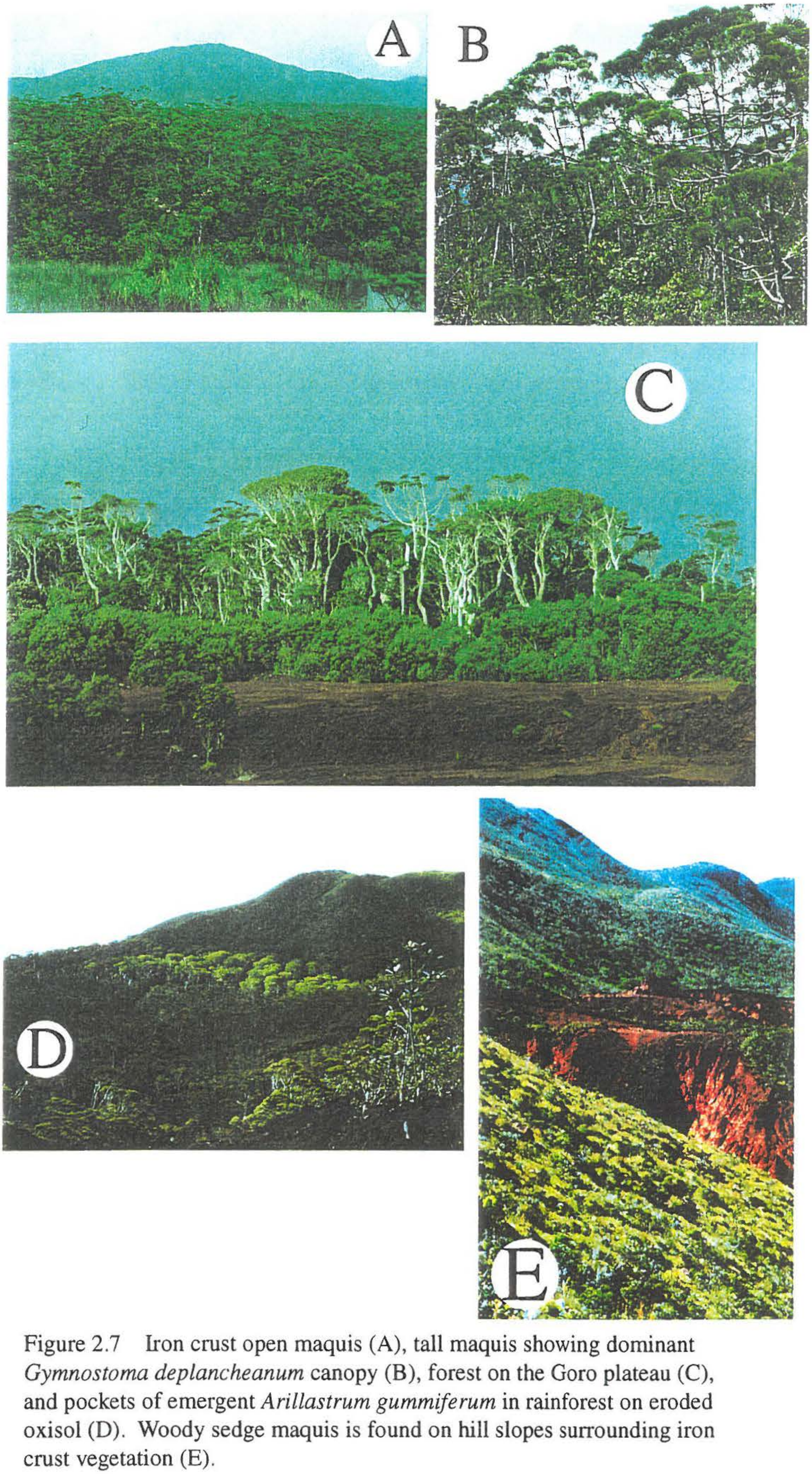


Figure 2.7 Iron crust open maquis (A), tall maquis showing dominant *Gymnostoma deplancheanum* canopy (B), forest on the Goro plateau (C), and pockets of emergent *Arillastrum gummiferum* in rainforest on eroded oxisol (D). Woody sedge maquis is found on hill slopes surrounding iron crust vegetation (E).

2.2.4 Vegetation

Vegetation patterns visible on aerial photos of the Goro plateau (fig. 2.6) in the Plaines des Lacs region form a mosaic (fig. 2.7) ranging from patches 1-10 ha of bare iron crust to a low woody maquis of scattered small shrubs, to a continuous tall maquis (maquis paraforestier) to forest. *Gymnostoma deplancheanum* is a characteristic tree component of the maquis and forest. Patches of *Arillastrum gummiferum* occur as forests 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 on peridotite ranges (Jaffré, 1980, Papineau, 1989). Swamplands and surrounding peridotite hill slopes typically support woody-sedge maquis (Jaffré, 1980; Jaffré *et al*, 1994 a).

The vegetation mosaic of maquis, forest and rainforest at Plaines des Lacs has a nearly random distribution pattern except that rainforest is most often located on south facing slopes on eroded oxisols. Open maquis and tall maquis are the most common vegetation types on iron crust. Forests occur as patches < 1 ha in size. Bare iron crust also covers extensive areas along ridgelines of the Goro plateau above 280 m a.s.l.. Jaffré (1980) suggested that vegetation on iron crust substrates represents a post-fire succession from open low maquis to tall maquis and forest, leading eventually to rainforest.

2.3 Kouaoua

(ii) Two study sites are located on the east coast Kouaoua range (Lat. 21°20'-30' S; Long. 165°40'-53' E; fig. 2.8) which is the north-eastern most extension of the Grand Massif du Sud. The Kouaoua ultramafics, which cover 300 km^2, consist of steep sided ranges which are separated by deep incised valleys (Guy *et al*, 1979) (fig. 2.9). Iron crust is found on the summit plateau regions at about 1000 m a.s.l. Serpentinite rock forms an irregular band (50-300 m a.s.l) at the base of these massifs along thrust zones and fault lines (Guy *et al*, 1979). Much of the landform between the iron crust plateaus and serpentinite belts has been heavily disturbed by nickel mine operations since 1875 (Guy *et al*, 1979). The study area is within the boundaries of Societe Le Nickel's (SLN) largest open cut mine operation, at Méa, below Mt Aréha (Lat. 21°27' S; Long. 165°46' to 165° 55' E; 700 m a.s.l). Most of the mid altitude slopes within the prospecting and mining zone are

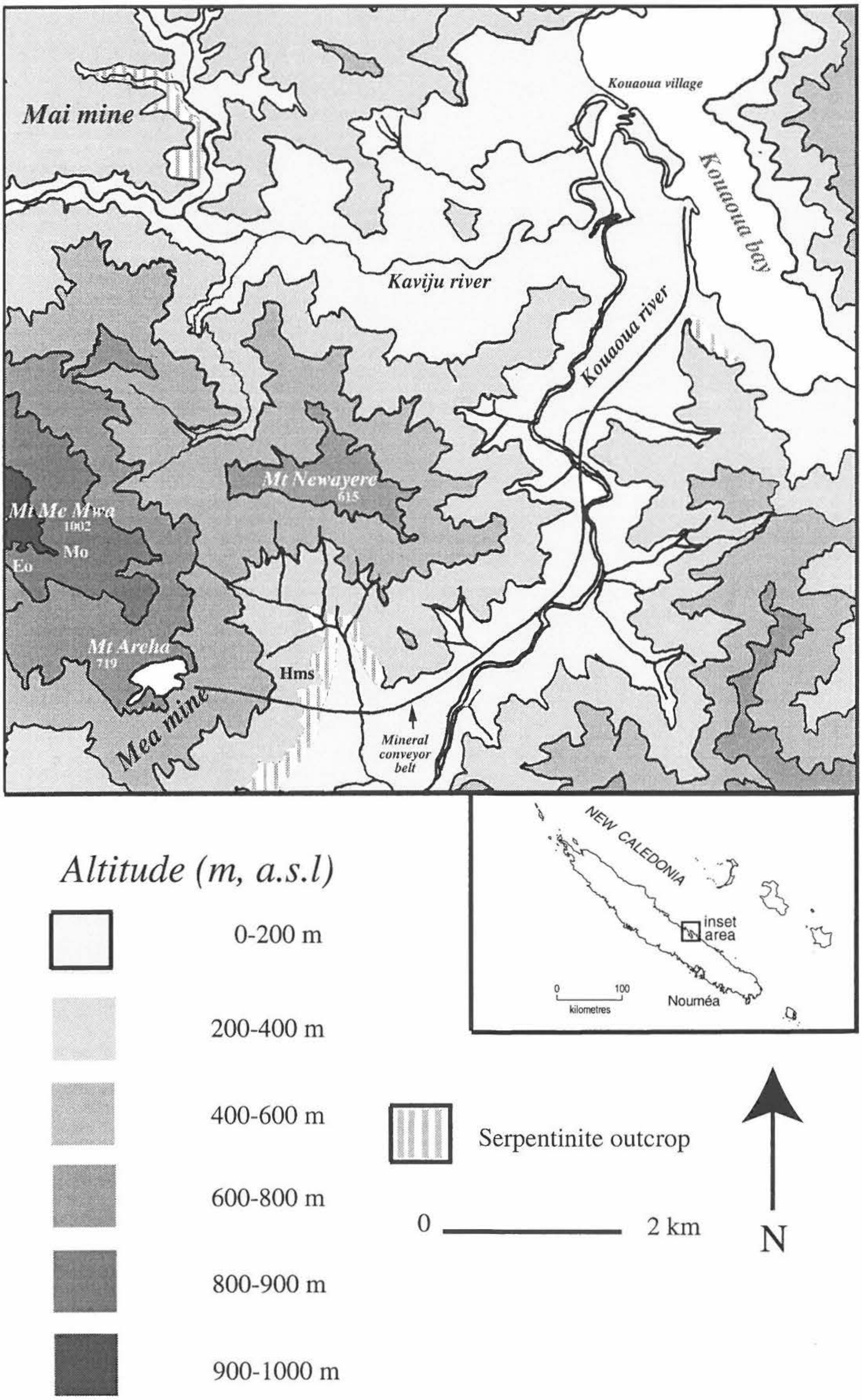


Figure 2.8 (i) Inset map shows the location of the study area. (ii) The main map shows the general topography of the Kouaoua region and serpentinite belts. Field trial plots (chapter 7) at the mine overburden site (Mo), the eroded oxisol site (Eo) and hypermagnesian soil site (Hms) are indicated at Mea Mine.

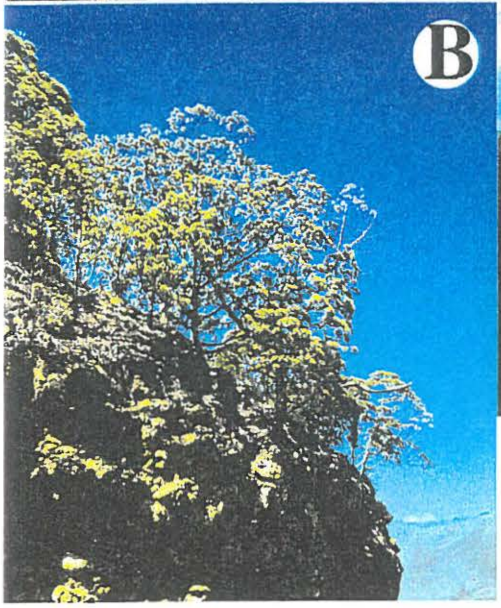


Figure 2.9 Landscapes of the Kouaoua region showing the Kouaoua valley (A), serpentinite outcrops on foot slopes of the Mea mine (B) and an aerial view of Mea mine (C). A diagrammatic profile of the valley (bottom) shows geology, geomorphology and soils of the study regions. Note that the diagram is not drawn to scale, in particular soil depths and slopes are exaggerated.

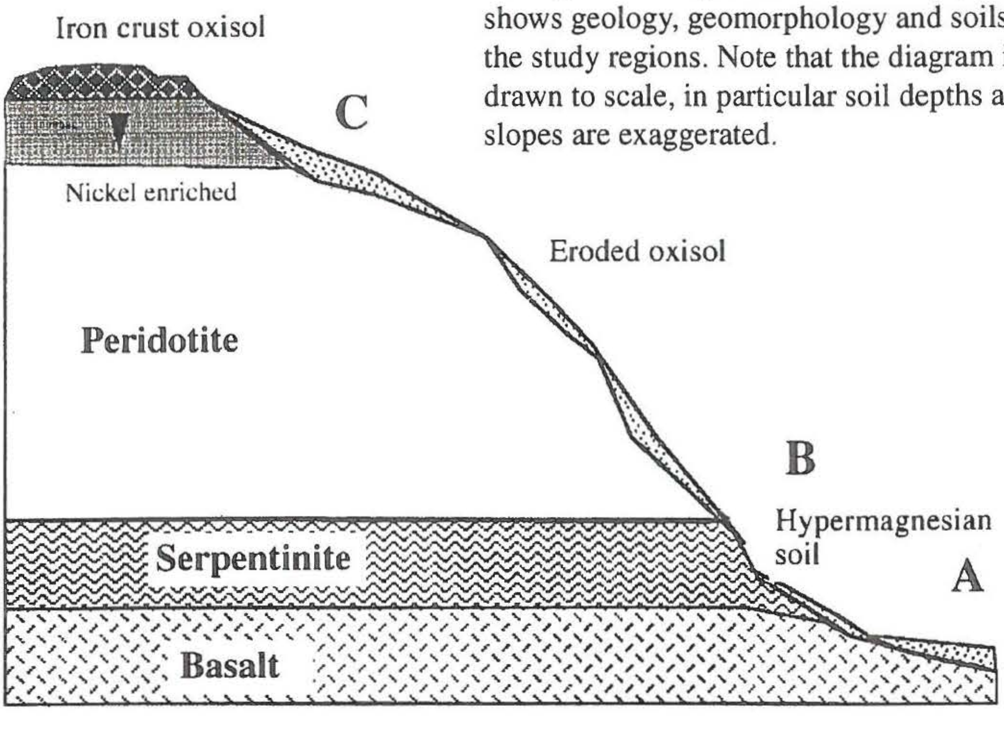


Figure 2.10 An aerial photograph taken in 1976 of ultramafic mountain ranges surrounding the Wa Kave creek to the north west of Mea mine at Kouaoua. Valley bottoms and lower facing slopes contain forest and rainforest (1). North facing slopes and ridgelines support a woody sedge maquis (2) that is often severely eroded (3).

very steep (30-40°) and are actively eroding, in particular serpentinite which is often bare. An aerial photograph of mid-altitude regions on mountain ranges outside the zone of direct mine activity to the north west of Méa mine reveals that north facing slopes support woody sedge maquis. Valleys and south facing slopes support forest and rainforest (fig. 2.10).

Surveys were conducted on vegetation formations on eroded oxisol above Méa mine and on serpentinite outcrops below zones of direct mining activity. Experimental work was conducted on mine overburden terraces and quarries situated at altitudes of 200 m a.s.l and 800 m a.s.l.

2.4 *Gymnostoma intermedium* communities on eroded oxisol

2.4.1 Geographic setting

The summital areas above Méa mine consist of a series of stepped ridge lines separated by deep valleys fed by erosional stream channels on slopes of 10-30°. Iron crust is found from Mt Aréha (722 m a.s.l) to Mé Mwa (1002 m) and Pic du Menazi (1,089m) along a band of low relief hill crests (fig. 2.8). Low relief areas below the ridge lines are heavily disturbed by mining and prospecting activity.

2.4.2 Climate

Mean monthly rainfall, evaporation and temperature for summit parts of the Kouaoua range are given in fig. 2.4. Mean temperatures reflect montane influences and rarely exceed 20°C. Temperatures often decline below 10°C. Rainfall records from Méa mine (765 m a.s.l) reveal that summital parts of Kouaoua are similar to the moist environments of other high altitude regions (Jaffré & Latham, 1974; Jaffré, 1980; Danloux, 1987) and receive approximately 3,000 mm yr^{-1}. Rainfall seasonality is less extreme compared to lower altitude parts of Kouaoua and varies between about 100 mm in September and 500 mm in February. Evaporation is low throughout the year because of humid conditions created by south-east trade winds maintaining frequent wet and foggy conditions with low solar radiation.

2.4.3 Eroded Oxisol

Four eroded oxisol profiles located along roads in close proximity to *Gymnostoma intermedium* forest formations were described using guidelines outlined by McDonald *et al* (1990). Morphological characteristics

Table 2.3: Generalised soil profile for hypermagnesian soil on ridgelines (2 profiles) and slopes (2 profiles), and for eroded oxisol (3 profiles) in valley bottoms at Kouaoua. All soil profile surveys were conducted in 1994 using guidelines given in MacDonald *et al* (1990).

		Ridgeline	Slope	Valley bottom
A 1 Horizon Morphology				
Depth	Upper (cm)	0	0	0
	Lower (cm)	26 to 40	15 to 60	40
Colour	Field	Grey brown	Browny grey	Dark reddish brown
	Munsell	5/2 5 YR	3/3 - 3/4 10 R	4/4 - 4/6 5 YR
Field texture		Medium clay	Clayey sand	Sandy loam
Coarse fragments	Abundance (%)	20 to 50	10 to 20	>90
	Material	Serpentinite	Serpentinite	Iron crust, peridotite
	Type	Fine - coarse gravel	Fine gravel - cobbles	Fine - coarse gravel
	Distribution	dispersed	dispersed	diffuse
	Size (mm)	2 to 60	2 to 200	2 to 60
	Shape	Angular, angular - tabular	Angular	Sub rounded, sub tabular
Structure	Pedality & fabric	Moderate & rough	Weak & rough	Weak & earthy
	Type	Polyhedral	Polyhedral	Polyhedral
	Size (mm)	2 to 5	2 to 5	2 to 5
	Cutans	Common & distinct	Few & Visible	Faint & few
Voids (cracks)	Type	Medium	Medium	Medium - coarse
	Size (mm)	5 to 10	< 10	5 to 20
Macropore abundance	Fine (mm^2)	1 - 5/100	1 - 5/100	> 5/100
	Medium - Coarse (m^2)	1 - 5/0.01	1 - 5/0.01	1 - 5/0.01
Horizon boundary		Clear & wavy (20 - 50 mm)	Sharp & irregular < 5 mm	Gradual (50 - 100 mm)
B Horizon morphology				
Depth	Upper (cm)	26 to 40	15 to 60	40
	Lower (cm)	90 to 120	40 to 70	140
Colour	Field	Dark yellowy brown	Orangy yellow brown	Brownish purple
	Munsell	4/2 - 5/2 5 YR	3/4 5 YR	4/2 - 4/4 2.5 YR
Field texture		Heavy clay	Very heavy clay	Medium clay
Coarse fragments	Abundance (%)	50 to 90	10 to 20	10 to 20
	Material	Serpentinite	Serpentinite	Peridotite
	Type	Gravel & stones	Gravel & stones	Cobbles & Stones
	Distribution	diffuse	diffuse	diffuse
	Size (mm)	2 to 200	2 to 200	< 1000
	Shape	Angular - platy	Angular	Sub rounded, sub platy
Structure	Pedality	Moderate	Moderate	Moderate
	Type	Polyhedral	Polyhedral	Polyhedral
	Ped diameter (mm)	5 to 10	20 to 50	5 to 20
	Cutans	Few & visible	Many & distinct	Common & distinct
Voids (cracks)	Size (mm)	5 to 20	Fine < 5	Fine < 5
Macropore abundance	Fine (mm^2)	1 - 5/100	1 - 5/100	< 1/100
	Medium - Coarse (m^2)	< 1/0.01	< 1/0.01	< 1/0.01
Depth to parent rock		90 to 120 cm	40 to 70 cm	5 to 10 m
Root distribution		Soil depth (cm)	Soil depth (cm)	Soil depth (cm)
Fine roots < 2 mm	Abundant > 200/0.01 m^2	0 to 26	0 to 20	0 to 24
	Few 1 - 10/0.01 m^2	26 to 40	10 to 38	24 to 40
	Absent	> 40	> 38	> 40
Coarse roots > 2 mm	Common >2 - 5/0.01 m^2	0 to 26	0 to 30	0 to 35
	Few 1 - 2/0.01 m^2	26 to 60	30 to 50	35 to 60
	Absent	> 60	> 50	> 60

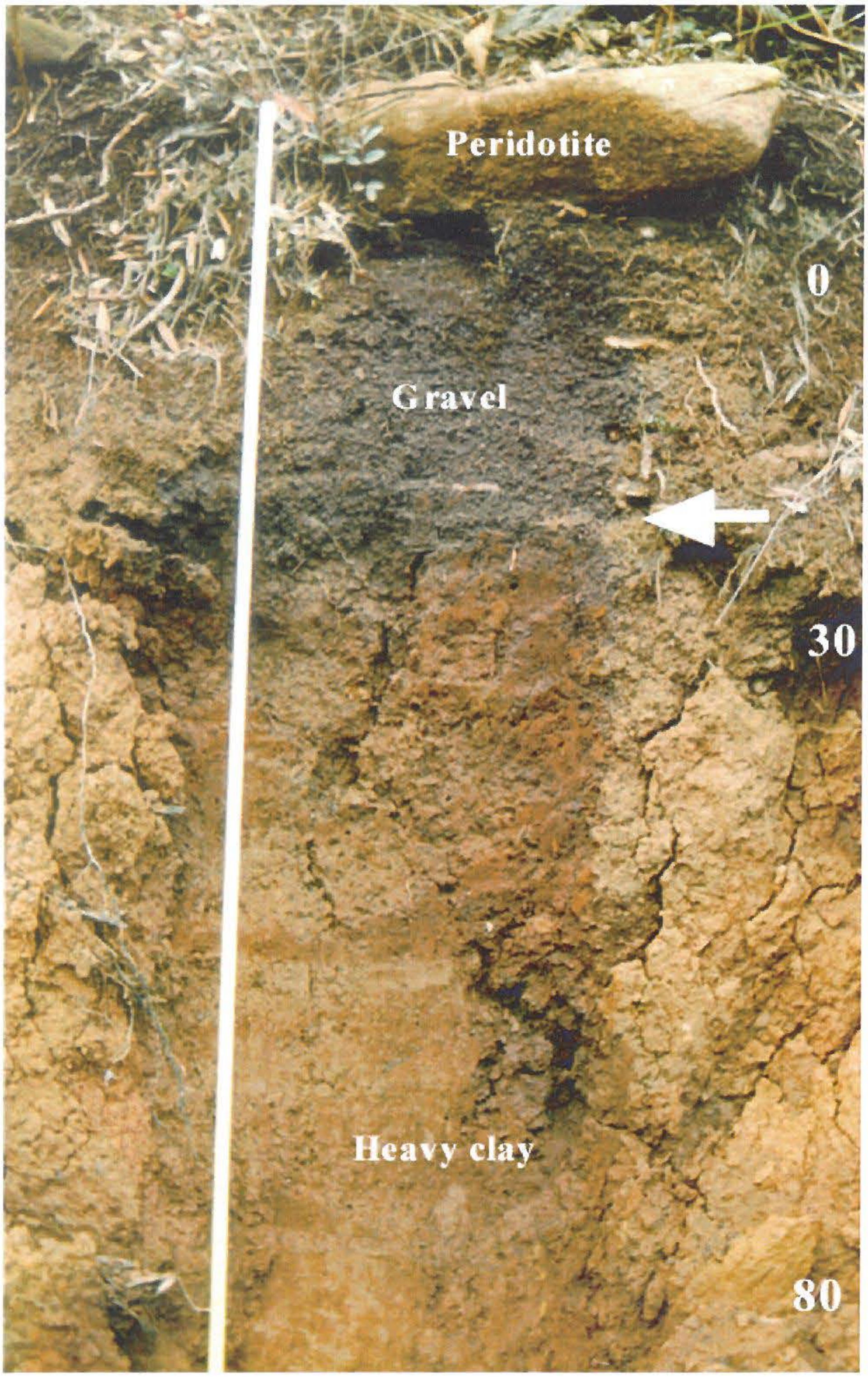


Figure 2.11 An eroded oxisol profile on a road cutting below Mt Me Mwa at Kouaoua. Peridotite rock is found throughout the profile. Gravel is abundant in the A horizon from 0-30 cm. The B horizon is composed of heavy clay. An arrow indicates the transition between the A and B horizons.

of these profiles is given in table 2.3. Measures of soil structure, hydraulic conductivity and chemical composition were carried out on flat bare eroded oxisol using techniques (table 2.2) given in Appendix 1 and Appendix 2.

Eroded oxisol (sol ferralitique ferritique erodé: Latham *et al*, 1978) physical and chemical properties vary depending on their location in the landscape. On steep slopes and ridgelines, eroded oxisol is often very shallow and interrupted by rocky outcrops of peridotite (Jaffré, 1980). Soil surveys of road cuttings (fig. 2.11) indicate that eroded oxisol in valleys are physically similar to iron crust oxisols except that they are much shallower (1-10 m deep) and contain erosion debris such as peridotite. The A horizon is composed of sandy loam containing coarse gravel (26% of sample weight) mixed with larger debris that may form a distinct layer (40 cm deep) above the ferrous clay B horizon. The average total porosity is very high (72% by volume) because gravels contain abundant pore spaces (average pore size 1.6 mm) between aggregates. However, measures of hydraulic conductivity (K) show that bare eroded oxisol is less permeable ($K > 300$ mm hr^{-1}) than iron crust oxisol and retains higher levels of moisture (9.4% by volume) because fine particle loam and clay are common in the A horizon. Roots < 2 mm in diametre exhibit a similar pattern of abundance to the A horizon of iron crust oxisols and become rare on contact with clayey B horizon which contains few macropores.

The A horizon tends to be less acidic (pH 5.2) and have a higher cation exchange capacity than iron crust oxisol at Plaines des Lacs (table 2.2). Heavy metals such as nickel and manganese are more abundant that in iron crust oxisols because weathered peridotite minerals are abundant throughout the profile.

2.4.4 Vegetation

An aerial photograph of Mt Mé Mwa indicates that high altitude parts of Kouaoua support three vegetation types (fig. 2.12). Montane rainforest is confined to the mountain summits above 800 m a.s.l, and contains rainforest tree species such as *Metrosideros nitida*, *Xanthomytrus heighenenesis*, *Gymnostoma glaucescens*, *Nothofagus balansae* and *Agathis ovata*. Between 600 and 800 m a.s.l, *Gymnostoma intermedium* is the most common tree species and forms pure canopy forests < 17 m tall (fig. 2.13) with an open emergent canopy of *Araucaria montana* < 30 m in height (Jaffré, 1995). The inter-plateau area between 400 and 600 m a.s.l has been heavily eroded by mining and contains extensive mine overburden terraces.

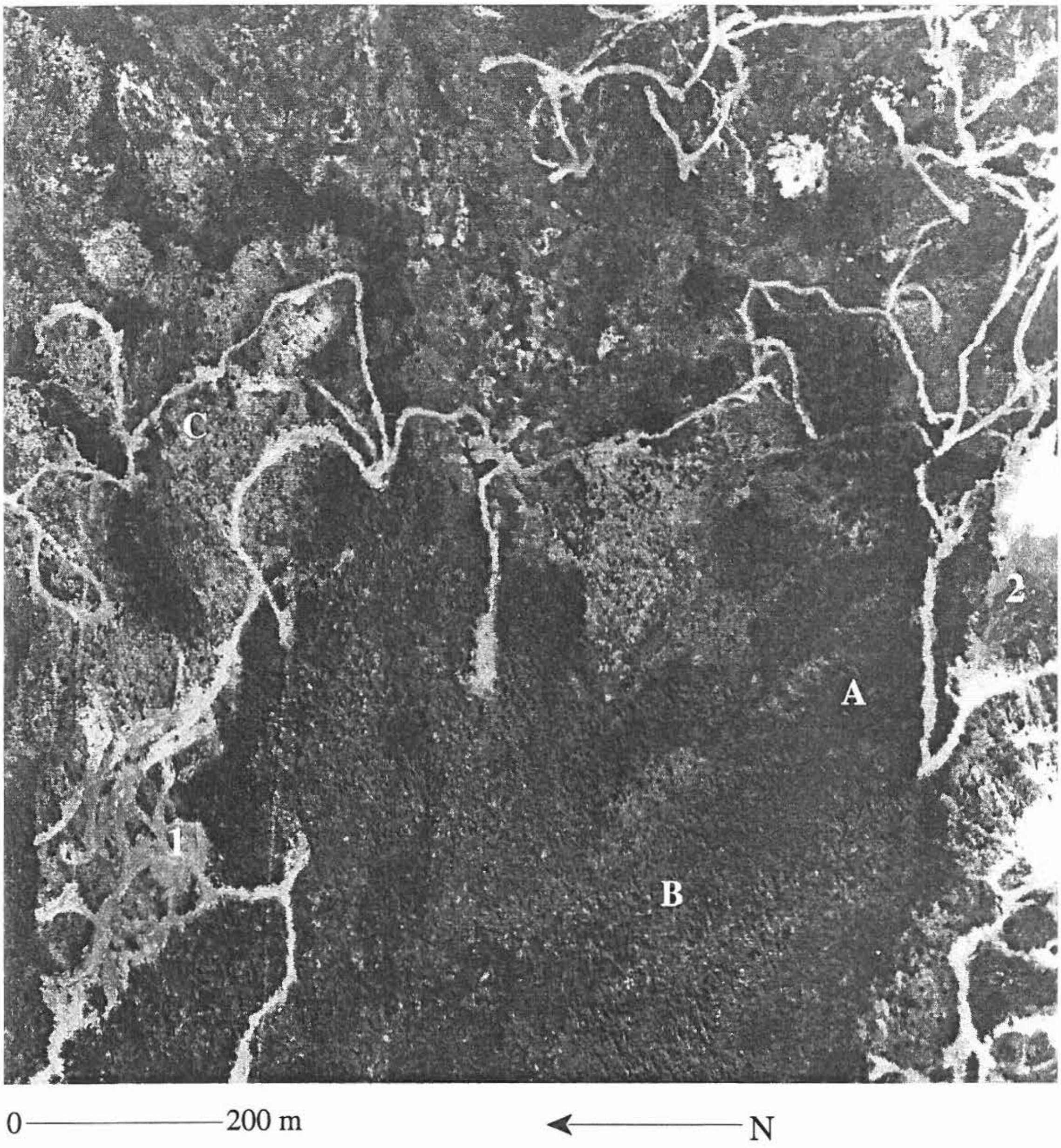


Figure 2.12 An aerial photograph taken in 1976 showing vegetation on Mt Me Mwa at Kouaoua. Black areas indicate *Gymnostoma intermedium* forest (A). Dark grey areas indicate a mixture of montane rainforest and *G. intermedium* forest (B) with emergent *Araucaria montana* trees. Light grey areas indicate woody sedge maquis with an open canopy of *A. muelleri* (C). The field sites on mine overburden and eroded oxisol are indicated as 1 and 2. Note numerous prospecting roads through woody sedge maquis.

Figure 2.13 Unburnt *Gymnostoma intermedium* dominated forest (right) and burnt forest (left) on slopes of Mt Me Mwa at Kouaoua. Note emergent *Araucaria montana* above the *G. intermedium* tree canopy and in the burnt area.

Figure 2.14 Woody sedge maquis with an open canopy of *Araucaria montana* trees on eroded oxisol slopes below *Gymnostoma intermedium* forest at Kouaoua.

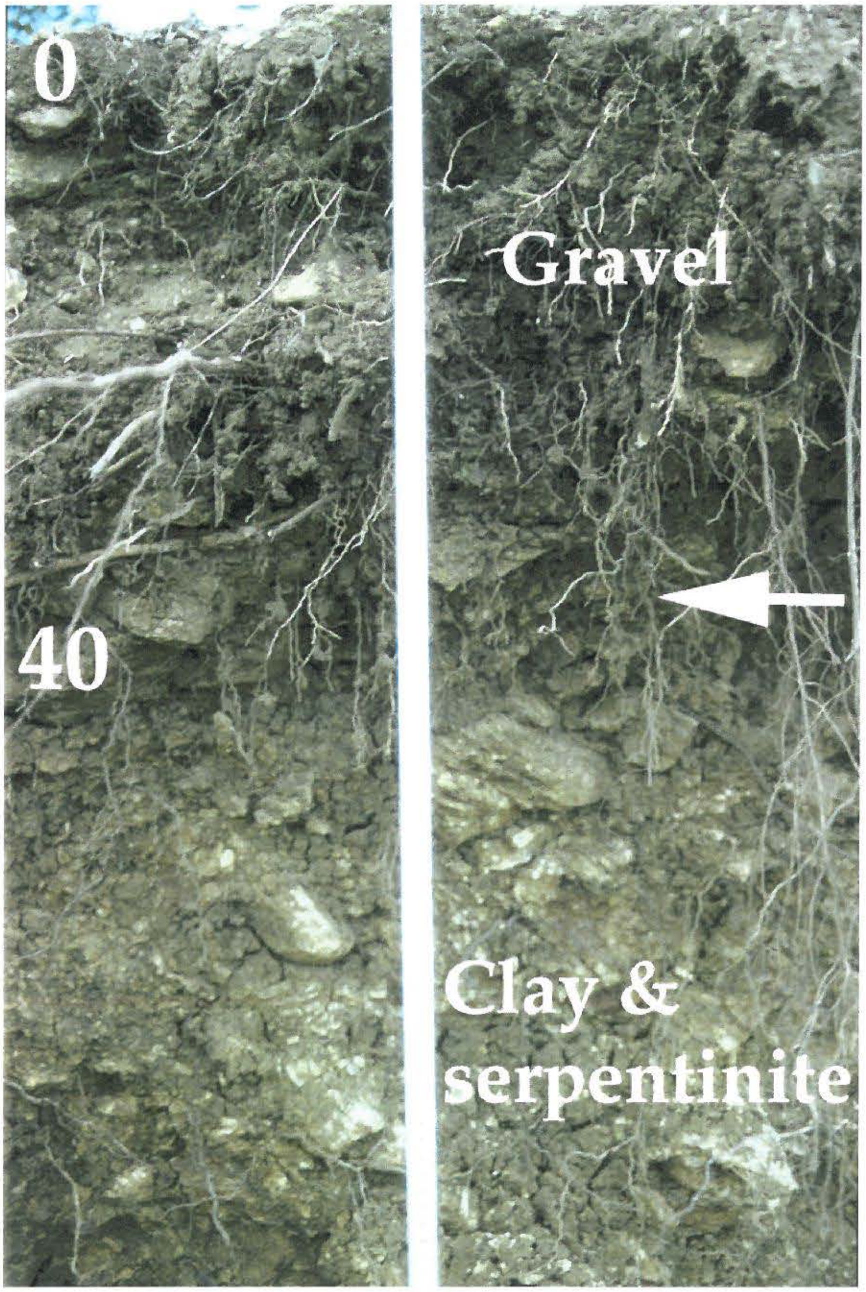


Figure 2.15 A hypermagnesian soil profile from a foot slopes road cutting at the base of the Mea mine at Kouaoua. The gravel A horizon contains abundant roots from 0-40 cm. The B horizon is composed of a mixture of serpentinite rocks and clay. An arrow indicates the transition between the A and B horizons.

A previous floristic survey above Méa mine indicates that terraced areas once supported forest and woody sedge maquis containing *Gymnostoma intermedium* (Veillon, 1978). Slopes and ridgelines surrounding these terraces contain a low open woody sedge maquis < 2 m tall with *Araucaria rulei* (Araucariaceae) forming an open strata of trees 10-15 m in height (fig. 2.14) (Jaffré, 1995). Woody sedge maquis is common on north facing slopes and has also invaded certain ridgelines to an altitude of 800 m a.s.l. Valleys often contain pockets of *Gymnostoma intermedium* forest surrounded by woody sedge maquis.

2.5 *Gymnostoma chamaecyparis* communities on serpentinite

2.5.1 Geographic setting

Serpentinite outcrops at Kouaoua are found at the base of valleys at altitudes ranging from 80 m to 300 m a.s.l. These outcrops are often very steep (30-40°) and contain numerous landslips arising from mine prospecting.

2.5.2 Climate

Mean monthly rainfall, evaporation and temperature for the Kouaoua valley are given in fig. 2.4. Average annual temperatures are slightly higher (23°C) than high altitude parts of Kouaoua, and maximum temperatures often exceed 30°C during summer. Minimum temperatures rarely descend below 15°C. Valleys at the base of the Kouaoua range receive less than 2,000 mm yr^{-1}. On average, rainfall varies seasonally between 60 mm in September and 300 mm in January. However, rainfall records indicate that valleys at the base of Kouaoua may receive less than 20 mm from July to December. Climatic records at Ponerihouen to the north of Kouaoua indicate that evaporation is high in coastal areas due to the higher average temperatures and continual influence of sea breezes.

2.5.3 Hypermagnesian soil

Four hypermagnesian soil profiles were described from road cuttings at the base of Méa mine using guidelines outlined by McDonald *et al* (1990). A summary of the morphological characteristics of these profiles is given in table 2.3. Measures of soil structure, hydraulic conductivity and chemical composition were carried out on level bare hypermagnesian soil using techniques (table 2.2) given in Appendix 1 and Appendix 2.

Hypermagnesian soils (sol brun hypermagnesien: Latham *et al*, 1978) (table 2.3) are the product of chemical weathering and erosion of serpentinite. Soils found on steep slopes are shallow (< 70 cm), highly erodable and restricted to depressions between extensive outcrops of platy serpentinite rock. Soil A and B horizons are poorly developed and composed of coarse textured clay containing a mixture of weathered serpentinite boulders, cobbles, gravel and clay smectites. Bare serpentinite rock surfaces surrounding soil pockets are often very friable and contain magnesium silicate deposits. Screes and active slips on steep slopes have created deeper, more developed (90-120 cm) soil deposits on foot slopes at the base of the Kouaoua range. Soil profile descriptions through foot-slope hypermagnesian soil (fig. 2.15) reveal that the clayey A horizon contains fine colluvial material which suggests greater landscape stability. Roots < 2 mm in diametre are abundant in the A horizon at both localities and may also penetrate to the weathered serpentinite rock because of the coarse textured nature of the clayey B horizons. The soil moisture of the A horizon is relatively high (29.2%) possibly due to the high clay content of fine soil fractions (table 2.2) which contains hydrophyllic montmorillonite as a common clay mineral (Latham *et al*, 1978). Hydraulic conductivity (K) is relatively high ($K = 200$ mm hr^{-1}) despite the high clay content and may contribute to frequent periods of water stress for plant communities because of the low rainfall.

The chemical composition of these soils (table 2.2) is similar to other serpentinite areas (Jaffré & Latham, 1974; Jaffré, 1980) except for higher levels of iron originating from colluvial oxisol slope material (Jaffré, 1969). The pH of hypermagnesian soil is slightly alkali due to the high magnesium silicate content of the soil. Nickel and manganese concentrations are moderately high in hypermagnesian soil, but are unlikely to exert toxic effects on plants because of their low solubility under alkali pH conditions (Jaffré, 1980; Becquer, 1997). However, the high levels of exchangeable magnesium may generate problems in calcium absorption by plants because of the very high Ca : Mg ratio imbalance found in this soil type (Jaffré, 1980).

2.5.4 Vegetation

An aerial photograph of the landscape below the Méa mine (fig. 2.16) reveals that vegetation on steep serpentinite outcrops above the Kouaoua valley floor occurs as isolated, disturbed stands of < 1 ha. These stands are separated from one another by active screes of eroded serpentinite rock arising from mine prospecting. The patches of vegetation are largely

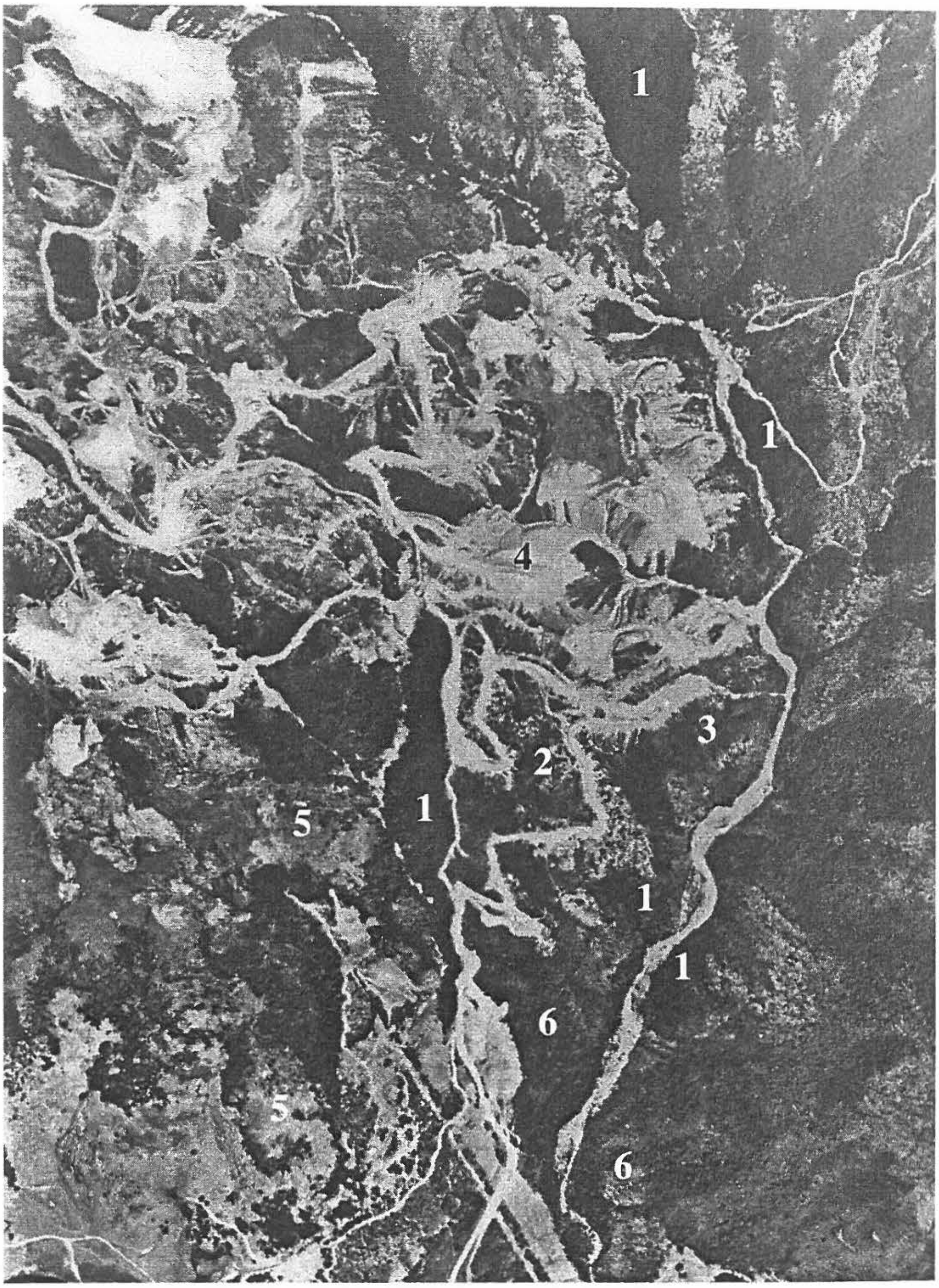


Figure 2.16 An aerial photograph of the valley bottom and serpentinite foot slopes at the base of Mea mine at Kouaoua (taken in1976). Forests on serpentinite occur in valley bottoms and on south facing slopes (1). Tall maquis (2) and open maquis (3) occur on steep serpentinite outcrops containing landslip debris from nickel mine excavations above (4). The valley floor consists of savanna grassland (5). Foot slopes adjacent to serpentinite outcrops support *Acacia spirorbis* shrubland (6).

Figure 2.17 Tall maquis on a serpentinite outcrop below Mea mine at Kouaoua. *Gymnostoma chamaecyparis* is the dominant tree species. Note erosion from prospecting roads on slopes above the vegetation formation.

dominated by a shrubby maquis < 5 m high (Jaffré, 1969). *Gymnostoma chamaecyparis* is the most common woody species in this maquis type and often forms a pure open canopy (fig. 2.17). *G. chamaecyparis* dominated forest formations < 10 m in height, occur as small stands < 0.5 ha in valley bottoms and on steep south facing slopes. Open maquis is more common on north facing serpentinite outcrops and is replaced by a tall maquis of large *G. chamaecyparis* trees on areas containing deeper hypermagnesian soil.

The vegetation on basalts and alluvium at the base of the Kouaoua massif consists of exotic pasture species, *Babingtonia pinifolia, Casuarina collina* and *Acacia spirorbis* (Jaffré, 1969). Stands of *Acacia spirorbis* will also extend to altitudes of 400 m a.s.l on serpentinite outcrops, but are largely restricted to areas containing eroded oxisol landslip material (Jaffré, 1969).

Chapter 3

Ultramafic plant succession & fire

3.1 Introduction

3.1.1 Aims

This chapter examines the floristics and structure of vegetation found on iron crust oxisol, eroded oxisol and hypermagnesian soils, and the effects of fire. Firstly, does the vegetation variation on each substrate primarily represent succession following fire rather than a response to local substrate or climate variation? Secondly, are the species fire tolerant, suggesting a long association and adaptations to cope with fire? Thirdly, 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? These questions are addressed at each of the study regions described in chapter 2; (i) iron crust oxisol sites at Plaines des Lacs[†], (ii) eroded oxisol sites at Kouaoua and (iii) hypermagnesian sites at Kouaoua.

Each study region is considered separately, using similar methods, and finally the three vegetation types are compared. The survey at Plaines des Lacs was the most extensive of the three surveys. It established patterns and suggested processes that could be examined more briefly at the Kouaoua sites.

3.2 *Plaines des Lacs*: Vegetation on iron crust oxisol

3.2.1 Methods

3.2.1.1 Survey of floristics and habitat

Study sites were selected at 88 accessible localities in five regions (Yaté Lake, Creek Pernod, Goro Plateau, Port Boisé and Prony; fig. 3.1) across the study area so as to sample the range of vegetation. All sites were located on massive iron crust or gravel substrates on low relief plateaus, avoiding

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[†] The analysis of the Plaines des Lacs region is published as McCoy *et al* (in press).

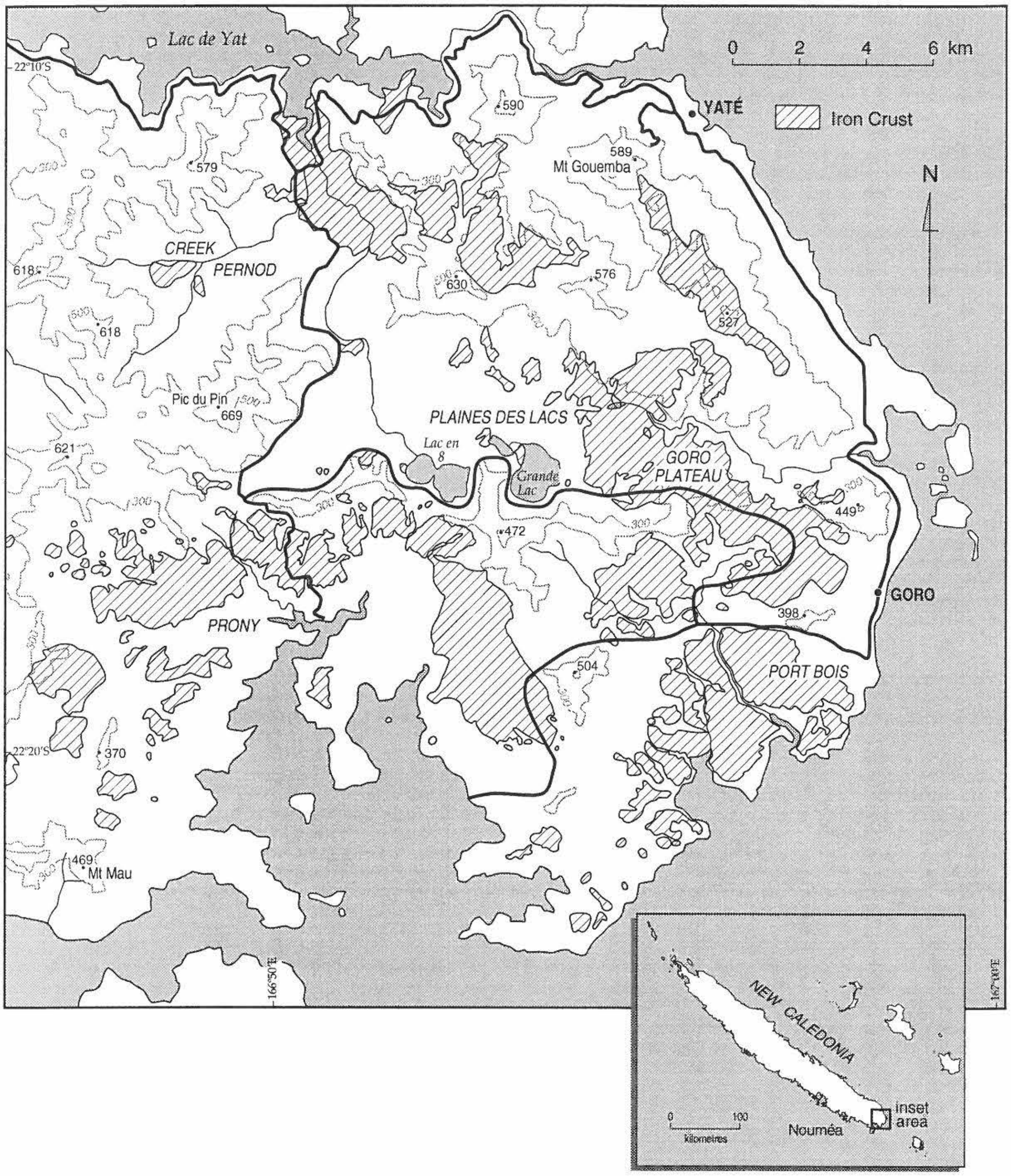


Figure 3.1 (i) Inset map shows the location of the study area. (ii) Main map shows the distribution of iron crust soils and the survey regions.

swamps and water courses. The most common vegetation type on such areas consists of open to tall maquis or forest containing abundant *Gymnostoma deplancheanum* trees. Certain forests types have a restricted geographic 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 composition and species diversity varied with the vegetation type, so the number of sites and their area was varied as follows: 35 sites of 100 m^2 in open maquis, 23 sites of 196 m^2 in tall maquis and 30 sites of 256 m^2 in forest. Due to the absence of large rainforest patches on iron crust, six sites of 500 m^2 in rainforest were sampled in neighbouring valleys on eroded oxisol. An additional three rainforest sites described by Jaffré & Veillon (1991) and Read *et al* (1995) are included for comparison. Records were made at each site of: altitude (m), slope (degrees), soil type (cover of surface iron crust (%) vs gravel), annual rainfall (mm) (Danloux, 1987), vegetation cover (%; estimated visually), canopy height (m), canopy cover (%), litter cover (%), average litter depth (cm; 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 (Goro clan elder; pers. comm) and M. Boulet (Service de l'Environnment, Province Sud; pers. comm.), Heckel (1892, 1913), Chevalier (1996), contemporary newspaper and gendarmerie 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* from various sites, and were sufficiently well defined and regular to suggest that they were of annual frequency. Annual rings are apparent in most conifers at similar latitudes and with seasonal climates elsewhere in the S. W. Pacific (Ash, 1985; Ash, 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 (characterised by abundant large vessels) were also noted in several *Arillastrum gummiferum* some of which possessed fire scars.

Statistical analysis focussed on maquis and forest. 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 multi dimensional scaling (MDS), using the PATN program (Belbin, 1989). Environmental and vegetation parameters were regressed on all 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 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 a succession index. The index was preferred to using the estimated time since the last fire because 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 relationship of environmental factors to the succession index.

3.2.1.2 Structure

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

3.2.1.3 Dispersal

All species recorded in the vegetation structure survey were scored as either wind dispersed or animal dispersed based on characteristics of their fruit or seed.

3.2.1.5 Fire tolerance

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: Lamont *et al*, 1991)(Gill, 1981).

3.2.1.5 Fire susceptibility

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

$$F_s = aL_d C e^{-bm}$$

where a and b are constants ($a \approx 50, b \approx 0.22$)

L_d = mean litter depth, cm.

C = connectance of fuel

= $2.77\,L_c^2$ if $L_c < 0.6$ and 1.0 if $L_c > 0.6$,

L_c = litter cover as a proportion.

m = wet weight of litter as a ratio to dry weight.

Litter moisture was recorded 7 - 10 days after the last rain at representative sites.

3.2.2 Results

3.2.2.1 Vegetation structure

Figure 3.2 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. The floristic survey of iron crust sites recorded 271 species of which 102 were excluded from further analysis because they occurred on less than three sites. A further 50 species only occurred in the rainforest sites.

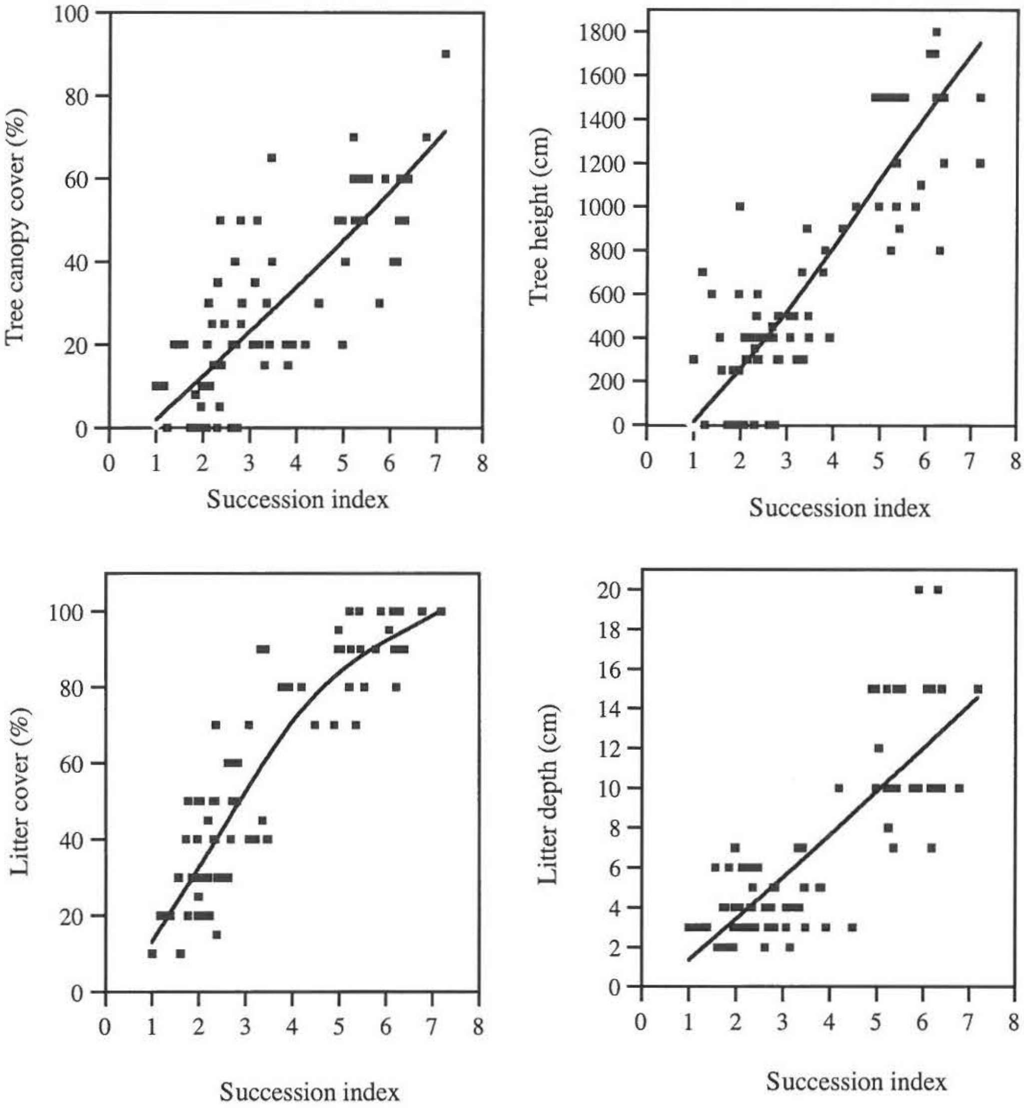


Figure 3.2 Tree canopy cover, tree height, litter cover and litter depth in the 88 sites at Plaines des Lacs plotted against the succession index based on a PCA axis. Trends are shown by fitted spline curves.

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 (Belbin, 1989). 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 weak relationships with altitude ($r^2 = 0.19$), rainfall ($r^2 = 0.14$), and slope ($r^2 = 0.07$) (table 3.1). 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 of the succession index indicated a significant regional effect ($F = 6.45$, $P < 0.0001$) and slope ($F = 6.47$, $p = 0.01$), however, the slope effect was attributable to 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 3.3 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. Figure 3.4 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 ($I < 3.0$) which are initially abundant but absent later. A second group of 29 persistent species are present from start to finish ($I = 3.0$-4.30) while the third ($I = 4.31 - 5.51$) and fourth ($I > 5.51$) groups of 59 and 56 species are only present from the middle and late stages.

3.2.2.2 Structure

Stem size class distributions for each vegetation type are shown in fig. 3.5 and distributions for selected species are shown in fig. 3.6. 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 species such as *Montrouziera sphaeriodea, Tristaniopsis guillanii* var. *balansae* and *T. callobuxus* exhibit a notable decline in regeneration. This decline coincides with increases in *Gymnostoma* trunk diametre and stem density from open maquis (1000 stems ha^{-1}) to tall maquis (2800 stems ha^{-1}).

Table 3.1: Results of multiple linear regression analysis of environmental factors in relation to the four MDS axis scores, fitted simultaneously, showing r^2 and F ratios. Significance is indicated, $p > 0.05$ = ns, $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = *** .

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

Family	Species		I
Cyp.	*Costularia pubescens* Raynal		1.94
Epac.	*Dracophyllum involucratum* Brongniart & Gris		2.16
Cyp.	*Costularia comosa* (C. B. Clarke) Kükenthal		2.18
Myrt.	*Xanthostemon aurantiacum* (Brongniart & Gris) Schlechter	F	2.20
Myrt.	*Eugenia* sp.	F	2.23
Myrt.	*Babingtonia leratti* Dawson	F	2.32
Sapot.	*Troettea lissophylla* Pierre ex Baillon	F	2.53
Prot.	*Grevillea gillvrayi* W. J. Hooker	F	2.54
Flac.	*Homalium kanaliensis* (Veillard) Briquet	F	2.55
Sant.	*Exocarpos baumanii* Stauffer	F	2.58
Cyp.	*Costularia arundinacea* (Solander ex Vahl) Kükenthal		2.59
Orch.	*Dendrobium steatoglossum* H. Reichenbach	F	2.62
Cun.	*Pancheria veillardii* Brongniart & Gris	F	2.64
Denn.	*Pteridium esculentum* (Forster) Cockayne	F	2.65
Myrt.	*Tristaniopsis callobuxus* Brongniart & Gris	F	2.66
Orch.	*Eriaxis rigida* H. Reichenbach	F	2.68
Cyp.	*Costularia nervosa* Raynal		2.74
Rham.	*Alphitonia neocaledonica* (Schlechter) Guillaumin		2.76
Rub.	*Moranda* sp.		2.79
Good.	*Scaevola beckii* Zahlbrucker	F	2.79
Prot.	*Stenocarpos comptonii* S. Moore	F	2.86
Celas.	*Geniostoma celastrenium* Baillon	F	2.87
Epac.	*Dracophyllum verticillatum* Labillardière		2.90
Prot.	*Stenocarpus umbelliferus* (Forster) Druce	F	2.92
Cun.	*Pancheria confusa* Guillaumin	F	2.92
Dill.	*Hibbertia lucens* Brongniart & Gris ex Pancher & Sébert	F	2.97
Myrt.	*Uromyrtus emarginatus* (Pancher ex Brongniart & Gris) Bur.	F	3.22
Euph.	*Longetia buxoides* (Baillon) A. Shaw	F	3.23
Cyp.	*Gahnia novacaledonensis* Benl	F	3.31
Epac.	*Dracophyllum ramosum* Pancher ex Brongniart & Gris		3.33
Flag.	*Flagellaria neocaledonica* Schlechter	F	3.41
Gutt.	*Montrouziera sphaeriodea* Pancher ex Planchon & Triana	F	3.45
Myrt.	*Tristaniopsis guillainii* Veillard ex Brongniart & Gris	F	3.45
Aral.	*Polyscias pancheri* (Veillard) Harms		3.49
Rut.	*Myrtopsis sellingii* Guillaumin	F	3.53
Lora.	*Amyema scandens* (Tieghem) Danser		3.57
Cyp.	*Lepidosperma perteres* C. B. Clarke	F	3.61
Rub.	*Tarenna hexamera* (Guillaumin) Jérémie	F	3.61
Rub.	*Tarenna microcarpa* (Guillaumin) Jérémie		3.89
Smi.	*Smilax* sp.	F	3.93
Sapin.	*Gioua glauca* (Labilliardière) Radlkofer	F	3.95
Podo.	*Dacrydium araucarioides* Brongniart & Gris		3.95
Epac.	*Styphelia veillonii* Virot		3.99
Cas.	*Gymnostoma deplancheanum* (Miquel) L. Johnson		4.02
Dill.	*Hibbertia pancheri* (Brongniart & Gris) Briquet	F	4.05
Rub.	*Gardenia aubryi* Veillard	F	4.12
Xanth.	*Lomandra insularis* Schlechter	F	4.16
Lil.	*Dianella intermedia* Endl.	F	4.19
Orch.	*Bulbophyllum* sp.		4.21
Myrt.	*Syzygium ngoyensis* (Schlechter) Burret	F	4.22
Rubi.	*Ixora francii* Schlechter & Krause	F	4.23
Apoc.	*Parsonsia carnea* Pancher	F	4.28
Sant.	*Exocarpos neocaledonicus* Schlechter & Pilger	F	4.28
Thym.	*Solmsia calophylla* Baillon		4.29
Cun.	*Codia montana* J. R. & G. Forster	F	4.29
Cyp.	*Gahnia serberiana* Kunth		4.34
Elae.	*Elaeocarpos alaternoides* Brongniart & Gris	F	4.37
Orch.	*Dendrobium verruciferum* H. Reichenbach	F	4.39
Dill.	*Hibbertia veillardii* (Brongniart & Gris) Gilg	F	4.43
Rut.	*Halphordia kendac* (Montrouzier) Guillaumin	F	4.48
Euph.	*Phyllanthus francii* Guillaumin		4.48
Thym.	*Wickstroemia indica* (L.) Meyer	F	4.49
Ruta.	*Medicosma leratti* (Guillaumin) Hartley	F	4.53
Schi.	*Schizaea laevigata* Mettenius	F	4.57
Myrt.	*Austromyrtus stricta*	F	4.63
Apoc.	*Alyxia sp.*		4.67
Aral.	*Mydocarpos lanceolata* Dubard & Viguier		4.68
Myrs.	*Rapanea diminuta* Mez	F	4.69
Cun.	*Pancheria elliptica* Pampanini	F	4.69
Apo.	*Alstonia coriaceae* Pancher ex S. Moore	F	4.70
Apoc.	*Rauvolfia semperflorens* (Mueller Argovie) Schlechter	F	4.71
Sapot.	*Beccariella baueri* (Montrouzier) Aubréville	F	4.80
Epac.	*Styphelia pancheri* (Brongniart & Gris) F. Mueller		4.81
Sapin.	*Cupaniopsis oedipoda* Radlkofer		4.91
Celas.	*Maytenus fournieri* (Pancher & Sébert) Loesener	F	4.94
Gutt.	*Garcinia neglecta* Veillard	F	4.94
Epac.	*Styphelia* gp *cymbulae* (Labilliardière) Sprengel		4.95
Rub.	*Psychotria rupicola* (Baillon) Schlechter	F	4.95
Orch.	*Liparis chalendei* Finet		4.96
Join.	*Joinvillea plicata*		4.96
Lin.	*Hugonia penicillanthemum* Baillon	F	4.98
Aral.	*Mydocarpos fraxinifolius* Brongniart & Gris		5.01
Mel.	*Dysoxylum canalensis* (Baillon) C. DC.		5.16
Rut.	*Comptonella drupacea* (Labillardière) Guillaumin		5.19

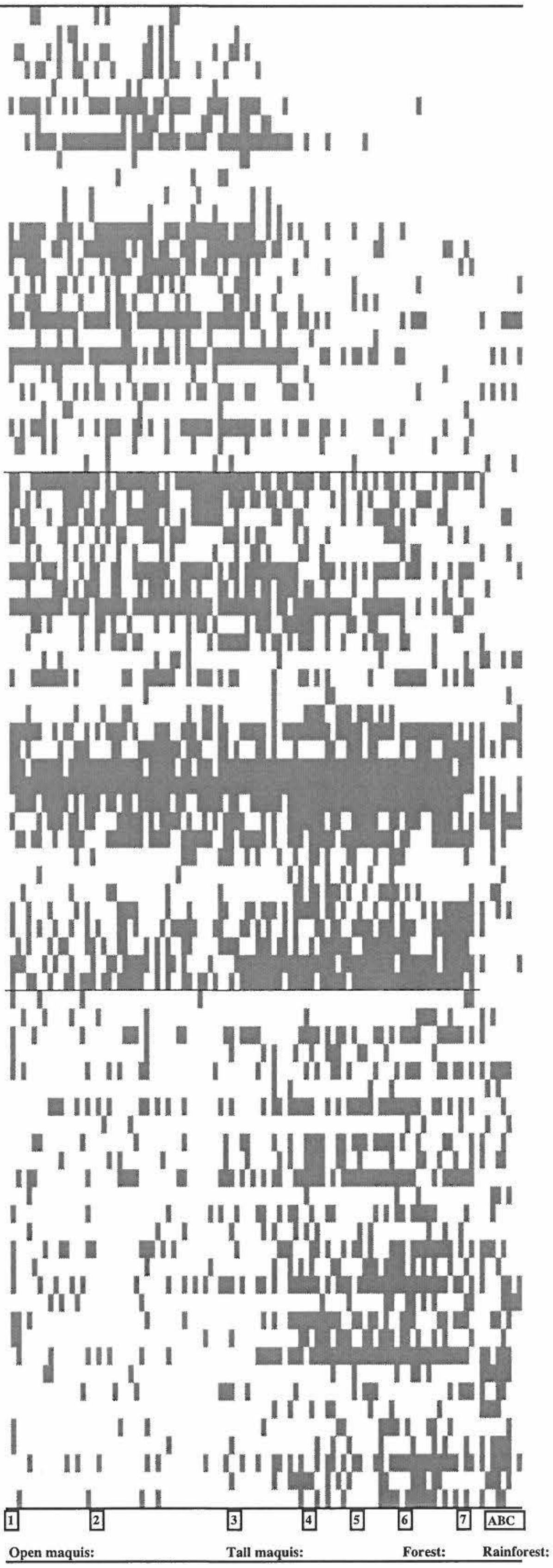


Figure 3.3 Presence of species (shaded) in the 88 iton crust sites ranked by the succession index (SI). Species are ranked by the species index (I). Horizontal lines indicate the boundaries between early, persistent, mid-late and late successional groups of species. F indicates resprouters from rootstocks. 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) Rivière Bleue on slopes (2.79 ha)(Jaffré & Veillon, 1990).

Family	Species		I
Myrt.	*Austromyrtus prolixa*		5.19
Flac.	*Casearia silvana* Schlechter		5.23
Verb.	*Oxera neriifolia* (Montrouzier) Beauvisage	F	5.23
Apoc.	*Pagiantha cerifera* (Sebert & Pancher) Markgraf	F	5.27
Viol.	*Agatea deplanchei* Brongniart & Gris ex Guillaumin	F	5.28
Pitt.	*Pittosporum haematomallum* Guillaumin		5.29
Myrt.	*Arillastrum gummiferum* Pancher ex Baillon		5.31
Laur.	*Litsea triflora* Guillaumin		5.31
Smil.	*Smilax purpurata* J. R. & G. Forster		5.32
Sapin.	*Guioa villosa* Radlkofer	F	5.33
Conn.	*Santalioides balanseanum* (Baillon) Schellenberg		5.36
Myrt.	*Tristaniopsis macphersonii* J. W. Dawson		5.37
Myrs.	*Rapanea assymetrica* Mez	F	5.38
Big.	*Deplanchei speciosa* Veillard		5.43
Orch.	*Malaxis torena* (H. Reichenbach) Kuntze		5.44
Euph.	*Phyllanthus pronyensis* Guillaumin		5.51
Annon.	*Xylopia pancheri* Baillon		5.52
Aqui.	*Ilex sebertii* Pancher & Sébert		5.52
Apoc.	*Alstonia lenormandii* Heurck & Mueller Argovie	F	5.53
Eben.	*Diospyros parviflora* (Schlechter) Bakhuizen		5.53
Monim.	*Hedycaryia parviflora* Perkins & Schlechter		5.54
Gutt.	*Garcinia balansae* Pierre	F	5.54
Euph.	*Bocquillonia spicata Baillon*		5.55
Gutt.	*Garcinia amplexicaulis* Veillard	F	5.56
Glei.	*Stromapteris sp.*		5.59
Rub.	*Psychotria cardioclamys* (Baillon) Schlechter		5.59
Rub.	*Tarenna rhypalostigma* (Schlechter) Bremekamp		5.60
Cun.	*Acsmithia meridionalis* (Brongniart & Gris) Hoogland	F	5.61
Thym.	*Lethodon tanaaensis* (Labillardière) Aymonin	F	5.63
Smil.	*Smilax orbiculata* Labillardière		5.66
Sapin.	*Cupaniopsis myrmoctana* Radlkofer		5.66
Hipp.	*Dicarpellum neocaledonica* (Guillaumin) A. C. Smith		5.67
Euph.	*Austrobuxus rubiginosus* (Guillaumin) A. Shaw		5.67
Ole.	*Osmanthus austrocaledonicus* (Veillard) Knoblauch	F	5.70
Sapot.	*Planchonella kuebuniensis* Aubréville		5.71
Sapin.	*Cupaniopsis glomerfolia* Radlkofer		5.72
Elae.	*Dubouzetia confusa* Guillaumin & Virot	F	5.80
Gram.	*Greslania rivularis* Balansa		5.82
Mel.	*Dysoxylum bijugum* (Labillardière) seeman		5.83
Pitt.	*Pittosporum gracile* Pancher ex Brongniart & Gris		5.85
Rut.	*Melicope veillardii* Baillon		5.87
Sapo.	Beccariella sebertii (Pancher) Pierre		5.90
Rub.	*Ixora kuakuensis* S. Moore	F	5.90
Myrt.	*Austromyrtus ploumensis* (Daeniker) Burret	F	5.91
Cun.	*Codia arborea* Brongniart ex Guillaumin		5.92
Flind.	*Flindersia fournieri* Pancher & Sébert		5.92
Myrt.	*Rhodamnia andromedoides* Guillaumin	F	5.94
Lind.	*Lindseae nervosa* Mettenius		5.98
Icac.	*Gastrolepis novacaledonensis* Benl		5.99
Eben.	*Diospyros austrocaledonica* Hiern		5.99
Good.	*Scaevola balanseae* Guillaumin		6.00
Pitt.	*Pittosporum deplanchei* Brongniart & Gris		6.01
Prot.	*Stenocarpos trinervis* (Montrouzier) Guillaumin		6.02
Pand.	*Freycinetia* sp. (large leaf)		6.02
Pand.	*Freycinetia novacaledonica* Warburg		6.03
Euph.	*Austrobuxus pauciflorus* A. Shaw		6.03
Myrs.	*Rapanea rouxii* Mez		6.04
Pand.	*Pandanus* sp.		6.05
Adia.	*Adianthum* sp.		6.05
Rub.	*Psychotria semperflorens* (Baillon) Pancher ex Beauvisage	F	6.05
Myrt.	*Metrosideros nitida* (Brongniart & Gris		6.07
Sapot.	*Pycnandra* sp. (J-M. Veillon 5139)		6.07
Myrs.	*Rapanea pronyensis* Guillaumin		6.07
Laur.	*Endiandra sebertii* Guillaumin		6.09
Cun.	*Cunonia veillardii* Brongniart & Gris		6.10
Laur.	*Cryptocarya guillanii* Veillard		6.10
Wint.	*Zygogynum crassifolium* Baillon		6.12
Myrt.	*Piliocalyx laurifolius* Brongniart & Gris		6.12
Aral.	*Arthrophyllum angustatum* (Baillon) Philipson		6.13
Myrt.	*Syzygium austrocaledonicum* (Seeman) Guillaumin		6.14
Pal.	*Basselinia pancheri* Veillard		6.15
Aral.	*Canacoschefflera* sp.		6.17
Rut.	*Dutaillyea trifoliolata* Baillon		6.18
Myrt.	*Piliocalyx eugenioides* Guillaumin		6.23
Sant.	*Exocarpos phyllanthoides* Endlicher	F	6.24
Ana.	*Euroschoenus verrucosus* Engler		6.26
Aral.	*Arthrophyllum balansae* (Baillon) Philipson		6.29
Apo.	*Alyxia clusiophylla* (Baillon) Guillaumin		6.35
Lin.	*Hugonia jenkensii* F. Mueller		6.42
Gutt.	*Calophyllum caledonicum* Veillard		6.42
Hipp.	*Dicarpellum pronyense* (Guillaumin) A. C. Smith		6.43
Aral.	*Mydocarpos crassifolius* Dubard & Viguier		6.46
Prot.	*Beauprea spathulaefolia* Brongniart & Gris		6.47

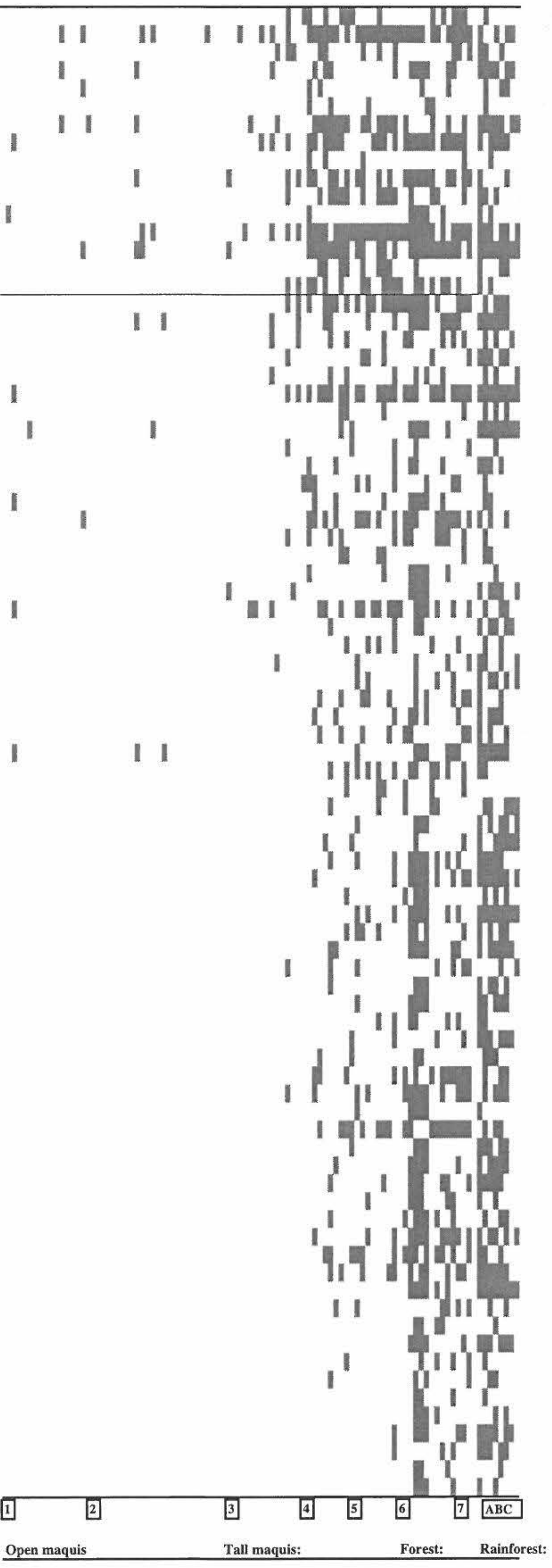


Figure 3.3 Presence of species (shaded) in the 88 iton crust sites ranked by the succession index (SI). Species are ranked by the species index (I). Horizontal lines indicate the boundaries between early, persistent, mid-late and late successional groups of species. F indicates resprouters from rootstocks. 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) Rivière Bleue on slopes (2.79 ha)(Jaffré & Veillon, 1990).

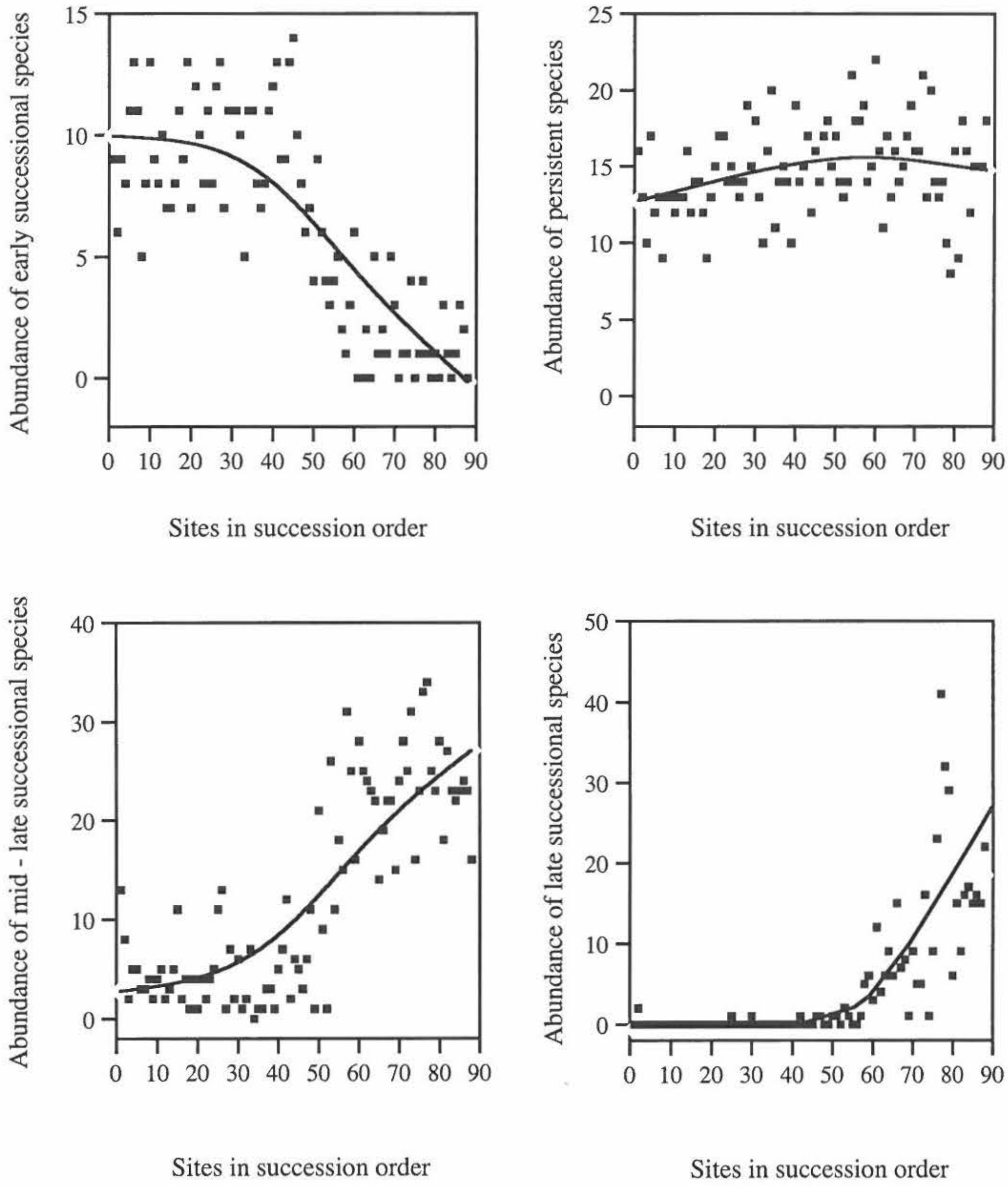


Figure 3.4 The number of early successional, persistent, mid-late successional and late successional species in relation to rank order of sites by the succession index. Trends are shown by fitted spline curves. Note that each successive group contains more species.

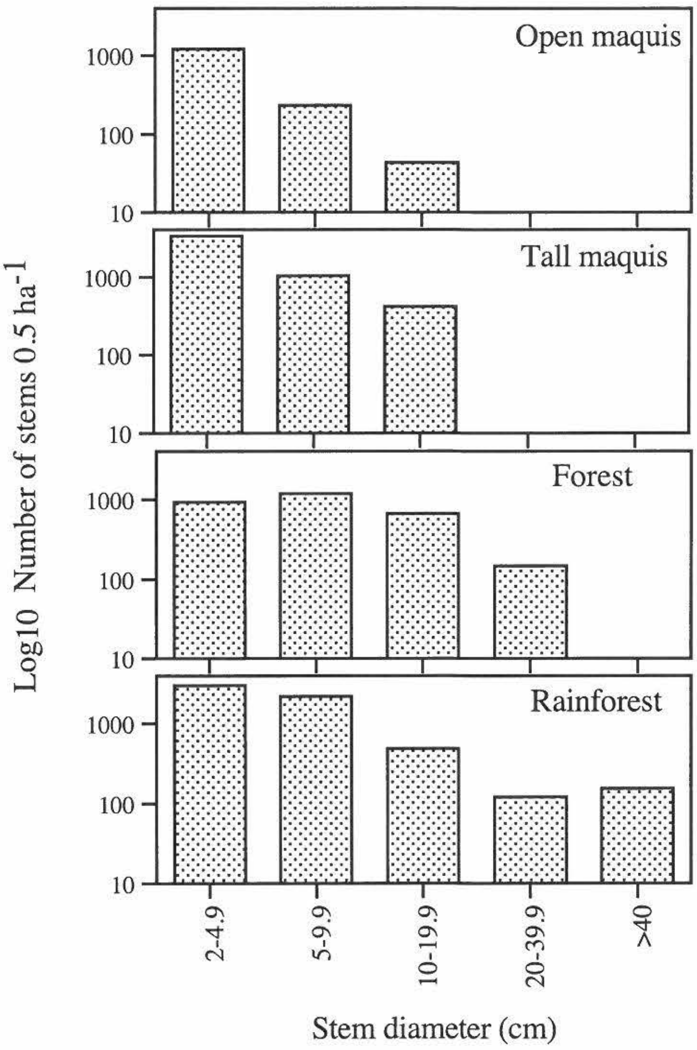


Figure 3.5 Size class distribution (d.b.h.) for all stems in open maquis, tall maquis, forest and rainforest at Plaines des Lacs.

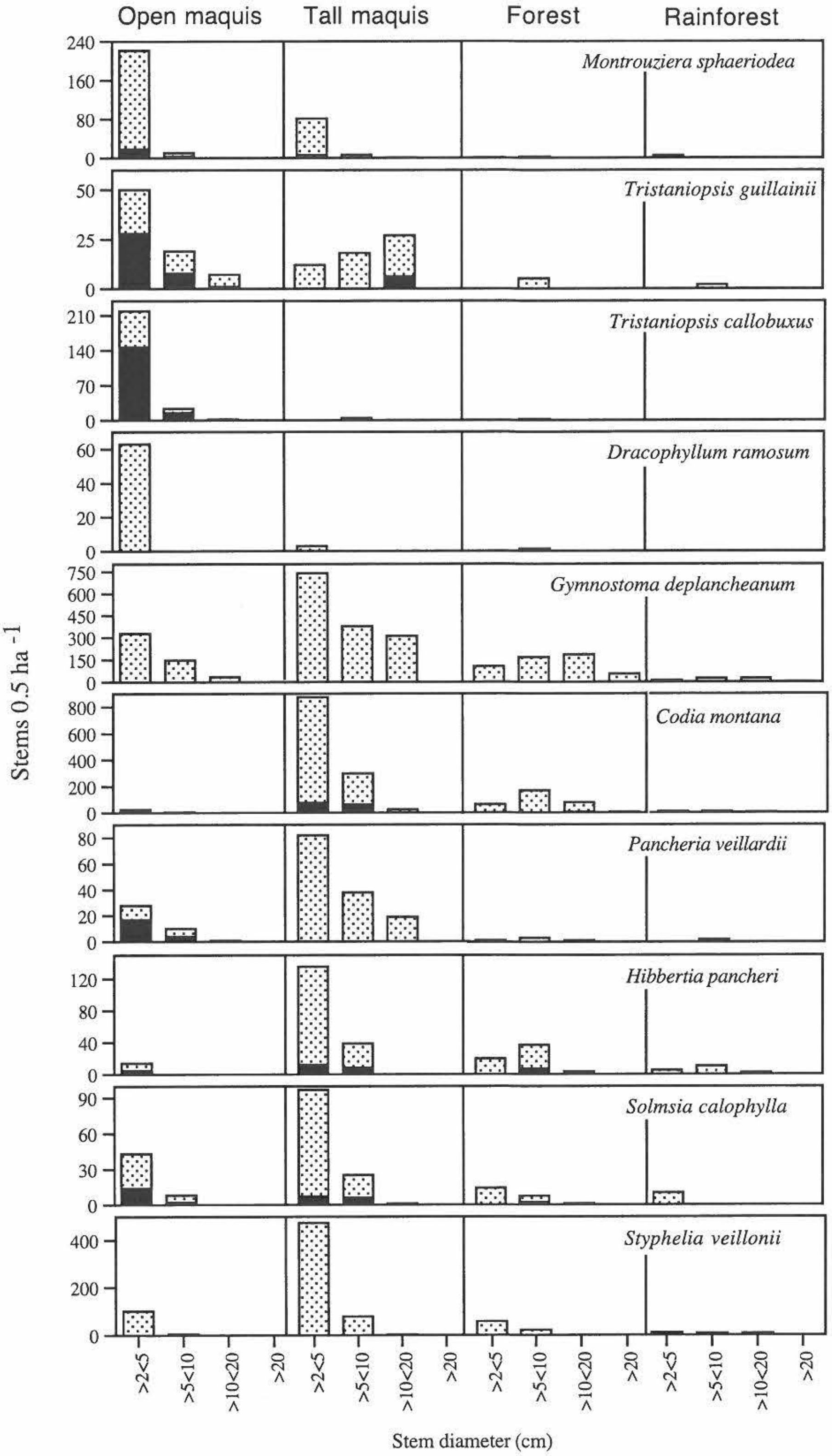


Figure 3.6 Size class distribution (d.b.h.) for stems of select species in open maquis, tall maquis, forest, and rainforest. Black bars represent total number of multistems treated as single stems.

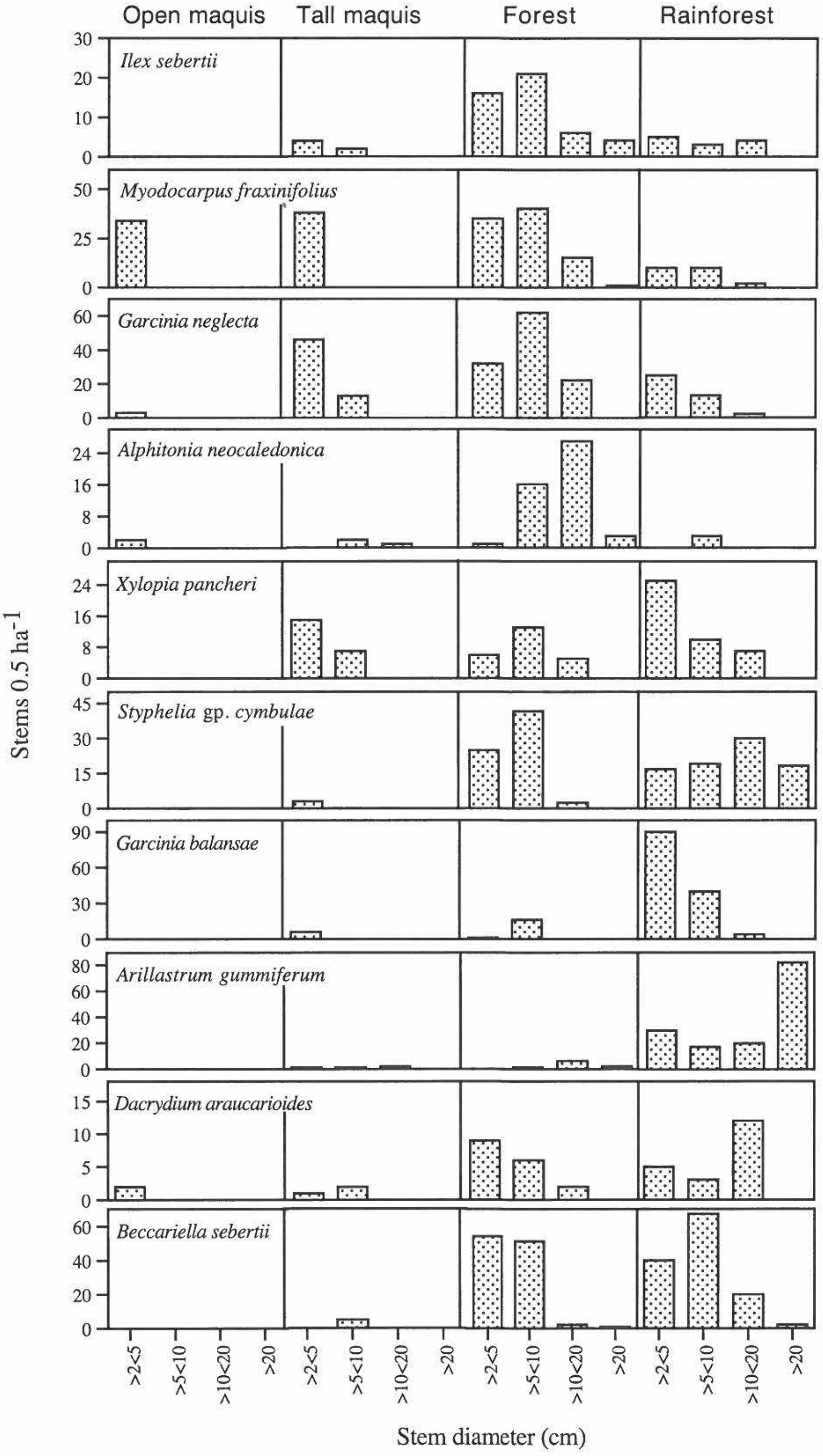


Figure 3.6 Size class distribution (d.b.h.) for stems of select species in open maquis, tall maquis, forest, and rainforest. Black bars represent total number of multistems treated as single stems.

Under this *Gymnostoma* canopy, species such as *Ilex sebertii, Myodocarpus fraxinifolius, Garcinia neglecta, Xylopia pancheri, Styphelia* gp. *cymbulae* first appear as small diametre 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* (fig. 3.6).

3.2.2.3 Growth rings of *Dacrydium araucarioides*

Growth rings in *Dacrydium araucarioides* sections (fig. 3.7) collected from a site which was completely cleared of vegetation in 1970 (C. Tessarolo, pers. comm), had 17-21 growth rings by 1996 suggesting that there is a delay of 5-9 yrs before a tree might be used to indicate the age of the site. Samples from the survey sites suggest that it takes about 55 yr to reach the tall maquis phase and 75 yr to reach the forest stage (fig. 3.8). 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 to 50 years to reach the forest canopy height (17 m), and 100-170 yr to reach 1 m d.b.h.

3.2.2.4 Fire tolerance

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 (fig. 3.9). Some later successional trees, such as *Arillastrum* had one or more fire scars suggesting some fire tolerance. However there are many locations where forests have been killed by fire. Isolated stands of mature *Arillastrum* in tall maquis suggests that the species may have been more widespread in this vegetation type (Papineau, 1989), before increases in the fire frequency restricted it to fire protected sites.

3.2.2.5 Dispersal

Dispersal of most (66%) early successional species is by wind (fig. 3.10). Many of these species (eg. *Gymnostoma, Codia, Grevillea* and *Tristaniopsis* ; refer to chapter 4) produce abundant seed during the wet season, and are often the first to colonise burnt maquis after dry season ground fires. Most (59%) later successional species rely more on animal dispersal (primarily birds, bats and perhaps geckkonid lizards: Bauer & Sadlier, in press). However, some common forest and rainforest species are wind dispersed (eg. *Alstonia, Nothofagus, Metrosideros, Arillastrum*) and may have limited dispersal distances.

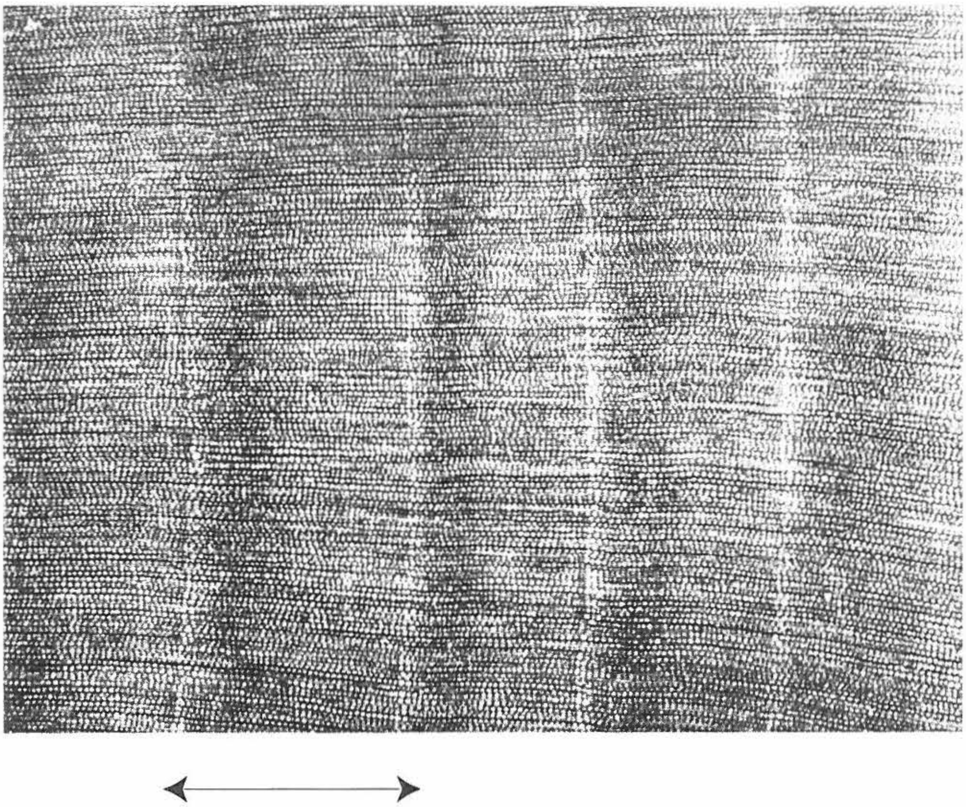


Figure 3.7 Transverse section of *Dacrydium araucarioides* wood showing growth rings. Scale bar is 1 mm.

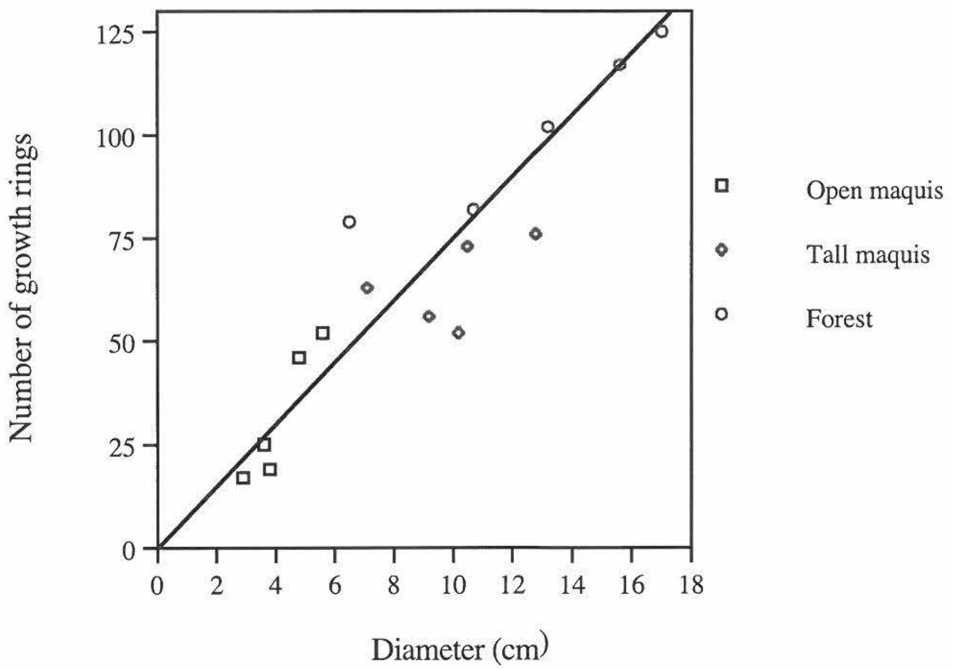


Figure 3.8 Growth ring counts on *Dacrydium araucarioides* from different iron crust vegetation formations. The trend is shown by a regression line fitted through the origin.

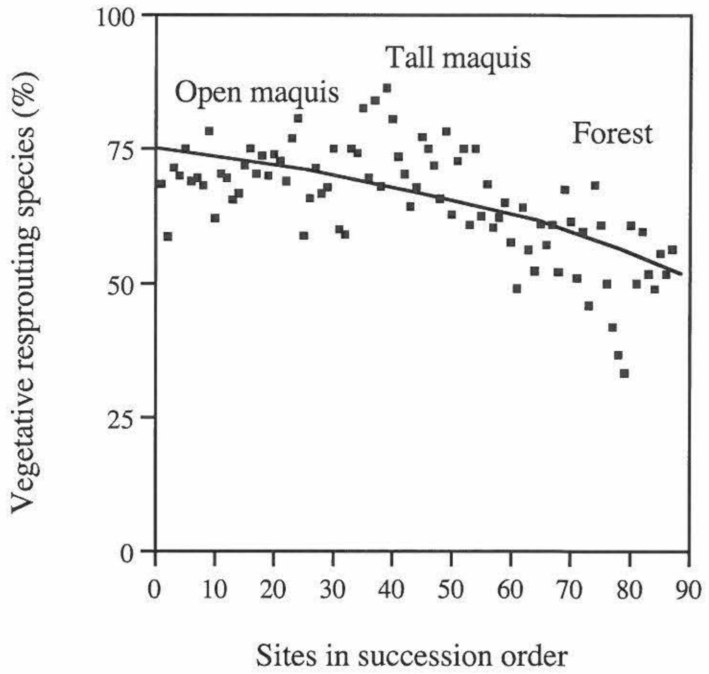


Figure 3.9 Percentage of species which resprout vegetatively in sites in successional order at Plaines des Lacs. The fitted spline curve shows a decrease from open to closed formations.

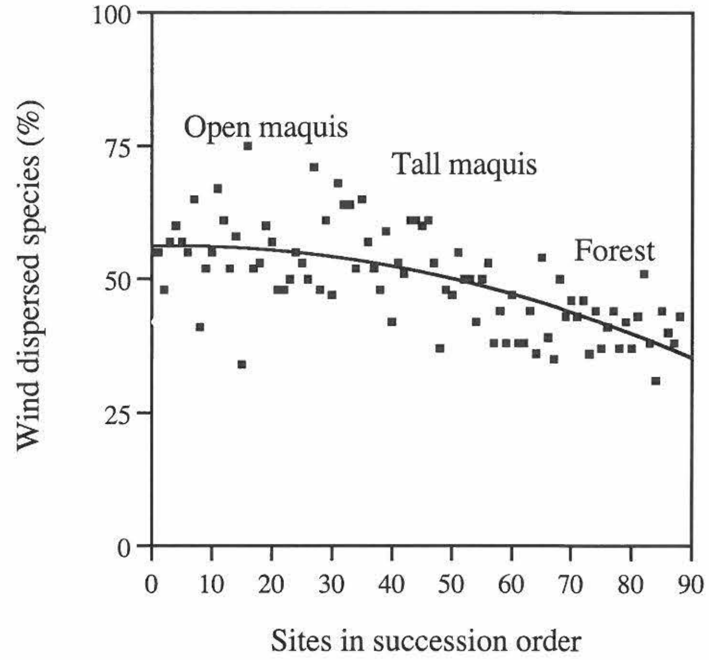


Figure 3.10 Percentage of wind dispersed species found in sites in succession order at Plaines des Lacs. The fitted spline curve shows a decrease from open to forest communities.

3.2.2.6 Fire susceptibility

The fire susceptibility index, *Fs*, (fig. 3.11) is highly variable in early successional sites (25-40 years old), reflecting the spatial 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 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 (25-70 years old) and forest (70-120 years old), 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. 3.12). 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, until the distribution was reaching a stable state. Figure 3.13 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 (ie. a fire expected every 17 years) virtually all forest is replaced by maquis.

3.2.3 Discussion of Plaines des Lacs survey

3.2.3.1 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

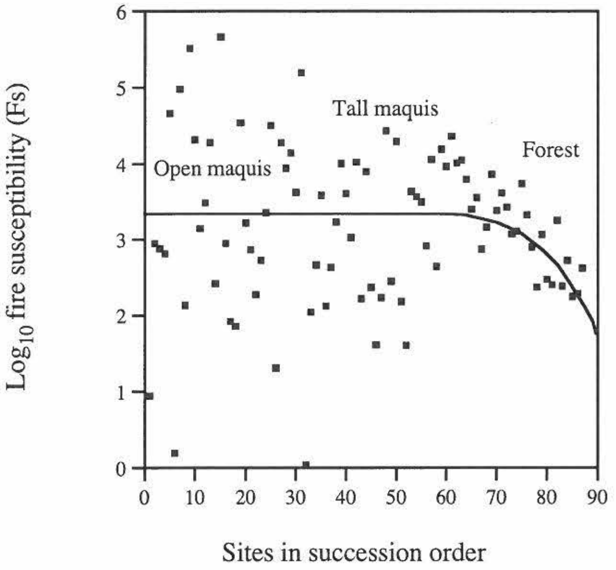


Figure 3.11 Fire susceptibility of sites in rank order of the succession index at Plaines des Lacs. Vegetation types are indicated and the trend is shown. Note that the youngest sites were burned 25 years previously and that variation in susceptibility decreases as succession proceeds.

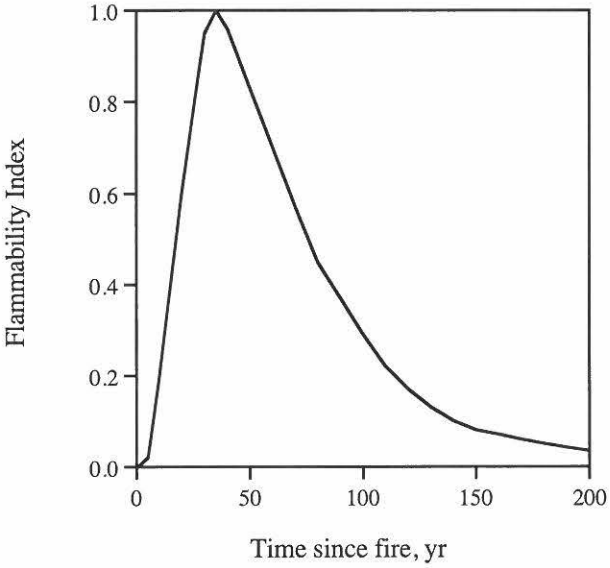


Figure 3.12 The relative flammability of different successional ages of vegetation used in the transition matrix model. Low fuel connectance limits flammability initially, whereas high moisture content limits flammability later.

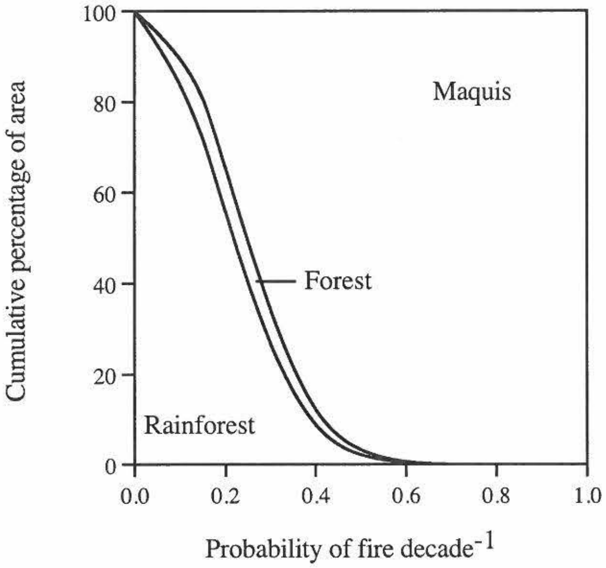


Figure 3.13 Composition of iron crust vegetation in relation to decadal ignition probability predicted using a transition matrix model over a 1000 yr period starting from burned sites.

unexplained. Some of this unexplained variation was correlated with environmental factors, notably rainfall, though this was confounded by 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 since rainforest species are recorded in the later forest stages.

From floristic records, suites of species can be identified as (i) early resprouters or seed colonists 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 (fig. 3.6). Based on historical sources and tree growth rings (fig. 3.8), the time scale for these changes appears to be about 40-75 yr to reach the closed maquis phase, 75-100 yr to reach the forest stage, and, possibly, >250 yr to reach a rainforest stage (assuming 100 yr for rainforest colonists to reach canopy height).

The succession appears to be similar to the facilitation model developed by Connell & Slatyer (1977) and consists of three phases. The post-fire successional phase is composed of maquis taxa which either resprout from rootstocks or establish from the seed bank of prior vegetation (eg. *Alphitonia*), and possibly from dispersed seed (*Gymnostoma*). These species gradually develop into patches of vegetation between iron crust boulders. *Gymnostoma deplancheanum* is generally the most abundant of the early post-fire successional species and appears to have a dominant influence on the second phase of the succession. This may be due to its nitrogen fixing *Frankia* association (Jaffré *et al*, 1994 b) which facilitates to its relatively rapid establishment, typically forming a nearly pure but open canopy 2-5 m in height after 50-70 years. This tree canopy alters the understorey environment in several ways (discussed in chapters 5 and 6) which appears to generally favour the establishment of later successional species.

Eventually broad-leaved forest trees such as *Arillastrum* may colonise. This forest phase apparently suppresses regeneration of most the early successional taxa including *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 stage successional species are limited to the localised forest and rainforest stands, possibly constraining succession. Rainforest stands are typically several kilometres from the iron crust forest sites.

3.2.3.2 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 trees is critical for fire spread at early stages. It may take several decades for some rocky sites to be colonised 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%), and the absence of rainforest on iron crust sites, may be compared with the values predicted from the transition matrix model (fig. 3.13). The model suggests that with a decadal 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 overestimated if there was an underestimate of the time for rainforest to develop or the flammability of rainforest was underestimated. Alternatively, the 2% rainforest component may be missing because dispersal is limiting. While the model may be imprecise in detail, the overall implications are robust. (i) Ignition probabilities of < 0.1 decade^{-1} could maintain a maquis component in predominantly rainforest vegetation. (ii) A shift of ignition probability from about 0.1 to 0.4 would radically change the vegetation composition from predominantly rainforest to predominantly maquis. (iii) At a high fire frequency (prob. > 0.6 decade^{-1}) all forest is likely to be excluded. Iron crust vegetation compostion is likely to be critically dependent on ignition frequency and is likely to shift disproportionately as the frequency changes. Stands of large fire scarred or killed *Arillastrum* within *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 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.

3.2.3.4 Vegetation history

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 & Pask, 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 iron crust oxisol.

The palynological record suggests that rainforest dominated for some periods which raises questions about the persistence of early succession species. Fifty maquis species were not recorded in the rainforest sites. Some early colonists (*Pteridium, Montrouziera, 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 fires to explain the maintenance of early successional species.

In summary, it is concluded that vegetation on iron crust oxisols is dynamic and represents a mosaic of post-fire successional stages. Over recent centuries the fire frequency has apparently been sufficient to maintain the succession at the early maquis and forest stages and there is no longer rainforest on this substrate.

3.3 Vegetation on eroded oxisol at Kouaoua

The objective of examining eroded oxisol communities containing *Gymnostoma intermedium* was to determine whether these formations are successional and whether changes in species composition reflect changes in the vegetation structure.

3.3.1 Methods

3.3.1.1 Survey of floristics and habitat

Methods described for the iron crust survey (3.2.1) were used to determine patterns on eroded oxisol but had to be modified because of the limited extent of vegetation containing *Gymnostoma intermedium* and the absence of information concerning fire history.

Ten forest sites were examined on the slopes of Mt Mé Mwa (Lat: 21°26'-21°27' S, Long: 165°43'-165°45' E; 700-900 m a.s.l) at points where there was easy access. All sites were located on eroded oxisol supporting forest dominated by a *Gymnostoma intermedium* canopy. Woody sedge maquis and forest presence/absence floristic data for six sites examined by Veillon (1978) and one site by Jaffré (1969) was added to the floristic data of the present survey to give an indication of the species composition of open maquis containing *G. intermedium*.

Floristic surveys, litter and vegetation structure were carried out using the same techniques as for the iron crust survey at Plaines des Lacs. Vegetation parameters (vegetation cover, litter depth, litter moisture) from open maquis at Plaines des Lacs were used as estimations of the structure of open *Gymnostoma intermedium* communities on eroded oxisol because of the limited information for these sites given in Jaffré (1969) and Veillon (1978). While these estimates may not be precise, they are approximately correct, and certainly indicate reliable trends when compared with forest. A quadrat area of 256 m^2 was chosen for forest sites.

Statistical analysis was carried out on the floristic data using the same ordination techniques as for the iron crust floristic survey, except that species only at one site were eliminated from the MDS. PCA ordination of correlation coefficients for vegetation structure was based on vegetation cover, canopy height and litter cover. This ordination yielded a first eigenvector accounting for 82% of the total variance, and the vector showed a high correlation ($r^2 > 0.66$) with the four vegetation structure components. A constant (2.73) was added to the first vector scores to obtain a succession index (SI) with values greater than 0.

3.3.1.2 Fire tolerance & susceptibility

Species tolerance and vegetation susceptibility to fire were estimated using the same method as at Plaines des Lacs.

3.3.1.3 Growth ring counts of *Araucaria montana*

Growth ring counts on fire scarred trunk sections of two *Araucaria montana* of 60 cm d.b.h. found in the open maquis where used to estimate the time since fires and ages of trees.

3.3.2 Results

3.3.2.1 Vegetation structure

Trends of increasing vegetation cover, canopy height and litter cover with the successional index for open maquis and forest sites are shown in fig. 3.14. Overall, vegetation parameter used in the PCA succession index show increases in vegetation structure with increasing number of species. 188 species were recorded from open and forest formations, of which 30 were excluded from the ordination because they occurred on only one site. 22 species were found only on sites studied by Jaffré (1969) and Veillon (1978). The MDS required three dimensions to attain a Kruskel stress of 0.15. Multiple linear regression of the succession index on MDS scores (table 3.2) revealed a strong correlation with the succession index ($r^2 = 0.69$). The strong relationship between the MDS floristic data and structurally derived succession index show a trend which could be interpreted as a successional pattern. However, since important historical information was missing for tall maquis, and incomplete for the open maquis, the pattern may be due to factors other than fire.

Figure 3.15 shows the inferred successional ranking of sites by (SI) and species (I). The floristic distribution across the succession axis shows considerable variation. Colonists species recorded only in open maquis sites are under-represented because of the low number of sites surveyed. Despite limitations in the floristic data there appears to be trend in species occurrence (fig. 3.16) which can be grouped into (i) early successional taxa which are absent from forest ($I < 1.4$), (ii) generalists which become scarce in forest ($I > 1.4$-4.05) and (iii) forest species ($I > 4.05$).

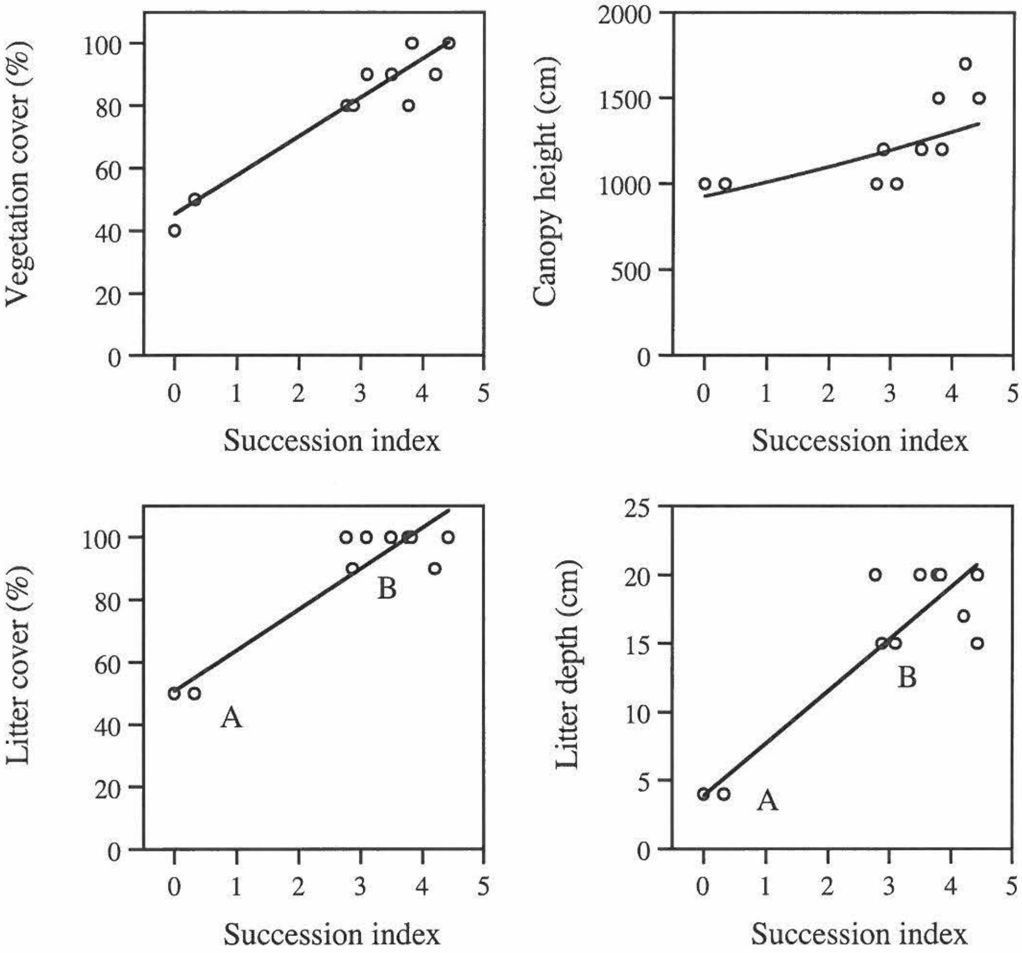


Figure 3.14 Vegetation cover, tree canopy height, litter cover and litter depth of the 17 sites on eroded oxisol at Kouaoua plotted against the succession index. Values for litter cover and depth for sites marked A and B are estimates based on iron crust communities with similar structure.

Table 3.2: Results of multiple linear regression of environmental factors fitted simultaneously to the 3 MDS axes of floristics for the eroded oxisol survey. Significance is indicated, $p > 0.05$ = ns, $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = *** .

Environmental factors	r^2	**MDS 1**	**MDS 2**	**MDS 3**
Succession index	0.70	1.49 ns	5.04 *	18.93 ***
Vegetation cover	0.57	0.38 ns	4.44 ns	9.7 ***
Canopy height	0.63	4.39 ns	0.91 ns	16.57 **
Litter depth	0.77	0.68 ns	10.27 **	26.32 **
Litter cover	0.71	0.26 ns	14.16 **	12.57 **

Family	Species		I
Cyp.	*Schoenus juvenis* C. B. Clarke		0.16
Euph.	*Austrobuxus clusiaceus* (Baillon) A. Shaw		0.16
Rub.	*Normandia neocaledonica* J. D. Hooker		0.16
Aral.	*Polyscias harmsii* Viguier		0.22
Cyp.	*Costularia arundinacea* (Solander ex Vahl) Kükenthal		0.22
Rub.	*Psychotria rupicola* (Baillon) Schlechter	**F**	0.22
Rut.	*Boronella* aff. *pancheri* Baillon		0.22
Cyp.	*Costularia nervosa* Raynal		0.33
Dill.	*Hibbertia altigena* Schlechter	**F**	0.33
Myrt.	*Tristaniopsis guillainii* Veillard ex Brongniart & Gris	**F**	0.33
Prot.	*Grevillea gillvrayi* W. J. Hooker	**F**	0.33
Epac.	*Dracophyllum verticillatum* Labillardière		1.2
Thym.	*Wickstroemia viridifolia* Meissn.	**F**	1.33
Glei.	*Gleichenia dicarpa* R. Br.	**F**	1.38
Denn.	*Pteridium esculentum* (Forster) Cockayne	**F**	1.6
Logan.	*Geniostoma densifolium* var. *oleifolium* Baillon	**F**	1.69
Apoc.	*Alstonia lenormandii* Heurck & Mueller Argovie		1.71
Rubi.	*Ixora francii* Schlechter & Krause	**F**	1.78
Orch.	*Eriaxis rigida* H. Reichenbach	**F**	1.92
Epac.	*Dracophyllum ramosum* Pancher ex Brongniart & Gris		1.97
Podo.	*Dacrydium araucarioides* Brongniart & Gris		1.98
Rut.	*Myrtopsis* (grands feuilles)		1.99
Cyp.	*Lepidosperma perteres* C. B. Clarke	**F**	2.09
Gutt.	*Montrouziera sphaerioides* Pancher ex Planchon & Triana	**F**	2.12
Euph.	*Longetia buxoides* (Baillon) A. Shaw	**F**	2.21
Sapin.	*Gioua glauca* (Labilliardière) Radlkofer	**F**	2.23
Cun.	*Codia montana* J. R. & G. Forster	**F**	2.29
Good.	*Scaevola balanseae* Guillaumin	**F**	2.31
Wint.	*Zygogynum baillonii* Tieghem		2.32
Hipp.	*Dicarpellum* sp.		2.34
Pitt.	*Pittosporum gracile* Pancher ex Brongniart & Gris		2.38
Dill.	*Hibbertia pancheri* (Brongniart & Gris) Briquet	**F**	2.44
Lil.	*Dianella intermedia* Endl.	**F**	2.47
Myrt.	*Carpolepis laurifolia* (Brongniart & Gris) Dawson	**F**	2.62
Sapin.	*Guioa villosa* Radlkofer	**F**	2.67
Arua.	*Araucaria montana* Brongniart & Gris		2.68
Rub.	Attractocarpus sp. (cf JMV 7168)		2.75
Rut.	*Comptonella drupacea* (Labillardière) Guillaumin		2.76
Xanth.	*Lomandra insularis* Schlechter	**F**	2.82
Cun.	*Codia ferruginea* Brongniart & Gris	**F**	2.82
Fag.	*Nothofagus balansae* (Baillon) Steenis		2.82
Epac.	*Styphelia* gp *cymbulae* (Labilliardière) Sprengel		2.84
Cun.	*Codia discolor* (Brongniart & Gris) Guillaumin	**F**	2.84
Casua.	*Gymnostoma intermedium* L. Johnston		2.9
Gutt.	*Montrouziera gabriellae* Baillon		2.93
Nepe.	*Nepenthes veillardii* J. D. Hooker	**F**	2.99
Icac.	*Gastrolepis novacaledonensis* Benl		3.04
Arau.	*Agathis ovata* (C. Moore) Warburg		3.05
Sapin.	*Guioa crenata* Radlkofer		3.07
Rut.	*Boronella verticillata* Baillon ex Guillaumin	**F**	3.08
Balan.	*Balanops* aff. *balansae* Baillon		3.1
Dill.	*Hibbertia* aff. *vanieri* Beauvisage		3.1
Elae.	*Elaeocarpus castanaefolius* Guillaumin		3.1
Euph.	*Bocquillonia* sp.		3.1
Orch.	*Megastylis glandulosa* (Schlechter) Schlechter		3.1
Prot.	*Beauprea pancheri* Brongniart & Gris		3.1
Rub.	*Psychotria douarrei* (Beauvisage) Daeniker		3.1
Myrs.	*Rapanea assymetrica* Mez	**F**	3.12
Psil.	*Tmesipteris veillardii* Dangeard		3.13
Alse.	*Wittsteinia balansae* (Baillon) Steenis		3.16
Aqui.	*Ilex sebertii* Pancher & Sébert		3.18
Epac.	*Styphelia balansae* Virot		3.18
Pal.	*Basselinia pancheri* Veillard		3.19
Glei.	*Stromopteris moniliformis*		3.19
Apoc.	*Rauvolfia schumanianna* var. *suavolans* (Schlechter) Boiteau		3.2
Sapot.	*Planchonella kuebuniensis* Aubréville		3.23
Epac.	*Styphelia macrocarpa* (Schlechter) Sleumer		3.24
Sapot.	*Troettea lissophylla* Pierre ex Baillon	**F**	3.25
Orch.	*Malaxis torena* (H. Reichenbach) Kuntze		3.26
Orch.	*Clematepistephium smilacifolium* (H. Reichenbach) Hallé		3.27
Aral.	*Apiopetalum velutinum* Baillon		3.29
Aral.	*Mydocarpos fraxinifolius* Brongniart & Gris		3.32
Orch.	*Bulbophyllum* sp.		3.32
Aral.	*Meryta coriacea* Baillon		3.33
Aral.	Mydocarpus cmf sp 21		3.38
Cun.	*Cunonia veillardii* Brongniart & Gris		3.38
Rub.	*Morinda* sp.		3.41
Sch.	*Schizaea dichotoma* Fournier	**F**	3.41
Gutt.	*Garcinia balansae* Pierre	**F**	3.43
Podo.	*Falcatifolium taxoides* (Brongniart & Gris) deLaubenfels		3.43
Phell.	*Phelline lucida* Veillard ex Baillon		3.43
Rham.	*Alphitonia xerocarpa* Baillon		3.47
Pitt.	*Pittosporum dzumacensis* Guillaumin		3.47
Myrt.	*Xanthomyrtus heighenensis* Guillaumin		3.48
Rub.	*Psychotria poissoniana* (Baillon) Guillaumin		3.49
Icac.	*Apodytes clusaefolium* (Baillon) Villiers		3.5

Succession index (SI)

Vegetation type

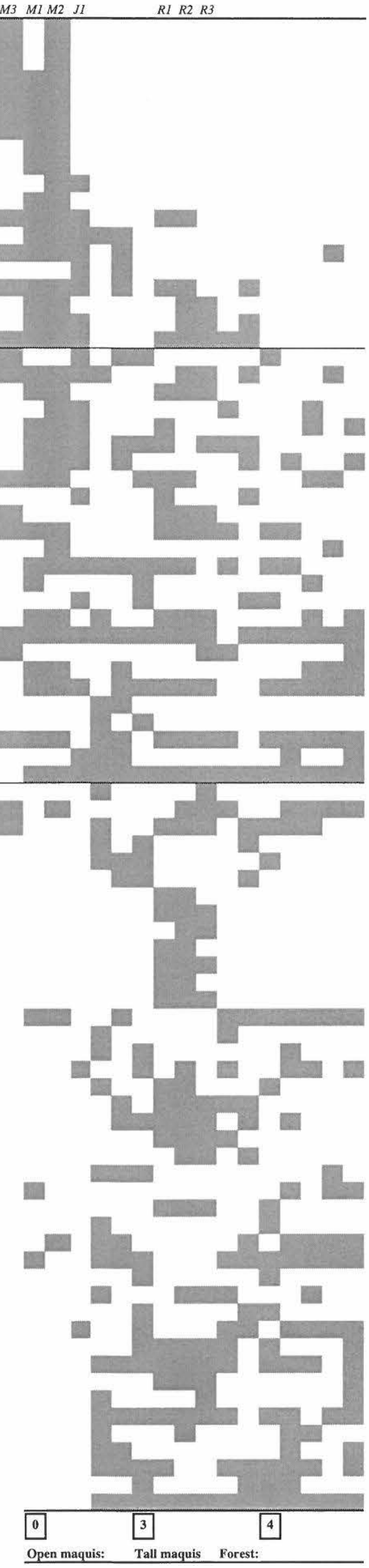


Figure 3.15 Presence of species (shaded) in the 17 eroded oxisol sites ranked by the succession index (SI). Species are ranked by the species index (I). Horizontal lines indicate the boundaries between early persistent and late successional groups of species. F indicates vegetative resprouters from rootstocks. *M1* , *M2* , *M3* , *R1* , *R2* , R3 are from Veillon (1978). J1 is from Jaffre (1969).

Family	Species		I
Cun.	*Acsmithia meridionalis* (Brongniart & Gris) Hoogland	F	3.5
Euph.	*Austrobuxus eugenifolius* (Guillaumin) A. Shaw		3.5
Laur.	*Cryptocarya transversa* Kostermans		3.5
Schi.	*Schizaea laevigata* Mettenius	F	3.5
Apo.	Parsonsia sp.		3.54
Celas.	*Maytenus fournieri* (Pancher & Sébert) Loesener	F	3.54
Lind.	*Lindseae nervosa* Mettenius		3.54
Myrt.	*Caryophyllus elliptica* Labillardière		3.54
Apo.	*Alyxia glaucophylla* Heurck. et Muell.		3.54
Cela	*Salaciopsis sparsiflora* Hürliman		3.55
Epac.	*Styphelia veillonii* Virot		3.58
Aral.	*Schefflera* aff. *gabriellae* Baillon		3.59
Pitt.	*Pittosporum* (rare)		3.6
Rub.	*Psychotria leratti* Guillaumin		3.6
Good.	*Scaevola beckii* Zahlbrucker	F	3.6
Cyath.	*Cyathea* sp.		3.6
Rub.	*Psychotria toninensis* S. Moore		3.61
Pand.	*Pandanus* sp. cf		3.62
Sapin.	*Cupaniopsis glomerfolia* Radlkofer		3.62
Palm.	*Basselinia gracilis* (Brongniart & Gris) Veillard		3.62
Balan.	*Balanops pachyphylla* Baillon ex Guillaumin		3.63
Rub.	*Ixora montana* Schlechter		3.63
Apo.	*Alstonia coriaceae* Pancher ex S. Moore		3.64
Pitt.	*Pittosporum mouanum* Guillaumin		3.64
Sapot.	*Pycnandra* sp.		3.64
Sapot.	*Beccariella rubicunda* (Pierre ex Baillon) Pierre		3.65
Phell.	*Phelline comosa* Labillardière		3.65
Myrt.	*Syzygium* sp.		3.66
Pand.	*Freycinetia novacaledonica* Warburg		3.67
Myrs.	*Rapanea diminuta* Mez	F	3.68
Rub.	*Psychotria balansanus* Guillaumin		3.69
Blech.	*Blechnum corbasonii* Brownlie		3.7
Laur.	*Beilschmidia* sp.		3.7
Rut.	*Comptonella oreophila* (Guillaumin) Hartley		3.7
Thym.	Lethodon calophylla (Guillaumin & MacKee), comb. ined.		3.79
Myrs.	*Tapeinosperma robustum* Mez		3.8
Myrt.	*Austromyrtus veillardii* (Brongniart & gris) Burret		3.8
Smil.	*Smilax orbiculata* Labillardière		3.8
Myrt.	*Uromyrtus artensis* (Montrouzier ex Guillau. & Beauvis.) Burret	F	3.82
Dill.	*Hibbertia podocarpifolia* Schlechter		3.82
Prot.	*Beauprea asplenioides* Schlechter		3.82
Wint.	*Zygogynum comptonii* Tieghem		3.83
Icac.	*Citronella sarmentosa* (Baillon) Howard		3.85
Hymen.	*Trichomanes veillardii* van den Bosch		3.85
Mel.	*Dysoxylum canalensis* (Baillon) C. DC.		3.85
Pitt.	*Pittosporum deplanchei* Brongniart & Gris		3.85
Dill.	*Hibbertia veillardii* (Brongniart & Gris) Gilg		3.86
Rut.	*Geijera balansae* (Baillon) Schinz & Guillaumin		3.91
Cun.	*Cunonia montana* Schlechter		3.94
Aral.	*Mydocarpus* (comf sp 6)		3.96
Euph.	*Phyllanthus houailouensis* Guillaumin		3.96
Hymen.	*Trichomanes antatum* van den Bosch		3.96
Rut.	*Comptonella sessilifoliola* (Guillaumin) Hartley		3.99
Symp.	*Symplocos montana* Brongniart & Gris		3.99
Lora.	*Amyema scandens* (Tieghem) Danser		4.04
Olea.	*Linociera brachystachys* (Schlechter) P. S. Green		4.04
Elae.	*Elaeocarpus yateensis* Guillaumin		4.1
Myrt.	*Austromyrtus pancheri* (Brongniart & Gris) Burret		4.1
Thym.	*Lethodon balansae* (Baillon) Kostermans		4.12
Laur.	*Beilschmidia neocaledonica* Kostermans		4.22
Hipp.	*Dicarpellum pronyense* (Guillaumin) A. C. Smith		4.31
Laur.	*Cryptocarya guillanii* Veillard		4.31
Aral.	*Myaocarpus elegans* Dubard & Viguier		4.42

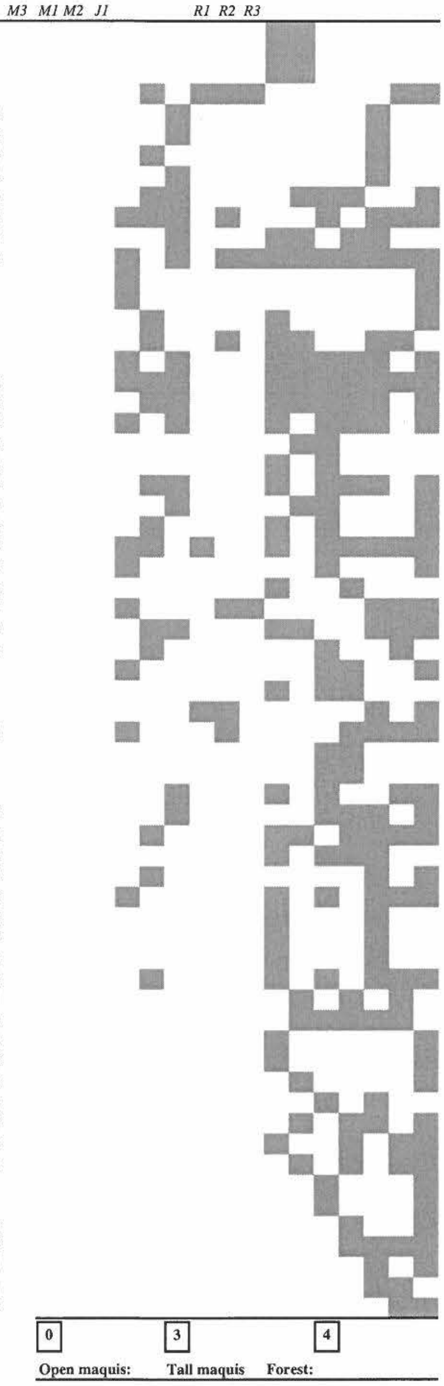


Figure 3.15 Presence of species (shaded) in the 17 eroded oxisol sites ranked by the succession index (SI). Species are ranked by the species index (I). Horizontal lines indicate the boundaries between early persistent and late successional groups of species. F indicates vegetative resprouters from rootstocks. *M1* , *M2* , *M3* , *R1* , *R2* , R3 are from Veillon (1978). J1 is from Jaffre (1969).

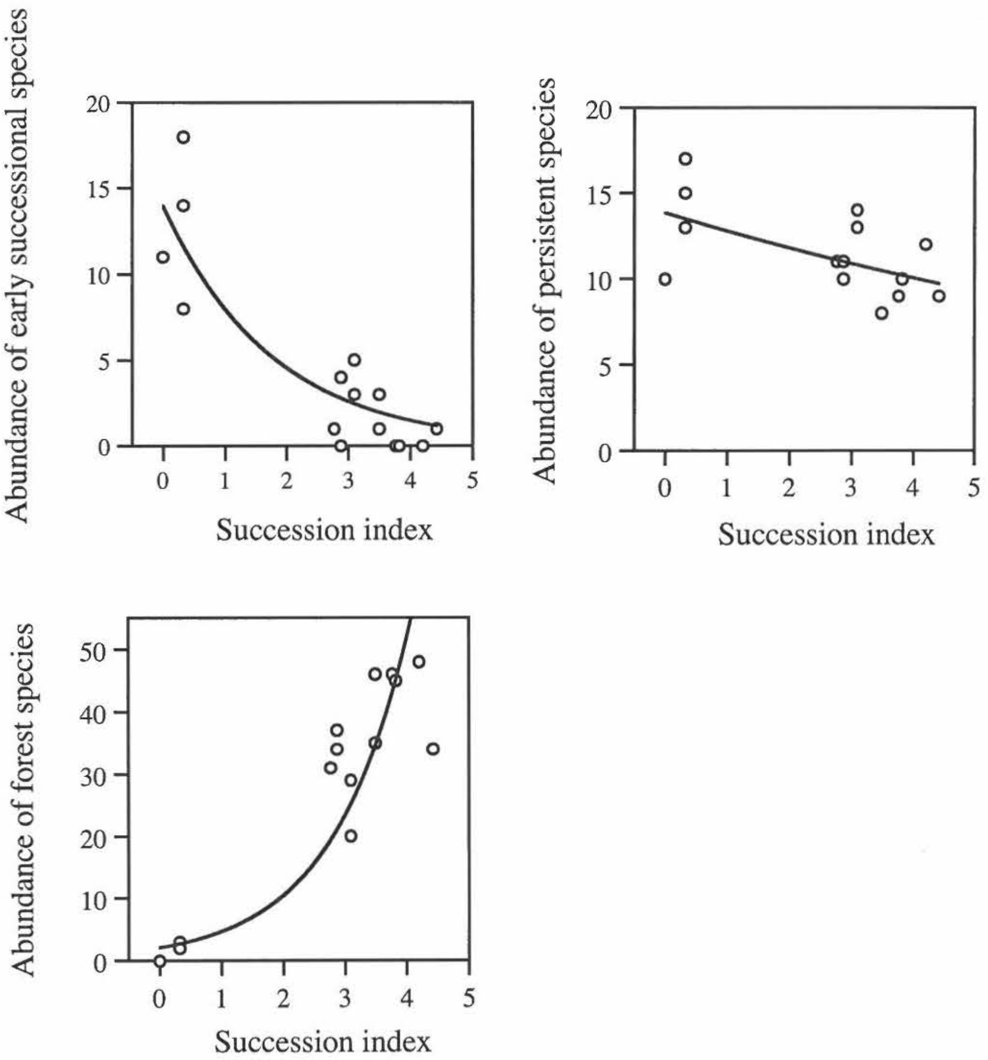


Figure 3.16 The number of early successional early successional, persistent and forest species in relation to rank order of sites by the succession index. Trends are shown by fitted spline curves.

3.3.2.2 Fire tolerance

Based on fire tolerance of species assessed largely at Plaines des Lacs, open maquis contains many species that resprout after fire. Many of these species are also present in forest formations. Non-resprouting species comprise about 50% of the open maquis flora and increase to 75% of the forest flora. (fig. 3.17).

3.3.2.3 Fire susceptibility

The fire susceptibility index, *Fs* (fig. 3.18) indicates a pattern similar to the iron crust succession, except that (i) open communities are more likely to burn when dry because connectance is high due to the higher abundance of sedges. (ii) Forest communities are less likely to burn because of the higher annual rainfall and frequent fog resulting in fuel remaining moist, resulting in lower values of flammability (fig. 3.19). Thus, fires may burn open maquis stands during dry months in most years, but only enter forest formations during exceptionally dry years.

3.3.2.4 Growth rings of *Araucaria montana*

Fire scarred *Araucaria rulei* and *A. montana* were found in woody sedge maquis on ridgelines and slopes below the *G. intermedium* forest indicating that the vegetation has been severely disturbed below 600 m a.s.l by widespread burning. Age determinations of two *A. montana* trees in the open maquis indicate that large individuals of about 60 cm d.b.h had rings that were approximately evenly spaced suggesting they were annual. Ring counts indicate that the trees were approximately 170-200 years old (fig. 3.20) and had been burnt several times over the past 20-40 years by fires that created scars. However since counts were based on only two trees, the values should be treated with caution.

3.3.3 Discussion of eroded oxisol survey

3.3.3.1 Successional patterns and processes

The survey of eroded oxisol vegetation indicated that the succession index explained for 59% of the floristic variation. This variation in species composition corresponds with increasing vegetation cover and height, suggesting a successional pattern similar to that found on iron crust Plaines des Lacs. The successional pattern contains three suites of species identified

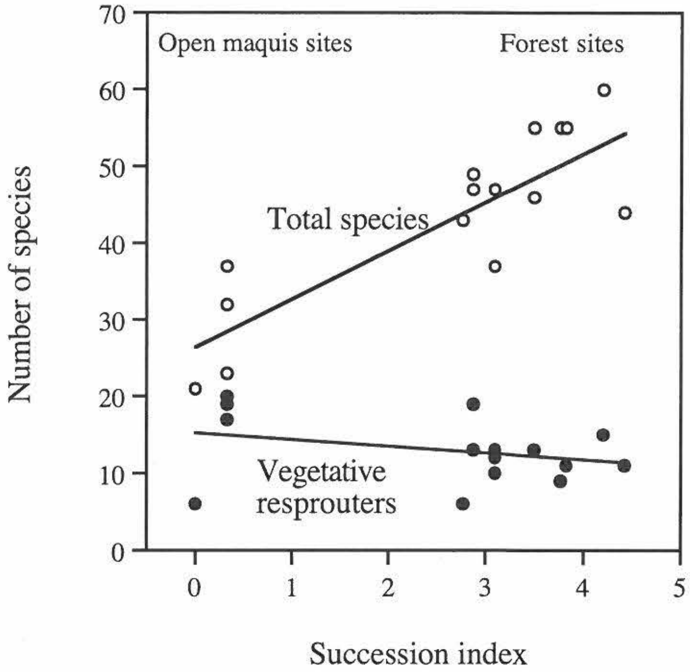


Figure 3.17 The number of vegetative resprouting species and all species on eroded oxisol sites at Kouaoua plotted against the succession index. Fitted splines show trends for the total number of species and number of vegetative resprouters.

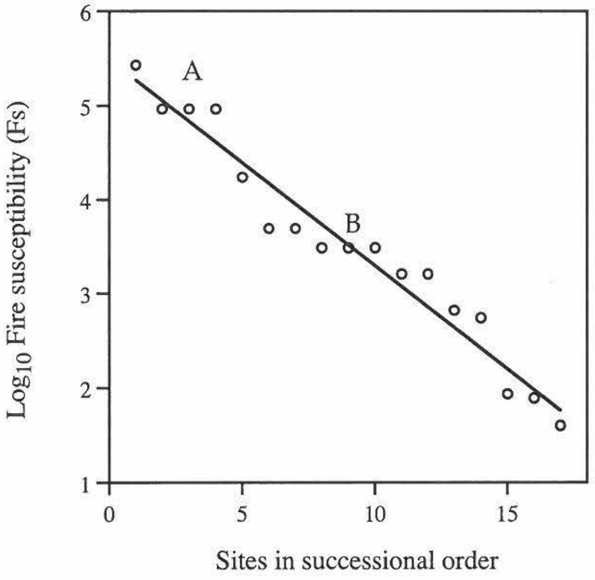


Figure 3. 18 Fire susceptibility of sites in rank order of the succession index. Fuel humidity values for sites (A) and (B) are taken from iron crust vegetation communities with similar vegetation structure.

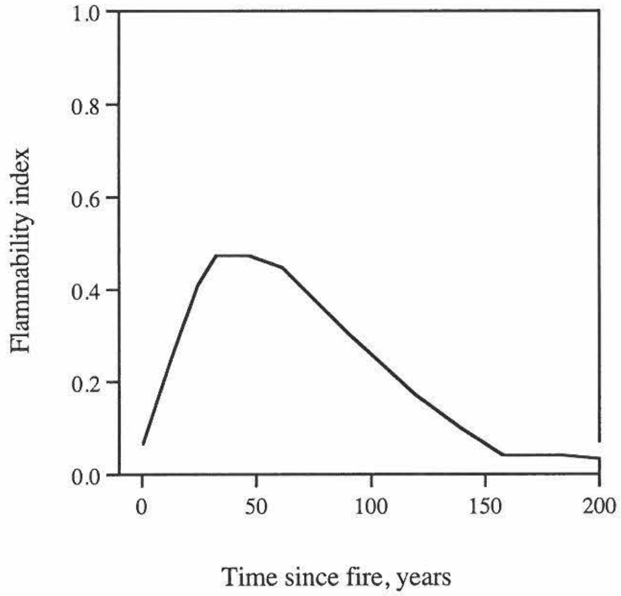


Figure 3.19 The relative flammability of different successional ages of vegetation used in the transition matrix model. Fuel connectance rises sooner than on iron crust sites. A maximum of 0.5 is used becuase these sites are considered much less flammable than maquis sites at Plaines des Lacs.

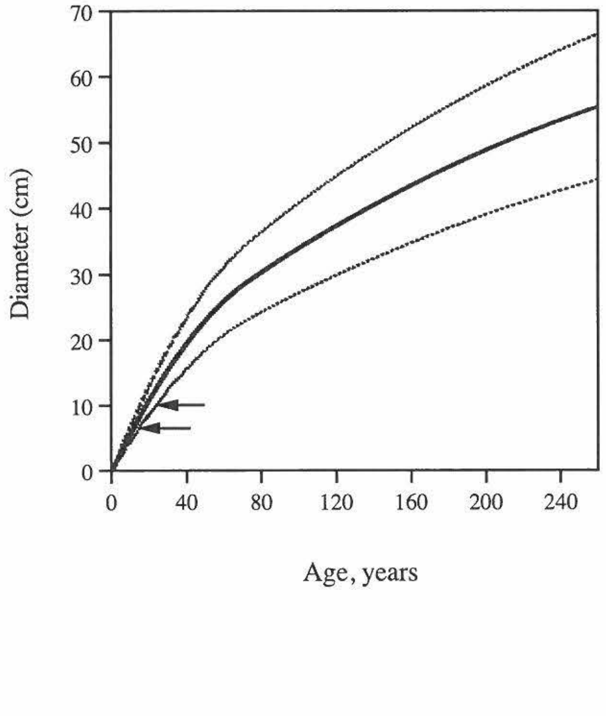


Figure 3.20 Estimated age *Araucaria montana* trees based on growth ring counts of 60 cm d.b.h individuals. The solid line is a fitted exponential curve indicating mean annual increase in trunk diameter based on tree ring counts of two individuals (approximately 50 cm d.b.h). The dotted lines are fitted exponential curves indicating maximum and minimum increase in trunk diameter of both species. Arrows indicate were fire scars were recorded.

as early successional which either (a) disappear in forest formations or (b) remain persistent. A third group of species is restricted to the forest formations. However 41% of the floristic variation was unexplained by the succession index which suggests that the successional pattern on eroded oxisol is partly confounded by local scale variations in species distribution because of limited sampling. Evidence that these are successional patterns following fire is outlined below.

At altitudes of 100-600 m a.s.l, aerial photographs (fig. 2.10) show that open maquis and forest occur in different parts of the landscape (fig. 3.21). Open maquis dominates north facing slopes and ridgelines, while forest is restricted to valleys and southern facing slopes, which may indicate an aspect controlled vegetation distribution pattern. Northern facing slopes experience higher levels of solar radiation, especially during winter months, (fig. 1.5) creating drier conditions by raising evaporation. Thus, north facing slopes during spring (August-October) would remain drier for longer periods of time. This would favour the development of a woody sedge maquis composed of species tolerant of periodic water stress. Floristic records show that Cyperaceae, Myrtaceae and Cunoniaceae are common in woody sedge maquis and generate a continuous ground cover of sclerophyllous fuel. These vegetation characteristics combined with steep terrain increase the magnitude and duration of the fire risk, and therefore influence the spread of fires on north facing slopes.

Valley bottoms support forest along drainage lines for reasons related to the topographic effects on the solar radiation balance and soil moisture conditions. Valleys experience lower solar radiation throughout the year and moist soil conditions because the underlying eroded oxisol is deeper and receives ground water from upper slopes. At altitudes above 600 m a.s.l, frequent cloud cover reduces solar radiation and evaporation effects of aspect and allow forest to persist. Furthermore, fires decelerate downhills, protecting valleys (Cheney, 1981).

Other sources of disturbance such as cyclone may have localised impacts on vegetation, however the aspect related patterns clearly indicate that fire is the most prevalent form of disturbance effecting the whole area.

Floristic records indicate that resprouting species in early facilitation succession stages of iron crust communities (*Pteridium esculentum, Tristaniopsis guillanii, Hibbertia pancheri, Codia montana, Longetia*

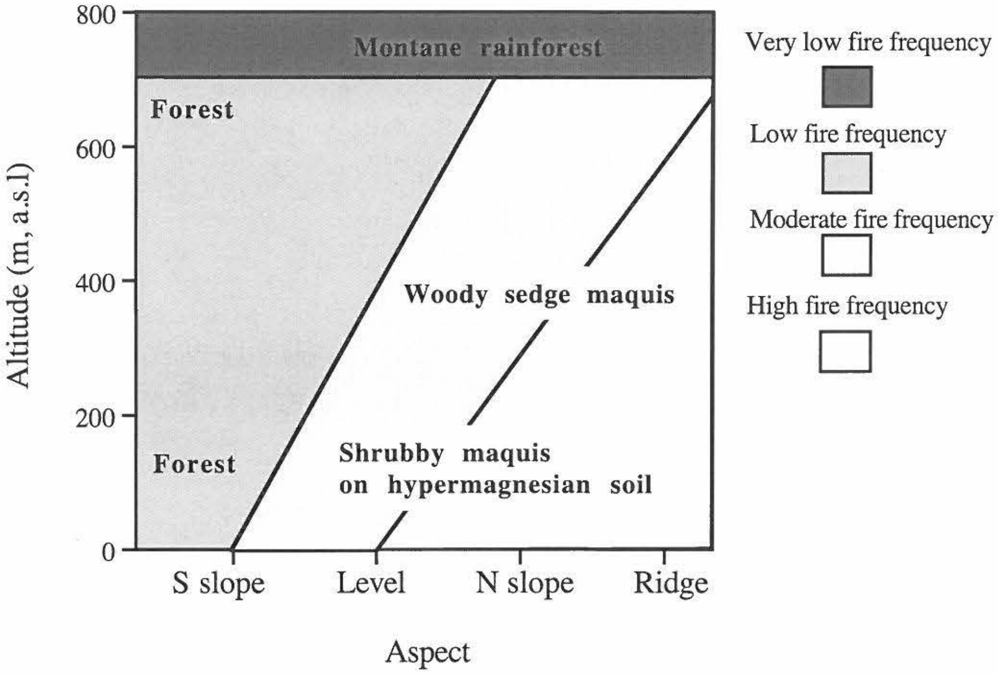


Figure 3.21 A schematic diagram indicating changes in fire frequency and vegetation with altitude at Kouaoua based on vegetation distribution patterns on aerial photographs.

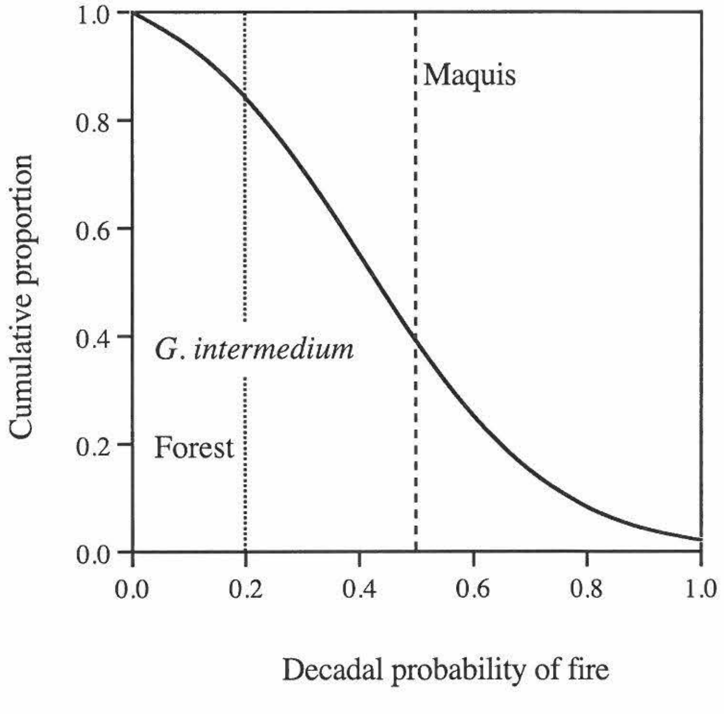


Figure 3.22 Composition of vegetation on eroded oxisol in relation to decadal ignition probability predicted using a transition matrix model over a 1000 yr period starting from burned sites. The fine dotted line respresents the observed frequency recorded in the floristic survey (fine dotted line). *G. intermedium* is likely to be excluded by fire frequencies >0.5 (dashed line).

buxioides and *Montrouziera sphaeroidea*) are abundant on eroded oxisol and are often charred at the base from previous fires. These species establish on burnt areas as individual or small shrub populations. Fire sensitive Cyperaceae gradually colonise bare ground between shrubs from wind dispersed seed in surrounding vegetation. This mixture of resprouters and seed dispersed species eventually develops into a low, continuous vegetation. At forest stages, broad leafed rainforest species belonging to Araliaceae, Cunoniaceae, Elaeocarpaceae, Lauraceae, Palmae, Pandanaceae, Sapotaceae, Phellinaceae, Rubiaceae, Rutaceae and Winteraceae form a well developed understorey of shrubs and trees < 7 m tall. Sedges and early successional shrubs are rare in the understorey which suggests that the environmental conditions of the understorey are unsuitable for sustaining large populations of open maquis species.

Gymnostoma intermedium seedlings, saplings and mature trees are common on bare ground along road cuttings at forests boundaries, but are rarely found in open maquis which suggests that *G. intermedium* may not be a key species in early stages. *Gymnostoma intermedium* annual seed production is often low and irregular compared to *Gymnostoma deplancheanum* (fig. 6.8). Frequent fires in open maquis of eroded oxisol would eliminate fire sensitive *G. intermedium* from these formations, because their low colonising potential would result in populations being killed before they could set seed.

3.3.3.2 Vegetation flammability and fire frequency

Open woody sedge maquis on eroded oxisol are highly flammable due to the extensive Cyperaceae cover forming a continuous fuel favouring fire spread. Fire spread in forest is reduced by increased litter moisture, rocky outcrops of peridotite and iron crust, and the absence of sedges in forest due to shade and possibly deep litter. Pure canopy stands of *Gymnostoma intermedium* forest occupy summit areas above 600 m altitude which experience frequent cloud and fog cover. Occasionally, dry cloud free conditions predominate such as during 1994, resulting in the drying of litter and an increased potential for fires. Extensive fires (500 ha) burnt forest and maquis communities between Mt Mé Mwa and Menazi in November 1994.

Vegetation communities in summit parts of Kouaoua are heavily degraded by mining activity which make it difficult to determine the past vegetation communities. The present ignition frequency of high altitude areas of Kouaoua is likely to be much higher than iron crust sites (> 0.5

decade^{-1}) because flammable woody sedge maquis extends down to agricultural land at the base of the Kouaoua valley where there are many sources of ignition. A transition matrix model constructed for communities at a median altitude of 600 m a.s.l relates approximate frequency for vegetation types (fig. 3.22). The model suggests that at regimes of > 0.1 decade^{-1}, an open woody sedge maquis component will remain in forest areas. Shifts in the fire probability from 0.1 to 0.6 decade^{-1} would substantially increase the maquis component and reduce forests to valley pockets. *Gymnostoma intermedium* would be virtually eliminated from open maquis under fire frequencies of > 0.5 decade^{-1} because there is insufficient time for it to reach reproductive maturity. Forest pockets would persist even under very high fire regimes (> 0.8 decade^{-1}) because foggy conditions experienced at high altitudes (> 700 m a.s.l) would maintain high fuel moisture. This forest is likely to be restricted to rocky valley slopes offering some additional protection from frequent fires.

3.3.3.3 Fire history

The presence of tumuli on coastal iron crust plateaus (500 m a.s.l) at Kouaoua (Guy *et al*, 1979) suggest that human impact was not restricted to coastal areas, and may have affected the vegetation in high altitude regions of Kouaoua through increasing fire frequencies. It is likely that mining, which began at Kouaoua in the 1870s (Guy *et al*, 1979), increased the incidence of fires at higher altitudes. Woody sedge maquis outside the proximity of mining contains evidence of past fires in the form of fire scarred *Araucaria rulei*, and *A. montana* trees. As *A. montana* is more abundant in rainforest formations as an emergent (Jaffré, 1995), this suggests that maquis which contains populations of this species may once have supported rainforest that has been reduced to the valley pockets by recent repeated fires. The frequency of fire events have been sufficient to maintain *G. intermedium* as a canopy species and exclude rainforest trees except on cloud capped peaks.

In summary, it is concluded that the mosaic of vegetation communities above 600 m altitude at Kouaoua represents a post fire successional pattern that has been generated by changing fire frequencies in the past. The post fire succession pattern differs from iron crust communities, in that sedge fuel produces high fire frequencies reducing the likelihood of maquis areas being eventually occupied by forest as would be the case on iron crust oxisol.

3.4 Vegetation on hypermagnesian soils at Kouaoua

The main objectives of examining *G. chamaecyparis* maquis was to determine (i) whether these formations are successional and (ii) whether changes in species composition reflect changes in the vegetation structure.

3.4.1 Methods

3.4.1.1 Survey of floristics and habitat

Methods described for the iron crust oxisol survey were used to determine patterns on hypermagnesian soil but were modified because of the limited distribution of this vegetation type to a few serpentinite outcrops, and the absence of information concerning fire history.

Serpentinite outcrops with hypermagnesian soil occur at the base of Méa mine, Mai mine and Kouaoua bay (Lat. 21°22'-28' S; Long. 165°45'-51' E; 80-400m a.s.l). These outcrops are very distant from each other (7-10 km) (fig. 2.12), and contain maquis and forest which have experienced disturbance from mining. All sites examined were located on slopes 10-30° which were unaffected by mine debris, landslips and erosion by water courses. These criteria were chosen to sample sites that were representative of vegetation prior to mining activities. The most common vegetation type was a tall maquis or forest containing abundant *Gymnostoma chamaecyparis* trees. Neighbouring *Acacia spirorbis* communities containing isolated *G. chamaecyparis* trees were not examined because they most often occurred on oxisol landslip debris, overlying serpentinite, which possesses different edaphic properties to hypermagnesian soil (table 2.2).

Floristic surveys were conducted below Méa mine in open maquis (3 sites), tall maquis (5 sites) and at 2 forest sites. At Mai mine, no open maquis was found and floristic surveys comprised of 3 tall maquis and 3 forest sites. Surveys at Kouaoua bay were confined to 2 open maquis sites and 2 tall maquis sites as forest formations were absent. All sites were situated in uniform stands which were at least 50 m from prospecting roads. Floristic comparisons between *G. chamaecyparis* forest and rainforest could not be made because rainforest was not found on serpentinite near Kouaoua, though such rainforest does occur elsewhere (Jaffré, pers. comm).

Floristic and structural surveys were carried out using the same methods described for the iron crust floristic survey at Plaines des Lacs (3.2.1). In addition, hypermagnesian soil cover (%) vs bare serpentinite was estimated for each site. A quadrat area of 196 m^2 was used for all sites surveyed. No species with distinct growth rings were found. Instead, sites were scored according to the presence/absence of burnt stumps or fire scarred individuals.

Floristic analysis was carried out using the same ordination techniques as for Plaines des Lacs (3.2.1.1). Species found on less than two sites were eliminated from the MDS ordination. PCA ordination of correlation coefficients for vegetation structure was based on vegetation cover, canopy height and litter cover. This ordination yielded a first eigenvector accounting for 36% of the total variation, and the vector showed a moderate correlation with vegetation cover ($r^2 = 0.63$) (refer to table 3.3). A constant (2.11) was added to the first vector scores to obtain a succession index (SI) with values greater than zero.

3.4.1.2 Structure

All woody stems > 2 cm d.b.h were measured for one plot of 25 x 50 m in open maquis and one plot in tall maquis on serpentinite outcrops at the base of the Méa mine. These plots were centered on the least disturbed parts of the vegetation formation to reduce edge effects caused by landslips.

3.4.1.3 Fire tolerance & susceptibility

No recently burnt (< 10 yr) *G. chamaecyparis* maquis was found at Kouaoua. Fire tolerance of maquis and forest species was assessed from the Plaines des Lacs survey, and for resprouting serpentinite species. The fire susceptibility model developed for the vegetation at Plaines des Lacs was applied to vegetation data for *G. chamaecyparis* formations.

3.4.2 Results

3.4.2.1 Vegetation structure

The floristic survey recorded 128 species of which 33 were excluded from further analysis because they occurred on less than two sites. Ordination of species abundance using MDS required four dimensions to reach a Kruskal stress value of 0.19. Multiple linear regression of the succession index and environmental factors (as a dependent variable) revealed a weak correlation with MDS axis 4 for the succession index (r^2 = 0.36), evidence of fire (r^2= 0.38), vegetation cover (r^2 = 0.35), litter cover (r^2 = 0.24) and soil cover (r^2 = 0.19)(table 3.3). The relationship between the succession index and MDS axis 4 suggest that there are variations in structure and floristics indicative of succession. A Hotell-Lawley MANOVA test for the effect of regions on the MDS axis scores was marginally significant ($F_{8, 26} = 2.36$, $p < 0.047$) on MDS axis 1 due largely to differences between Méa mine and the two other outcrops surveyed. Such regional scale floristic variations may also explain the strong correlation between shrub height (r^2 = 0.55) and MDS 1 and MDS 3, though this possibly reflects regional variation in vegetation structure. Multiple linear regression analysis of the succession index tested against independent environmental variables showed a slight positive correlation with the number of species (r^2 = 0.62, F = 29.53, $p < 0.0001$), evidence of fire (r^2 = 0.49, F = 17.27, $p < 0.0006$) and soil cover (r^2 = 0.40, F = 12.13, $p < 0.0027$).

Figure 3.23 shows that vegetation cover, canopy height, litter cover and litter depth increases with the succession index. Figure 3.24 shows the ranking of sites in successional order by (SI) and by species (I). It is apparent that species presence shows considerable variation between successive sites, but most species show trends in occurrence, and may be grouped into two categories. Figure 3.25 shows the total number of species in each category in relation to rank order of sites by the succession index. There is group of 44 persistent species ($I < 2.4$) which are present from start to finish and a second group 51 species which are absent in early stages.

3.4.2.2 Structure

Stem size class distributions for open and tall maquis are shown in fig. 3.26, and distribution for common woody species are shown in fig. 3.27. *Gymnostoma chamaecyparis* accounts for nearly half of the stems in both formations, and is the most common tree species > 10 cm d.b.h. Understorey multi-stemmed tall shrubs < 10 cm d.b.h. such as *Stenocarpus milnei, Xanthostemon gugerlii* become more abundant in tall maquis. Other multi-stemmed species such as *Pancheria ferruginia, Hibbertia pancheri* and *Soulamea pancheri* are less abundant in tall maquis and mainly occupy stem classes < 5 cm d.b.h as low shrubs.

Table 3.3: Results of multiple linear regression of environmental factors fitted simulataneously to the four axes of the MDS analysis of floristics on hypermagnesian sites. r^2 and F ratios are given for each MDS axes. Significance is indicated, $p > 0.05$ = ns, $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = *** .

Environmental factors	**r^2**	**MDS 1**	**MDS 2**	**MDS 3**	**MDS 4**
Succession index	0.36	2.56 ns	0.82 ns	0.56 ns	4.24 *
Vegetation cover	0.41	1.00 ns	0.21 ns	0.24 ns	8.76 **
Litter cover	0.34	5.32 *	0.40 ns	0.60 ns	0.39
Soil	0.19	2.72 ns	3.93 *	1.28 ns	0.37 ns

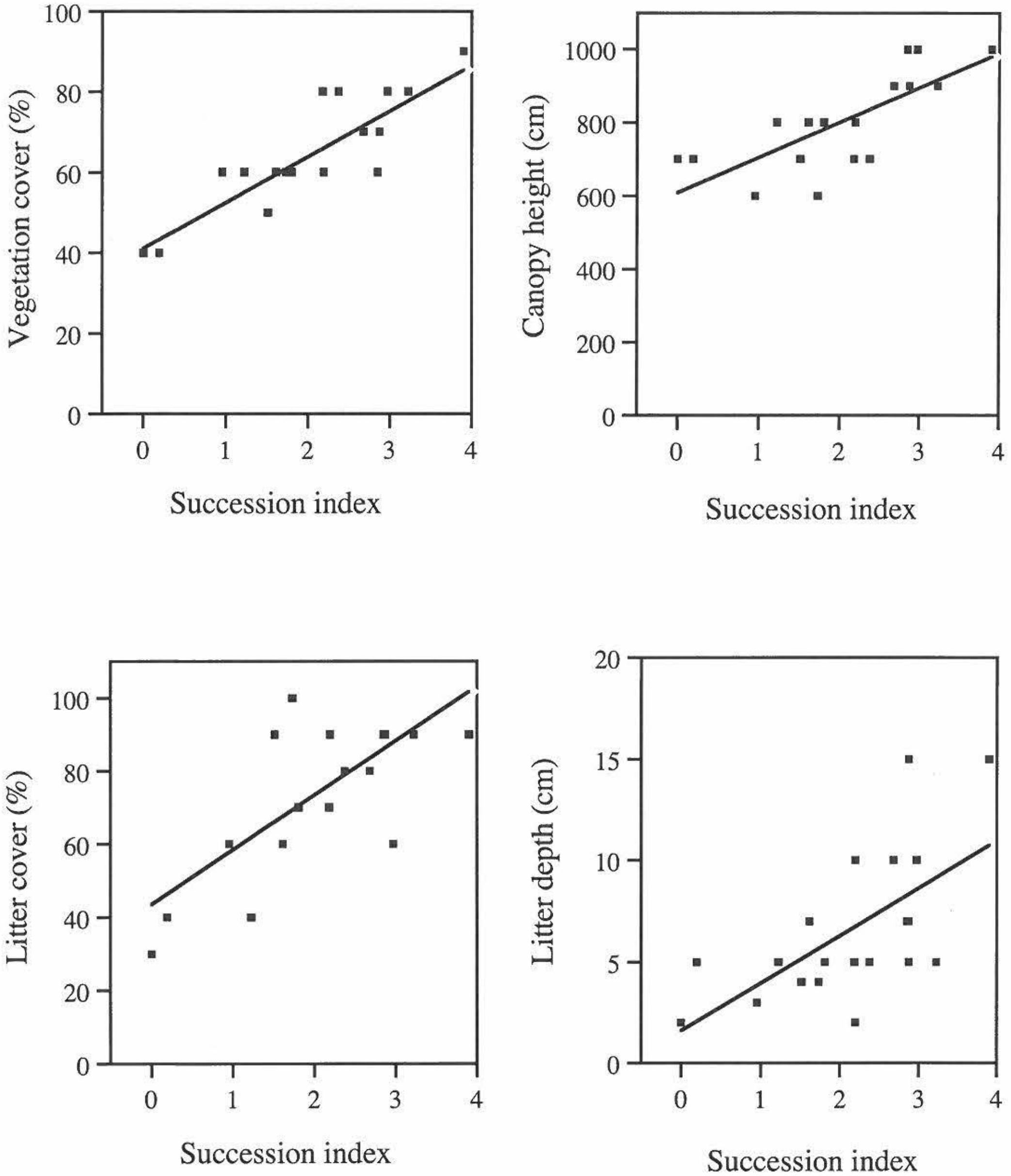


Figure 3.23 Vegetation cover, tree canopy height, litter cover and litter depth for 20 hypermagnesian soil sites plotted against the succession index. Trends are shown by the fitted spline curves.

Family	Species		
Cyp.	*Scleria brownii* Kunth		1.22
Apo.	*Alyxia microbuxus* (R. Br.) Guillau.	F	1.58
Smil.	*Smilax orbiculata* Labillardière	F	1.63
Apo.	*Alyxia glaucophylla* Heurck. et Muell.	F	1.78
Myrt.	*Babingtonia leratti* Dawson	F	1.79
Elae.	*Dubouzetia campanulata* Pancher ex Brongniart & Gris		1.81
Cyp.	*Costularia comosa* (C. B. Clarke) Kükenthal		1.87
Good.	*Scaevola montana* Labillardière	F	1.88
Denn.	*Pteridium esculentum* (Forster) Cockayne	F	1.89
Sapin.	*Gioua glauca* (Labilliardière) Radlkofer	F	1.90
Dill.	*Hibbertia wagapii* Gilg	F	1.95
Rub.	*Normandia neocaledonica* J. D. Hooker	F	1.96
Euph.	*Phyllanthus chrysanthus* Baillon		1.99
Myrt.	*Xanthostemon macrophyllum* Pampan.	F	2.00
Cun.	*Pancheria ferruginea* Brongniart & Gris	F	2.00
Sim.	*Soulamea pancheri* Brongniart & gris		2.02
Lind.	*Sphenomeris deltoidea* (C. Chr.) Copeland		2.03
Casua.	*Casuarina collina* Poisson	F	2.04
Rham.	*Alphitonia neocaledonica* (Schlechter) Guillaumin		2.05
Prot.	*Stenocarpus milnei* W. J. Hooker	F	2.06
Sant.	*Exocarpos neocaledonicus* Schlechter & Pilger	F	2.07
Prot.	*Grevillea gillvrayi* W. J. Hooker	F	2.11
Dill.	*Hibbertia veillardii* (Brongniart & Gris) Gilg	F	2.12
Epac.	*Styphelia veillonii* Virot		2.12
Myrt.	*Tristaniopsis callobuxus* Brongniart & Gris	F	2.12
Dill.	*Hibbertia pancheri* (Brongniart & Gris) Briquet	F	2.15
Celas.	*Maytenus fournieri* (Pancher & Sébert) Loesener	F	2.16
Thym.	*Solmsia calophylla* Baillon		2.17
Casua.	*Gymnostoma chamaecyparis* (Poisson) L. Johnston		2.17
Lilia.	*Dianella adenanthera* Schittler	F	2.18
Thym.	*Wickstroemia viridiflora* Meissn.	F	2.19
Cun.	*Codia montana* J. R. & G. Forster	F	2.20
Logan.	*Geniostoma densifolium* var. *oleifolium* Baillon	F	2.20
Aral.	*Polyscias pancheri* (Veillard) Harms		2.21
Epac.	*Styphelia albicans* (Brongniart & Gris) Sleumer		2.22
Cyp.	*Lepidosperma perteres* C. B. Clarke	F	2.23
Apoc.	*Rauvolfia semperflorens* (Mueller Argovie) Schlechter	F	2.24
Schi.	*Schizaea laevigata* Mettenius	F	2.24
Dill.	*Hibbertia lucens* Brongniart & Gris ex Pancher & Sébert	F	2.25
Apo.	*Alstonia coriaceae* Pancher ex S. Moore	F	2.28
Euph.	*Longetia buxoides* (Baillon) A. Shaw	F	2.29
Ole.	*Osmanthus austrocaledonicus* (Veillard) Knoblauch	F	2.34
Mim.	*Acacia spirorbis* Labillardière	F	2.35
Myrt.	*Piliocalyx eugenioides* Guillaumin		2.39
Myrt.	*Xanthostemon gugerlii* Merrill	F	2.39
Myrt.	*Austromyrtus stricta* Brongniart & Gris	F	2.41
Euph.	*Phyllanthus kouaouaensis* Guillaumin		2.41
Myrt.	*Uromyrtus artensis* (Montrouzier ex Guillau. & Beauvis.) E	F	2.41
Rub.	*Moranda* sp.		2.42
Epac.	*Dracophyllum verticillatum* Labillardière		2.43
Myrs.	*Rapanea assymetrica* Mez	F	2.43
Sapin.	*Cupaniopsis glomerfolia* Radlkofer		2.43
Xanth.	*Lomandra insularis* Schlechter	F	2.44
Myrt.	*Cloezia floribunda* Brongniart & Gris	F	2.44
Rut.	*Eriostemon pallidum* Schlechter	F	2.45
Sapin.	*Guioa villosa* Radlkofer	F	2.48
Flac.	*Casearia silvana* Schlechter		2.53
Smil.	*Smilax purpurata* J. R. & G. Forster	F	2.53
Euph.	*Austrobuxus carunculatus* (Baillon) A. Shaw		2.53
Thym.	*Wickstroemia elegans* L. Meyer	F	2.53
Cyp.	*Costularia pubescens* Raynal		2.54
Sapin.	*Dodonea viscosa* (L.) Jacquin	F	2.55
Mel.	*Dysoxylum rufescens* Veillard ex Pancher & Sébert		2.57
Rut.	*Comptonella albiflora* Hartley		2.58
Mel.	*Dysoxylum roseum* DC.		2.58
Sapot.	*Beccariella abrifolia* (Montrouzier) Sébert		2.59
Sapin.	*Storthocalyx leioneurus* Radlkofer	F	2.60
Apo.	*Rauvolfia balansae (Baillon) Boiteau*		2.61
Olea.	*Osmanthus austrocaledonicus* var. *crassifolius* (Veillard) I	F	2.61
Cyp.	*Baumea deplanchei* Boeckler		2.63
Malp.	*Acridocarpus austrocaledonicus* Baillon		2.68
Prot.	*Beauprea gracilis* Brongniart & Gris		2.70
Apo.	*Alyxia breviflora* Heurch & Mueller Argovie		2.70
Rub.	*Guettarda platycarpa* (Montrouzier) Guillaumin		2.70
Myrt.	*Cloezia artensis* var. *basilaris* (Montrouzier) P. S. Green	F	2.72
Rham.	*Ventilago neocaledonica* Schlechter		2.73
Eben.	*Diospyros labillardierii* Kostermans		2.75
Gutt.	*Garcinia balansae* Pierre	F	2.75
Sapin.	*Guioa crenata* Radlkofer		2.76
Eben.	*Diospyros veillardii* Kostermans		2.76
Cyp.	*Costularia nervosa* Raynal		2.77
Flac.	*Homalium austrocaledonicum* Seemann		2.77
Aral.	*Mydocarpus crassifolius* Dubard & Viguier		2.80
Gutt.	*Montrouziera sphaerioides* Pancher ex Planchon & Triana	F	2.83
Pitt.	*Pittosporum gracile* Pancher ex Brongniart & Gris		2.90
Euph.	*Phyllanthus aeneus* var. *aeneus* Baillon		2.94
Myrt.	*Austromyrtus ellipticus*		2.94
Sapot.	*Rhamnoluma calomeris* (Baillon) Aubréville		2.98
Rub.	*Tarenna microcarpa* (Guillaumin) Jérémie		2.99
Rub.	*Gardenia aubryi* Veillard	F	3.04
Aqui.	*Ilex sebertii* Pancher & Sébert		3.05
Lora.	*Amyema scandens* (Tieghem) Danser		3.05
Rub.	*Psychotria collina* Labillardière		3.05
Rub.	*Psychotria semperflorens* (Baillon) Pancher ex Beauvisage	F	3.06
Prot.	*Stenocarpos tremuloides* Brongniart & Gris		3.22
Celas.	*Geniostoma rupestre* Baillon		3.50

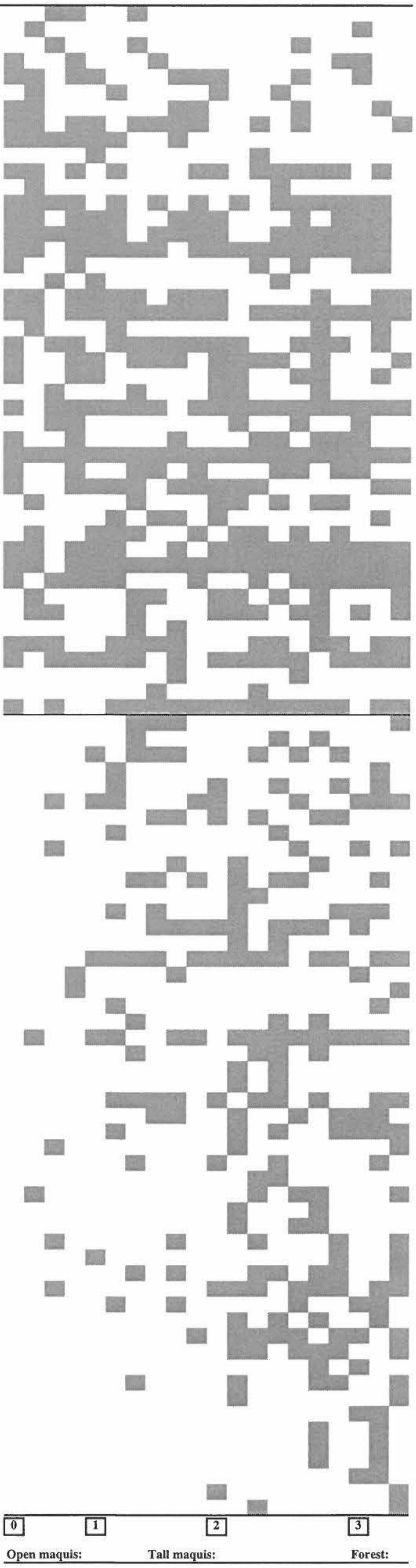


Figure 3.24 Presence of species (shaded) in the 20 hypermagnesian soil sites ranked by the succession index (SI). Species are ranked by the species index (I). Horizontal lines indicate the boundaries between early persistent and late successional groups of species. F indicates vegetative resprouters from rootstocks.

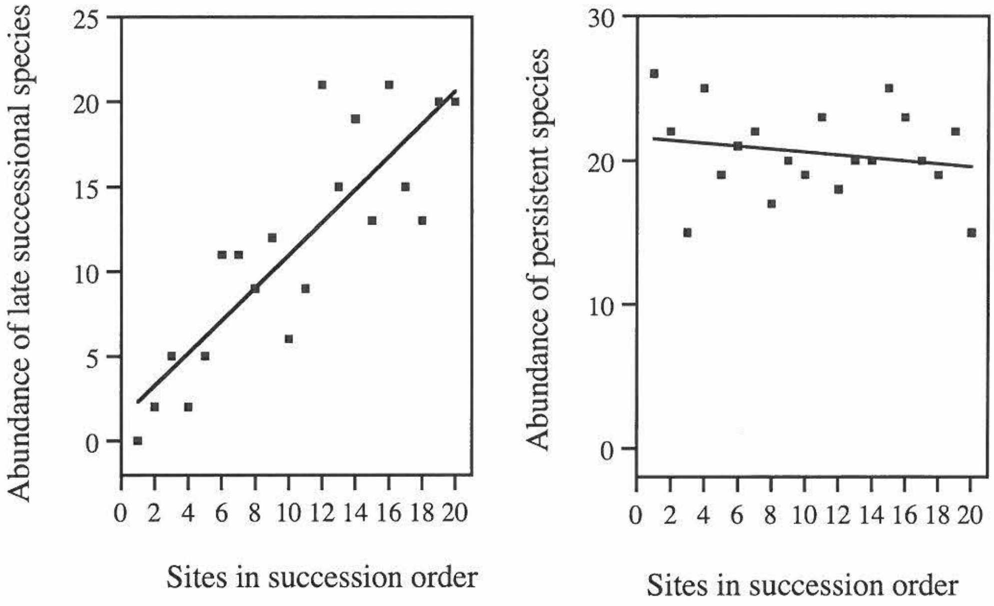


Figure 3.25 The number of persistent and late successional species in relation to rank order of sites on serpentinite at Kouaoua by the succession index. Trends are shown by the fitted spline lines.

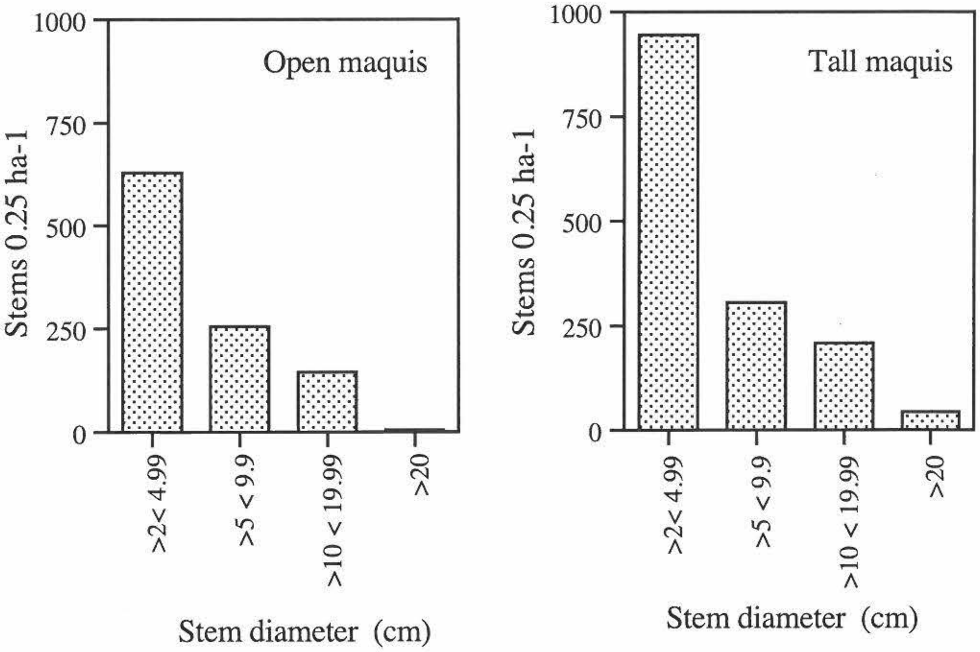


Figure 3.26 Size class distribution for all stems for maquis communities on serpentinite at Kouaoua.

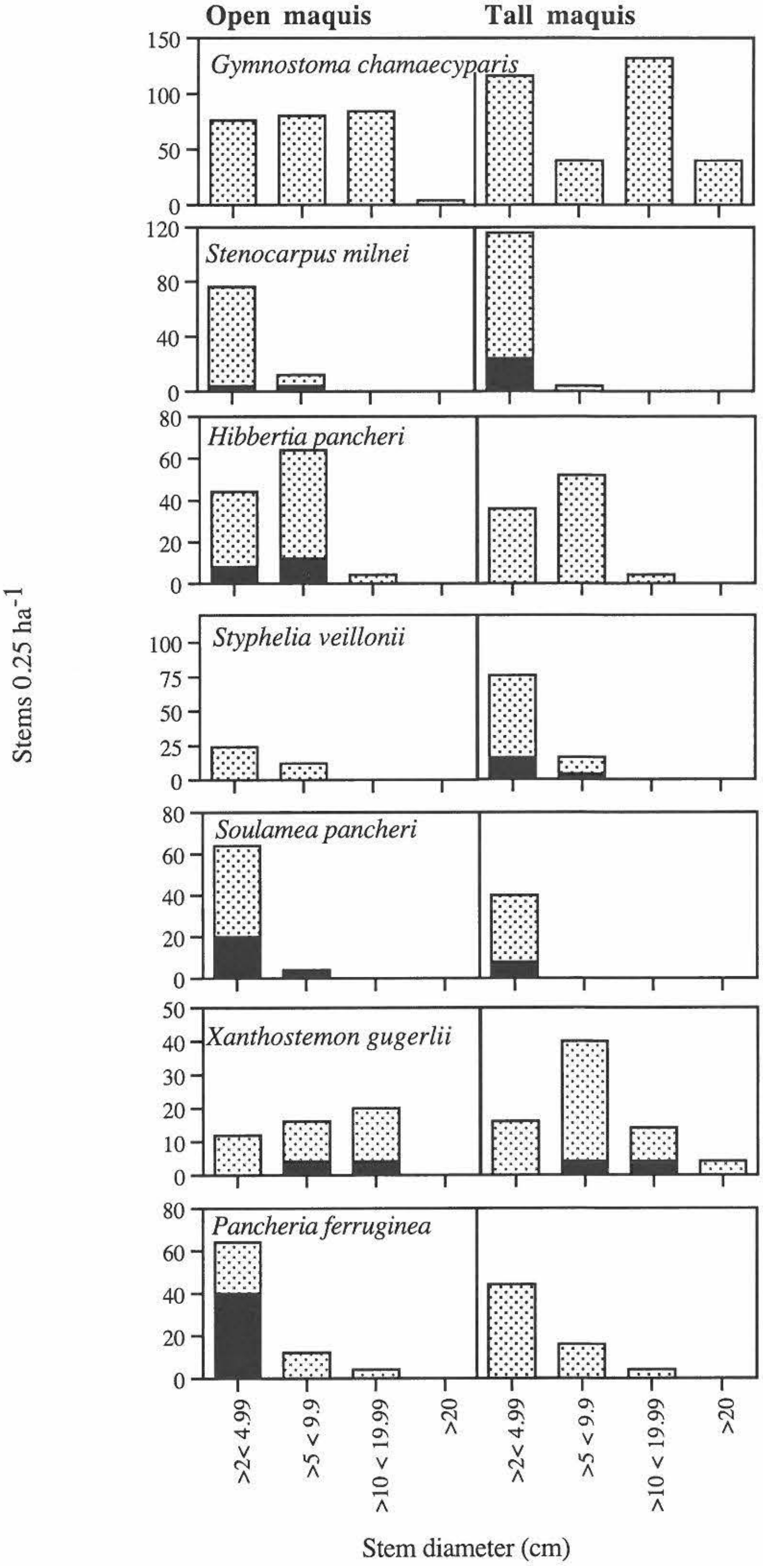


Figure 3.27 Size class distributions (d.b.h.) for stems of select species in open maquis and tall maquis on serpentinites at Kouaoua. Black bars represent total nu mber of multistems treated as single stems.
Note: Values for the number of stems per species have been transformed to 0.5 hectares.

3.4.2.3 Fire tolerance

Maquis formations on serpentinite outcrops below Méa, and Mai frequently contained burnt stumps and fire scarred shrubs. The floristic survey of *G. chamaecyparis* communities indicated that thirty nine percent of species in the maquis have a resprouting growth habit which may confer fire tolerance. Many of these are persistent species which constitute approximately half of the cover of these maquis formations (fig. 3.28).

3.4.2.4 Fire susceptibility

The estimated fire susceptibility of *Gymnostoma chamaecyparis* sites is shown in fig. 3.29. Bare areas in open maquis are likely to have a major effect by spatially reducing fire spread between vegetation patches. Open and tall maquis formations possessing more continuous vegetation cover are very susceptible to fire and maintain very high flammability ($Fs > 7$) because ground fuel cover is continuous and is frequently dry beneath open canopy conditions. *G. chamaecyparis* forest appears to be less susceptible to fire than tall maquis, but is relatively susceptible compared to forests on oxisols because of the absence of large broad leaf canopy trees which cast shade and thereby increase the moisture content of ground fuel.

The flammability index (fig. 3.30) was based on the trends of fire susceptibility. Since precise ages are unavailable for *G. chamaecyparis* formations at Kouaoua, tree growth rates were estimated by comparing the height/trunk diametre ratios of *G. deplancheanum* trees from iron crust formations of known age with *G. chamaecyparis* trees (fig. 3.31). It appears that *G. chamaecyparis* trees are 40% slower growing, perhaps because of limited soil on serpentinite and the chemical constraints imposed on plants by this soil type (Jaffré, 1980). Slow growth rates might delay peak flammability of vegetation formations on hypermagnesian soil by approximately 20 years compared with iron crust vegetation. However the forest may remain more flammable than its equivalent on iron crust because the steepness of sites would promote the rapid spread of fire. Furthermore, the canopy is more open compared to forest communities on oxisol and therefore promotes drier more flammable conditions in the understorey.

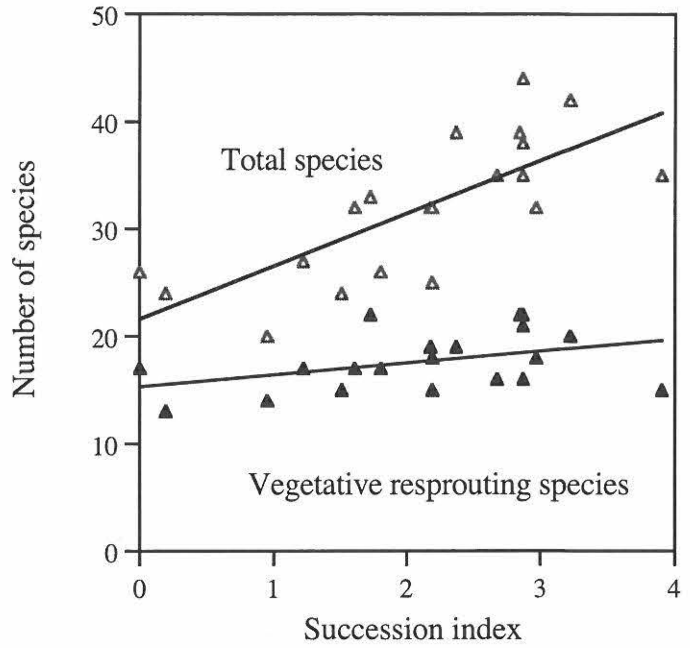


Figure 3.28 The number of vegetative resprouting species in relation to rank order of sites by the succession index on serpentinite at Kouaoua. Trends are shown by fitted spline curves.

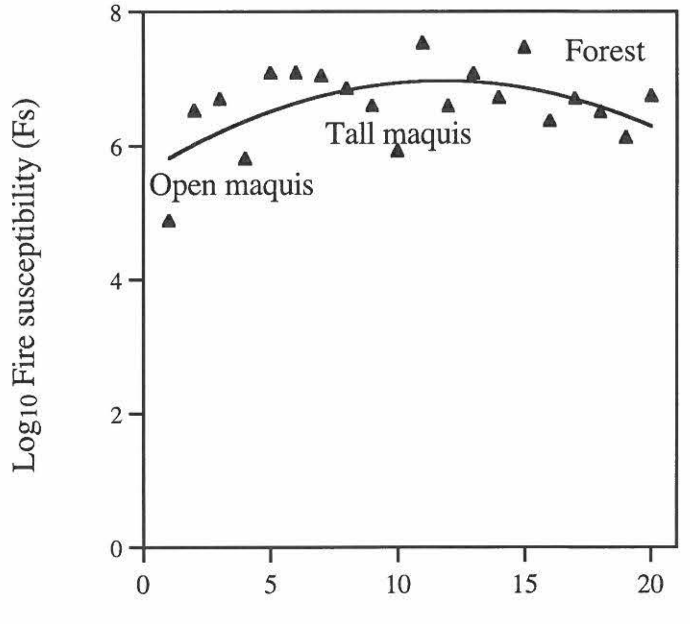


Figure 3.29 Fire susceptibility of sites in rank order of the succession index. Vegetation types are indicated and a fitted spline shows the trend from open to forest formations. The earliest sites have apparently not burned for at least 25 years.

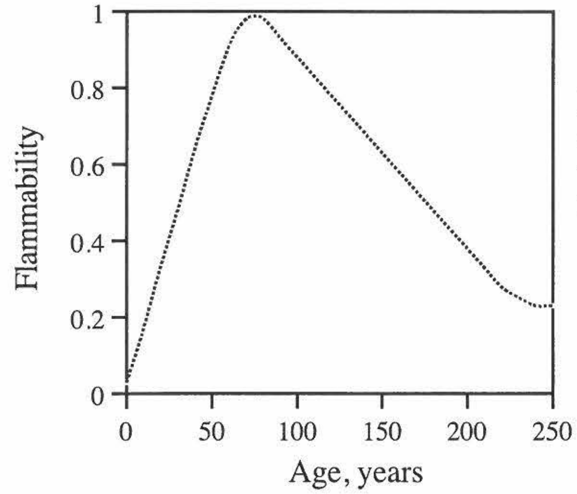


Figure 3.30 Relative flammability of different successional ages of vegetation used in the transition matrix model.

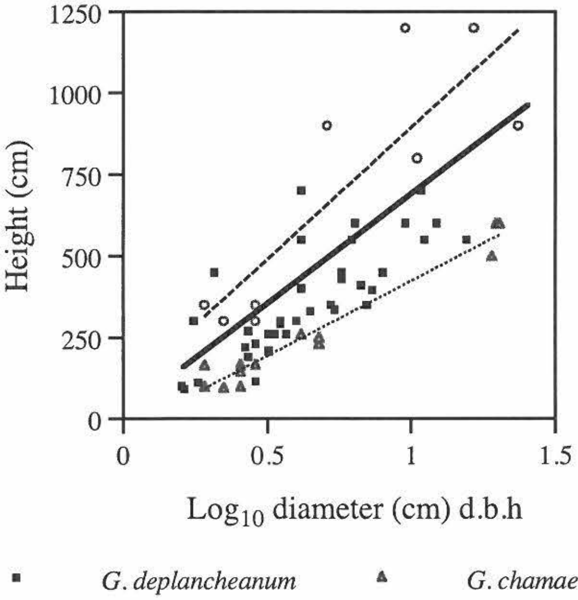


Figure 3.31 Height of *Gymnostoma deplancheanum* (dark square, thick line), *Gymnostoma chamaecyparis* (triangle, dotted line) and*Gymnostoma intermedium* (circle, dashed line) plotted against trunk diameter (d.b.h). Fitted regression lines show that *G. chamaecyparis* produce shorter trees of equivalent diameter to *G. deplancheanum* and *G. intermedium*.

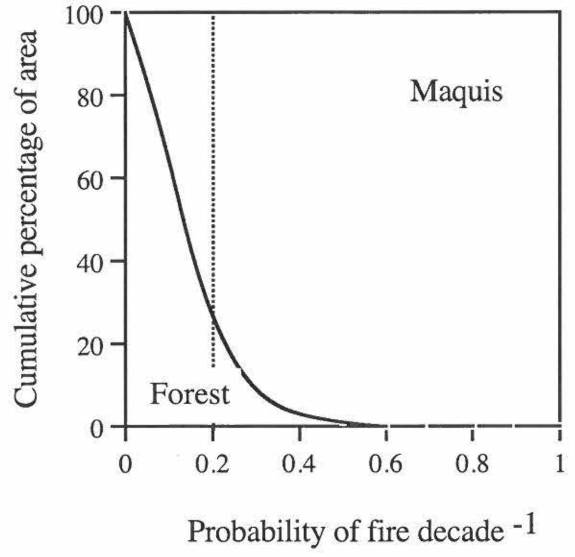


Figure 3.32 Composition of vegetation on hypermagnesian soil in relation to decadal ignition probablity predicted using a transition matrix model over a 1000 yr period starting with burnt sites. The fine dotted line represents the observed frequency recorded from the floristic survey.

3.4.3 Discussion of the hypermagnesian soil survey

3.4.3.1 Succession patterns & processes

The succession index derived from vegetation structure parameters only explained 35% of the variation in the MDS floristic analysis, and was therefore a poor predictor of successional change in vegetation. This lack of correlation arose partly because certain vegetation types on serpentinite, in particular open maquis, were under-sampled on eroded parts of the serpentinite landscape where they were most common. Most of the samples were at a tall maquis stage, so much of the variation reflects differences within this stage of the succession rather than between successional stages. This problem is exacerbated because several tall maquis and forest sites retained large areas of bare serpentinite outcrop which maintained suitable conditions for the persistence of open maquis species (eg: Cyperaceae). Also, large *G. chamaecyparis* trees in open maquis produced conditions which were also suitable for the establishment of certain forest species.

Despite the low correlation of the succession index against MDS axes, floristic diversity increases with (i) soil cover and (ii) vegetation cover and height. This pattern might be interpreted as variations in soil depending on the slope. Jaffré (1974) suggests that *Gymnostoma chamaecyparis* occupy parts of the serpentinite landscape which posses higher soil moisture conditions, such as drainage lines. However, this fails to explain the broad distribution of common serpentinite species such as *Gymnostoma* which are also found on rocky serpentinite sites. Species diversity also shows an inverse correlation with evidence of fire, suggesting that serpentinite communities form part of a post-fire succession progressing from open maquis, to tall maquis and forest, but not to rainforest. Ages for when these stages developed at Kouaoua are unclear. However, height/trunk diametre ratios of *G. chamaecyparis* trees have been used to infer that the transition between successional stages on hypermagnesian soil takes perhaps 20 years longer than post-fire successional communities on iron crust.

Vegetation communities on serpentinite appear to be composed of (i) a group of persistent species found from open maquis to forest and (ii) a group of shade tolerant species found only in closed formations. The persistent group is composed of species which resprout in soil pockets (*Hibbertia, Stenocarpus, Soulamea*), and sedges (*Costularia, Baumea,* *Schoenus* and *Scleria*) and woody species (*Gymnostoma*) which establish from either seed banks or wind dispersed seed. Increases in floristic diversity within soil pockets may be affected by the depth of soil, with deeper soil pockets able to support a rapid development of shrubs and large *G. chamaecyparis* trees (up to 20 cm d.b.h). Vegetation spread onto adjacent areas with shallow soil is slow and characterised by a prolonged sedge phase and gradual colonisation by shrubs. As these shrubs become more abundant in later successional stages (fig. 3.27). Cyperaceae cover declines because sedges are excluded by greater shade and litter or competition from shrub species which are favoured by more closed conditions.

3.3.3.2 Vegetation flammability and fire frequency

Gymnostoma chamaecyparis has a major influence on the flammability because (i) it produces a deep persistent fuel bed which (ii) dries rapidly during rain-free periods because of the open crown and sparsely developed shrub understorey. 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 colonised and support fires. Fire is more likely to spread in tall maquis formations because of the continuous litter and an open canopy which maintains dry understorey conditions.

Fires accelerate and burn more intensely as the slope increases up to about 30° in the direction of the fire spread, and are capable of jumping bare ground (Gill, 1981). The steepness of the serpentinite terrain would favour rapid fire spread between vegetation patches and burning of forest despite the higher fuel moisture.

Results of the floristic survey suggest the frequency of maquis and forest to be 80% and 20% respectively. This corresponds with a decadal ignition probability of 0.2 (fig. 3.32). Such an ignition probability prediction is possibly too low because serpentinite communities are in close proximity to mines and agricultural land (fig. 2.16) containing numerous sources of ignition. Mine prospecting in the Kouaoua region peaked in the 1960s (Guy *et al*, 1979), and fires lit during this period would have had a major impact on steep serpentinite maquis and could explain the presence of charcoal in fire scars of shrubs and burnt stumps. A more realistic ignition probability of > 0.4 decade^{-1} reflects actual connectance and ignition frequency. Lower connectance between patches would also explain the restriction of forest to areas protected from fire by bare rock along ridge lines or steep slopes observed from aerial photographs (fig. 2.16).

3.3.3.3 Vegetation history

Serpentinite belts at Kouaoua represent a steep geological contact zone which is often in close proximity to coastal agricultural areas (Jaffré, 1969). Sediment cores from a coastal swamp site at Canala contain abundant charcoal from 3000 BP to the present suggesting that valleys and surrounding slopes have been frequently burnt since human arrival (Stevenson, 1998). Fires escaping from agricultural land over this period are likely to have had a profound effect on the vegetation of surrounding slopes and explain the restricted distribution of rainforest to small pockets within valleys conferring some protection from fire.

Several serpentinite localities in the central mountain range of New Caledonia contain rainforest (eg: Koné Tiwaka). These high altitude areas experience rainfall sufficient to maintain fire sensitive rainforest communities. In contrast, hypermagnesian soils on low altitude serpentinite outcrops of the Boulinda (Jaffré & Latham, 1974) and Koniambo ultramafic ranges (Jaffré, 1974) are generally much drier environments that no longer support rainforest possibly due to repeated burning by fires from neighbouring agricultural land (Latham & Jaffré, 1974; Jaffré, 1980). Patches of forest with large *G. chamaecyparis* trees occur along water courses on serpentinite, but contain few rainforest species despite the close proximity of rainforest in eroded oxisol valleys adjacent to these serpentinite outcrops (Jaffré, 1974). The remaining eroded oxisol landscape surrounding rainforest patches and serpentinite outcrops supports extensive thickets of flammable *Acacia spirorbis* (Jaffré, 1974; Jaffré & Latham, 1974). Such a flammable vegetation in close proximity to high ignition sources in valleys would effectively eliminate low altitude rainforest species from establishing populations outside of valley pockets would be unlikely because of the frequent fires. Seed from rainforest patches is unlikely to establish in forest on serpentinite because of (i) the limited extent of suitable forest habitat on serpentinite, and (ii) the large distance between forest and rainforest. Rainforest species which do establish in serpentinite forests will require adaptations to the chemical properties of hypermagnesian soils (table 2.2) which are very different from other ultramafic substrates (Jaffré, 1980).

Serpentinite shrubby maquis and forest occupy a very limited area compared to other vegetation types on ultramafic soil at Kouaoua. *Acacia* *spirorbis* will form extensive stands (> 100 ha) on soils composed of a mixture of eroded oxisol and serpentinite debris (Jaffré, 1969). *A. spirorbis* rapidly establishes after fire because germination is stimulated by heat. Moreover, *Acacia spirorbis* shrubs are able to reproduce 3-5 years after initial establishment (Sarrailh, pers.comm). In contrast, *G. chamaecyparis* trees require much longer to reach reproductive maturity and are possibly excluded by *Acacia spirorbis* through direct competition. Furthermore, high fire frequencies in *Acacia spirorbis* thickets would kill fire sensitive *G. chamaecyparis* trees before they reaches maturity. Individual *G. chamaecyparis* trees have been recorded in *Acacia spirobis* formations (Jaffré, 1969, Jaffré, 1974), however they are likely to only remain abundant on steep rocky outcrops with low fire frequencies.

3.5 General discussion

Floristic and demographic analysis of maquis and forest at Kouaoua and Plaines des Lacs has raised several issues which are the focus of this discussion. (i) Does vegetation variation represent succession after fire? (ii) (ii) Are all three systems similar in terms of (a) general patterns / dynamics and (b) response to fire? (iii) What is the role of *Gymnostoma*? (iv) How do changes in susceptibility and fire frequency affect vegetation composition?

Results presented in this chapter suggest that variation in vegetation at Plaines des Lacs and Kouaoua is primarily indicative of succession after fire. However, the proportion of the floristic variation explained by fire differs between substrate types. This difference is partially explained by the different size of the areas sampled.

Iron crust oxisol covers extensive areas of Plaines des Lacs and allowed for vegetation sampling at a broad scale, reducing the effects of local scale floristic variations on the general succession pattern. Regional scale differences in precipitation, altitude and slope explained 20% of floristic variation in plant communities on iron crust. However the remaining 80% of the floristic variation correlated with vegetation structure and known fire events at different times in the past. Growth rings of fire sensitive species (fig. 3.8) and the declining abundance of fire tolerant species with time since fire (fig. 3.6), also lend support to a fire driven succession pattern on iron crusts.

Changes in floristic composition due to fire were much less obvious at Kouaoua and confounded by local scale site effects because sampling was limited to small areas of vegetation that had not been disturbed by mining. Aerial photos reveal the extent recent mining disturbance has had on vegetation on eroded oxisol and hypermagnesian soil at Kouaoua (figs. 2.12 & 2.16). Both cyclones and landslides may also generate local successional patterns that may differ from those due to fire. In the case of communities found on eroded oxisol at Kouaoua, there is uncertainty as to when fires occurred, but evidence that fire has had an important role in expanding fire tolerant woody sedge maquis into areas once occupied by rainforest. Recent fire scars (20 yr ago) on *Araucaria montana* trees (fig. 3.20) indicate that woody sedge maquis is maintained by a high fire frequency. In the case of serpentinite vegetation at the base of Kouaoua, the distribution of maquis and forest may be related to soil moisture gradients (Jaffré, 1996), though there is evidence in the form of burnt stumps and charcoal to suggest that these communities have also been burnt in the past. Moreover, floristic changes from maquis to forest on hypermagnesian soil coincide with decreases in the abundance of fire tolerant species and burnt material.

Successional vegetation at Plaines des Lacs and Kouaoua can be grouped into suites of species characteristic of a sere in a successional sequence. The early successional group exhibits abundant regeneration in open maquis that either (a) abruptly declines in later formations where canopy cover and litter are more abundant, or (b) persist as a main structural component of tall maquis and forest formations (fig. 3.33). Species belonging to the forest group first appear as isolated individuals in tall maquis and eventually become the characteristic component of later forest stages.

From the iron crust survey, it appears that early successional species may take up to 50 years to develop a continuous canopy and another 50-70 years for late successional species to establish as an abundant understorey in forest. Rates of establishment of maquis and forest at Kouaoua are poorly understood on hypermagnesian soil but are likely to be slower than on oxisols because of slower growth intrinsic on this substrate. The rate of vegetation development at all areas surveyed is slow compared to many other tropical regions (Brown & Lugo, 1990). However they are similar to those on lava fields (Kitayama *et al*, 1995)(fig. 3.34). This suggests that the processes constraining establishment at Plaines des Lacs and Kouaoua may be similar.

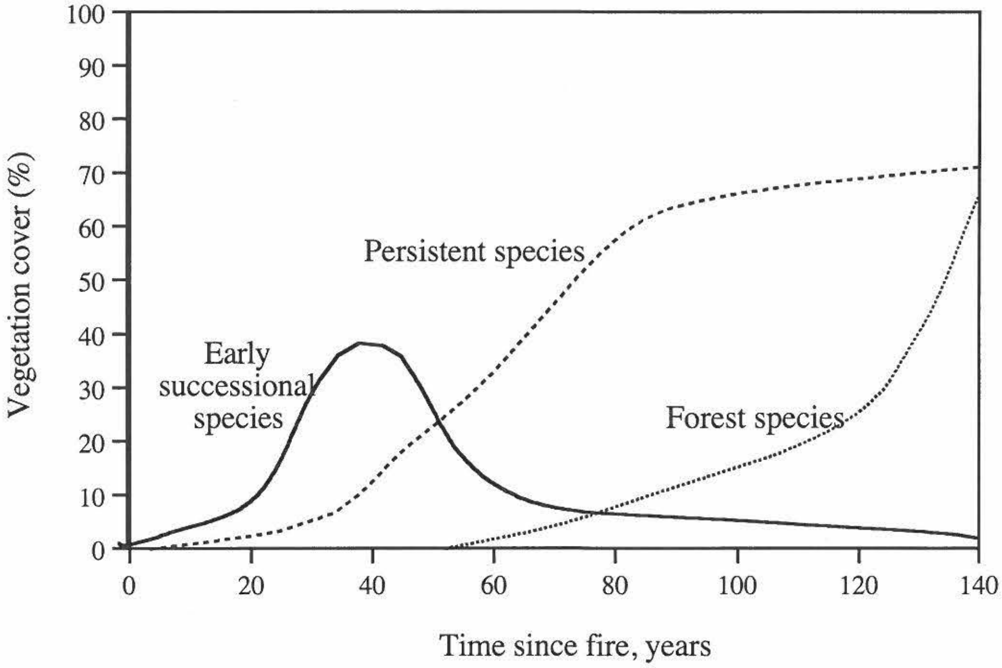


Figure 3.33 Schematic diagram of changes in abundance (vegetation cover) of the three successional floristic groups with time since fire.

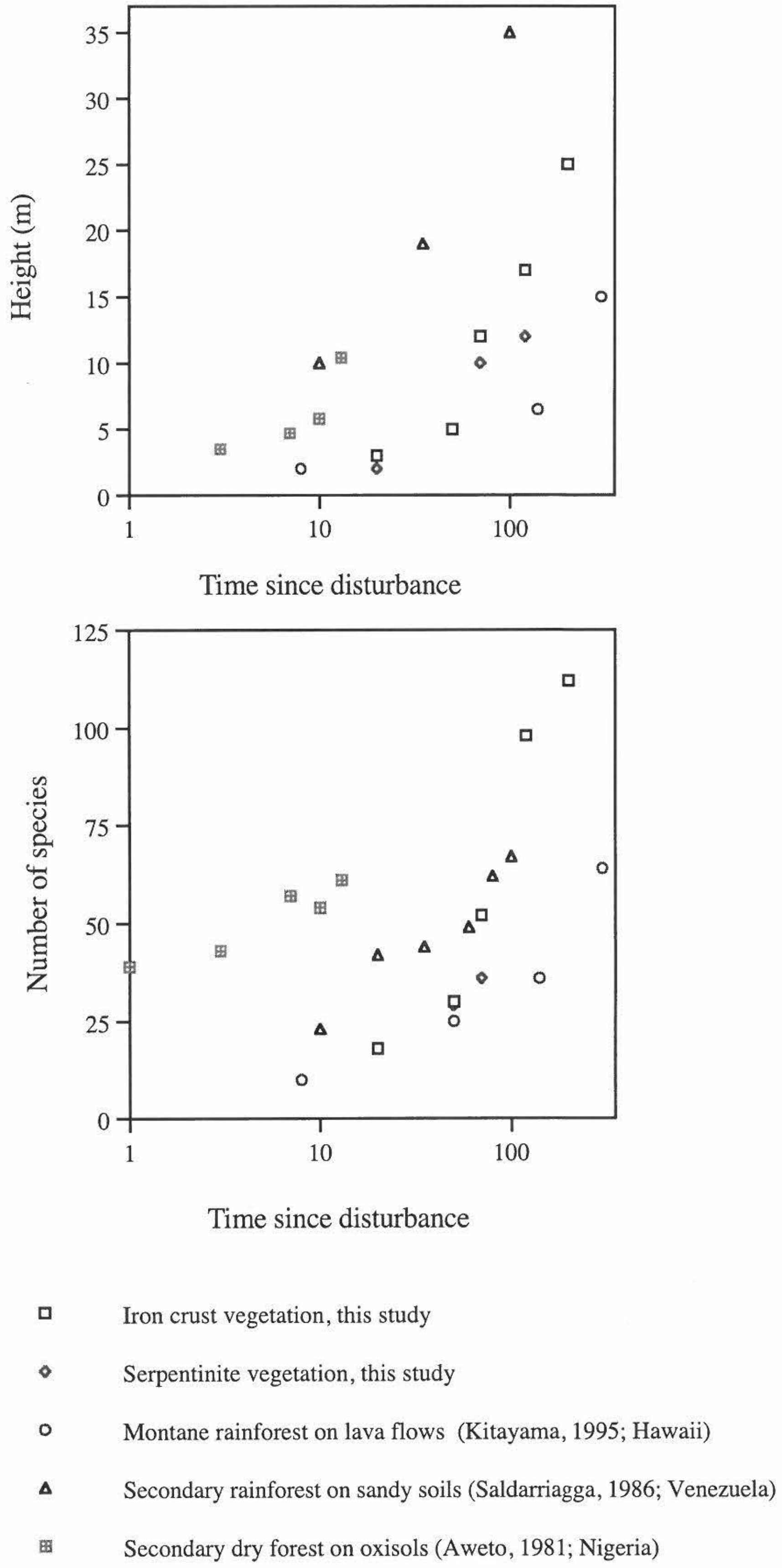


Figure 3.34 Change in tree canopy height, and number of species with time for iron crust, serpentinite sites, and other tropical rainforest.

A major pattern to emerge from vegetation surveys is the strong floristic similarity between maquis communities. Maquis at Kouaoua and Plaines des Lacs share a core of early successional taxa that can be subdivided into three distinct groups.

(i) Resprouters - such as *Pteridium esculentum, Montrouziera sphaeriodea, Eriaxis rigida, Lepidosperma perteres,* and *Babingtonia leratti* are the first species to appear after fire, mostly through rapid resprouting, but become rare in later formations because they either regenerate poorly through seed or spores or require conditions that are not present in later successional stages.

(ii) Resprouters which produce abundant seed - such as *Hibbertia pancheri, Tristaniopsis callobuxus, T. guillanii, Lomandra insularis, Codia montana. Grevillea gillvrayii, G. exul* and *Longetia buxioides.* These species are able to re-establish after a disturbance such as fire either through vegetative resprouting, from seed in seed banks or from surrounding vegetation. They may persist in later successional stages by being either long lived (*Tristaniopsis* spp., *Codia montana*) or able to undergo several short life cycles that maintain populations.

(iii) - Fire sensitive obligate seeders - such as *Gymnostoma* spp., *Alphitonia neocaledonica, Styphelia veillonii, Dracophyllum verticillatum* and *Costularia* spp. establish from abundant seed that may remain in the seed bank after fire or arrive through dispersal from outside the burnt area. They are able to persist, with the exception of *Costularia,* into later successional stages by being either long lived (*Gymnostoma* spp.) or by maintaining short lived populations from seed banks. *Gymnostoma, Costularia* and *Alphitonia* tend to show greater levels of regeneration in areas that area frequently disturbed.

The most common form of fire tolerance in maquis species is through vegetative resprouting from lignotubers. This form of fire tolerance is common to many families. Myrtaceae contains the highest number of lignotuber resprouting genera followed by Cunoniaceae, Euphorbiaceae, Proteaceae, Dilleniaceae, Goodeniaceae, Flacourtiaceae, Sapindaceae, Guttifereae, Myrsinaceae, Apocynaceae, Thymeliaceae, Rubiaceae and Verbenaceae. Woody species such as *Montrouziera sphaeriodea, Guioa glauca, G. villosa* and *G. crenata* are able to resprout from suckers on horizontal roots. Certain orchids (*Eriaxis rigida*) and ferns (*Pteridium esculentum*) resprout from subterranean rhizomes. Other physiological adaptations to tolerate fire such as thick bark are rare in ultramafic maquis and restricted to mature trees (eg: *Araucaria* and *Arillastrum*).

Species may also escape fire as refugia populations in unburnt patches. Rocky outcrops of iron crust at Plaines des Lacs and serpentinite at Kouaoua are effective barriers against fires and often protect a mix of maquis and forest species. Surrounding burnt areas are initially occupied by resprouters then by wind dispersed maquis species from vegetation islands. Forest species may also establish on burnt areas, but are rare, which suggests that they are either dispersal limited or require forest conditions that are not present at early successional stages.

Gymnostoma is potentially a key modifier of succession processes at tall maquis and forest stages because of its abundant regeneration and persistence as a dominant canopy tree in these communities. *Gymnostoma deplancheanum* and *G. chamaecyparis* contributes up to 66% of the stems in maquis formations and 80% of the canopy trees > 10 cm d.b.h. Such an important dominance of the canopy is likely to have a major impact on succession processes by modifying the light and litter regimes (chapter 5 and 6) which in turn influence the susceptibility of the community to fire.

Vegetation susceptibility to fire is largely dependent on (i) the abundance of flammable components of the vegetation, (ii) the rate of fuel accumulation of these species and (iii) the connectance between fuel loads. Changes to these vegetation properties will occur over time and generate vegetation types containing different levels of susceptibility depending on the conditions produced by the structurally dominant vegetation groups. Vegetation structure may influence rates of evaporation in fuels by affecting microclimatic conditions such as light and wind (Whelan, 1995). Local scale (iv) climatic and (v) topographic influences will also have an impact on fuel flammability independently of the characteristics of the vegetation (Whelan, 1995).

The tree and shrub stratum of open maquis on iron crust and serpentinite is composed of isolated *Gymnostoma* trees and shrubs such as *Tristaniopsis, Xanthostemon* and *Babingtonia* which produce a thin litter layer separated by extensive areas of bare ground. Woody sedge maquis at Kouaoua is similar in structure to maquis communities on iron crust and serpentinite except that *Gymnostoma* is absent and sedges produce a continuous ground cover between shrubs and trees. This fuel is prone to rapid drying and is therefore highly flammable because the isolated shrubs and trees produce insufficient cover to greatly reduce evaporation. During rain-free periods, fuels on northern slopes dry more rapidly and to lower moisture contents because of the longer duration of solar radiation. Woody sedge maquis on eroded oxisol is also more susceptible to fire on dry north facing aspects because Cyperaceae and *Pteridium esculentum* fernland typically produce a high fuel connectance. This situation is likely to favour high rates of fire spread because of the steep terrain associated with many woody sedge communities. In contrast, open maquis on iron crust and serpentinite are less susceptible to fire even on north facing aspects, because extensive areas of bare rock reduce fuel connectance between trees and vegetation patches. Fire spread is likely to be low in maquis on steep hypermagnesian soil pockets because of the low connectance of fuels, and even lower on iron crust for the same reason and also the low relief of iron crust landscapes.

The development of a continuous *Gymnostoma* canopy after 20-50 years increases the susceptibility of tall maquis formations to fire by producing a deep continuous litter cover that can promote fire spread despite the higher fuel moisture content. The open crown of *Gymnostoma* allows both greater solar radiation and possibly wind to enter and increase evaporation of moisture from understorey fuel beds. Tall maquis on hypermagnesian soil is likely to be even more susceptible to fire than tall maquis on iron crust because canopy and understorey cover is less abundant and casts very little shade between soil pockets. Large areas of bare ground between vegetation pockets might also facilitate greater evaporation of fuel by winds. Tall maquis formations on north facing serpentinite outcrops are likely to be very susceptible to drying because of longer periods of solar radiation which increase the duration of evaporation and high temperatures. Such dry fuels on steep slopes may facilitate high rates of fire spread in tall maquis on serpentinite outcrops.

Forest on iron crust oxisol and eroded oxisol are characterised by a canopy largely dominated by *Gymnostoma*, and by a tall dense understorey of broad leafed forest and rainforest species. The susceptibility of these communities to fire is lower than younger tall maquis sites because the dense broad leaf understorey casts heavy shade and may reduce wind evaporation of fuel moisture. Forests on eroded oxisol appear to be even less susceptible to fire than forests on iron crust because high altitude parts of Kouaoua experience more frequent cloud and fog which lower solar radiation and reduce evaporation of forest fuels. In contrast, forest communities on hypermagnesian soil are likely to remain fire prone compared to other forests due to the absence of broad leaf tree species which could cast more shade and maintain litter moisture.

It is apparent from a broader geographic context or from vegetation history (Hope, 1996; Hope & Pask, 1998) that rainforest can occur on all three substrates. However, rainforest is now much more restricted and occurs as small fragments on moist summits, valley bottoms or south facing slopes where moister microclimates reduce the duration of dry fire prone conditions. Maquis communities have expanded in their place and developed into a series of distinct communities. The rate at which these communities develop appears to be dependent on the suitability of ultramafic soil chemical and physical properties for establishment and growth. Rates of growth and development of communities will in turn generate communities with different fire frequencies.

On peridotite slopes surrounding forest at Kouaoua, and maquis and forest at Plaines des Lacs, frequent fires have led to the development of woody sedge maquis. This maquis type is composed of a continuous ground cover of sedges and fire tolerant shrubs, which in many areas is maintained in a pyric succession by very frequent fires that favour the rapid growth of a flammable *Pteridium esculentum* fern land after 20 years (Jaffré *et al*, 1998 a). Fire spread in such formations leaves very few islands of unburnt vegetation, because there is very little rocky ground to reduce the connectance between fuel patches. Under such situations, many fire sensitive colonists are likely to be either eliminated before they reach reproductive maturity or confined to patches of bare ground. This appears to be the case for *Gymnostoma intermedium*, and fire sensitive Epacridaceae which only show abundant regeneration on large areas of bare ground (eg: road sides).

Vegetation development after fire on iron crusts and serpentinite is much slower than on eroded oxisol slopes because rocky outcrops restrict vegetation establishment to soil pockets between outcrops. Slow vegetation development on iron crust and serpentinite outcrops has in turn reduced the susceptibility of these maquis formations being burnt by frequent fires. Maquis on iron crust and serpentinite contain large numbers of fire sensitive colonists such as *Gymnostoma*. Fire sensitive species are able to persist in these maquis formations even in areas where there are numerous sources of human ignition because fire spread is effectively reduced by low fuel connectance and rocky outcrops. In contrast, fire sensitive species, in particular forest species, may suffer localised extinctions in forest because fire spread is likely to be facilitated by continuous fuel connectance between trees and shrubs.

Forests at Plaines des Lacs are likely to remain dominated by *Gymnostoma* trees because (i) the fire frequency has been sufficient to reduce rainforest seed sources to isolated pockets which are spatially very distant from suitable forest habitats. (ii) Seedling regeneration is sufficiently abundant in forest formations for fast growing *Gymnostoma* to colonise canopy gaps created by disturbances (eg: cyclones, tree fall). This interpretation may also explain for the persistence of *G. chamaecyparis* on serpentinite and the maintenance of pure canopy forest stands of *G. intermedium* at Kouaoua. Certain rainforest species such as *Nothofagus* behave in a similar manner and also establish pure canopy stands through progressive replacement of adults trees by saplings during episodic disturbance events (Ash, 1982; Read & Hope, 1996).

Transition matrix models generated for communities at Plaines des Lacs and Kouaoua suggest that fire frequencies > 0.6 decade^{-1} are likely to reduce tall maquis and forest communities on iron crust and serpentinite outcrops to smaller unburnt vegetation patches and eliminate of rainforest species found in forest formations. Forest would be reduced to areas protected by rocky mounds in climatically wet parts of the landscape. Mature trees (eg: *Araucaria, Arillastrum*) which tolerate infrequent fires would also suffer localised extinctions. Colonist species which produce seed irregularly such as *Gymnostoma intermedium* might also suffer localised extinction because fire frequencies would eliminate colonists before they were able to produce seed. The absence of resprouters in these communities would result in much slower rates of establishment on burnt patches largely dependent on seed arriving from surrounding vegetation. In contrast, maquis containing *Gymnostoma deplancheanum*, and *G. chamaecyparis* is unlikely to a major suffer floristic impoverishment at fire frequencies of > 0.6 decade^{-1} because slow vegetation establishment would ensure that fuel connectance remained low enough to reduce fire spread into these formations.

At fire frequencies < 0.4 decade^{-1}, the floristic composition of forest containing many fire sensitive species are likely to expand into areas once occupied by maquis. *Gymnostoma deplancheanum* and *G. intermedium* might persist as a canopy tree, but it would eventually be replaced by rainforest species as rainforest expanded from valleys or summits. In contrast, *Gymnostoma chamaecyparis* is likely to remain a major component of the forest canopy on serpentinite outcrops because of the absence of rainforest on serpentinite at Kouaoua. At fire frequencies of < 0.4 decade^{-1}, colonist species more suited to the open conditions of rocky outcrops or recently disturbed bare ground (*Pteridium, Costularia*) would be excluded from much of their former range by forest and occur in swamplands or rocky outcrops where substrate conditions would reduce forest colonisation.

3.6 Conclusion

Field surveys indicate that changes in vegetation structure and floristics at Plaines des Lacs are indicative of different stages of a post fire succession. These post fire patterns appear to have arisen from a low fire frequency consisting of short peak fire events separated by long fire free periods which allowed the development of later successional stages. A similar fire frequency scenario may also explain for floristic and structural changes in vegetation on hypermagnesian soils at Kouaoua. However, frequent large fires from agricultural land in the valley bottom appear to have reduced maquis and forest over much of its former serpentinite range to relictual pockets and replaced it with *Acacia spirorbis* shrubland. Successional development is likely to be much slower on serpentinite outcrops than on iron crust because of the limited suite of species tolerant of the particular chemical properties of this soil type. Furthermore, forest formations in valleys are likely to represent climax formations due to the lack of serpentinite rainforest seed sources.

Chapter 4

Colonisation of bare ground

4.1 Introduction

An analysis of vegetation at Plaines des lacs and Kouaoua in chapter 3 has shown that vegetation patterns largely represent post-fire successional mosaics. The progression of these communities will depend not only on rates of colonisation, generally referred to as the immigration of seed or spores (Willson, 1992; Ash *et al*, 1994), but also on the degree to which the previous vegetation has been disturbed. Small scale disturbances such as canopy removal by natural tree death in the maquis to forest stages are unlikely to greatly affect the composition of these communities because early successional species are sufficiently abundant to colonise gaps. In contrast, large scale disturbance events such as fire and cyclones are likely to alter the floristic composition of communities by removing the aerial vegetation component containing seed and nutrient sources. Ground surfaces produced by these disturbance events, typically contain undisturbed seed banks and root systems, and create different conditions for colonisation from seedfall (fig. 4.1). However, early stages of successional development from resprouters and seed is slow and it may take 20 to 50 years for species to develop into a maquis.

Mining generally involves even more disturbance than fire and cyclones, removing not only the above ground parts but also top soil containing root systems, seed banks and organic matter (Williamson *et al*, 1982: Bradshaw, 1987, 1997). Colonisation of mined areas is slower than in post-fire areas and limited to seed colonisation which decline in abundance away from the periphery of surrounding vegetation (fig. 4.2). Central areas of mined surfaces usually contain a random distribution of isolated sedges and woody primary colonists often surrounded by a variety of secondary colonist species that are rarely found in open conditions (fig. 4.3). Determining what processes are limiting plant colonisation on these disturbed substrates is a particularly relevant issue in New Caledonia because of the widespread extent of bare ground arising from mining.

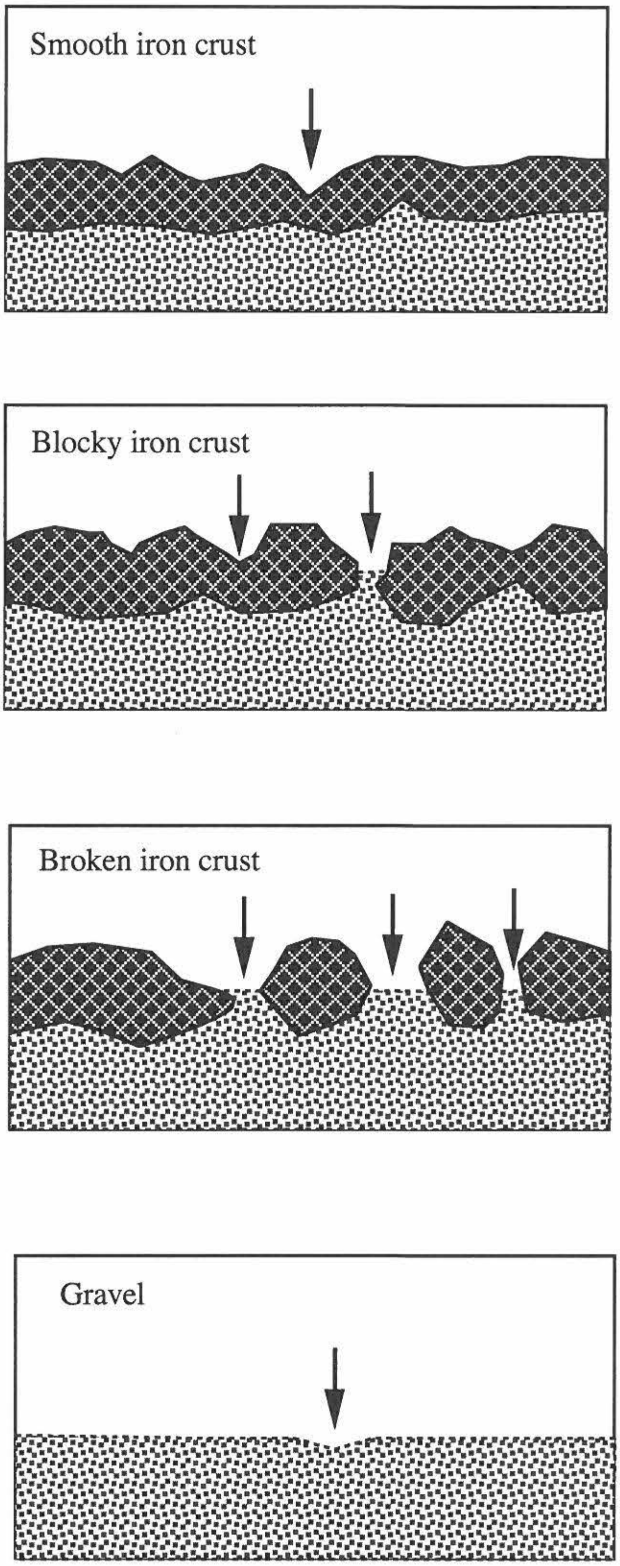


Figure 4.1 Abundance of micro-site crevices in different types of iron crust surface. Arrows indicate large crevices.

Figure 4.2 Abundant regeneration of *Gymnostoma deplancheanum* on a prospecting road adjacent to forest cleared in 1988.

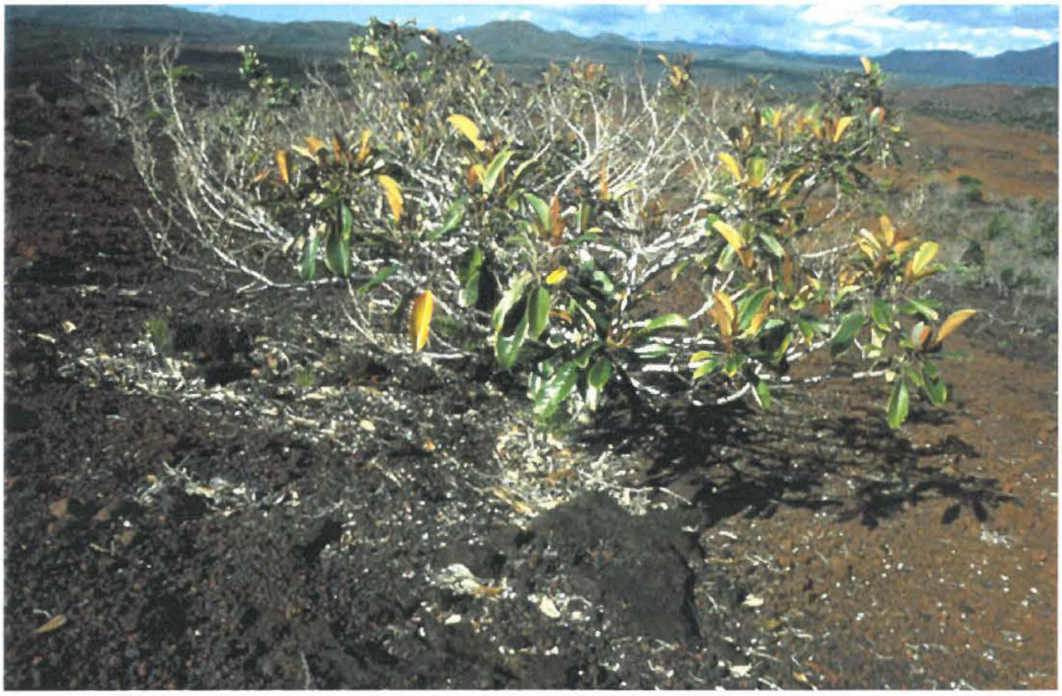


Figure 4.3 Isolated primary colonist tree (*Alphitonia neocaledonia*) on the iron mine at Prony (abandoned in 1968). Note secondary colonist seedlings establishment underneath the primary colonist.

To date, the processes influencing plant establishment on bare ultramafic sites in New Caledonia have received little attention. Elsewhere, literature relating to plant establishment on natural rocky surfaces such as lava flows and on mine sites have shown that colonisation is dependent on factors such as (i) the extent of bare ground (Ash *et al*, 1994), (ii) the dispersal ability of primary colonist species (Burrows, 1986; McClanahan, 1986, 1988; Augsperger & Kitajima, 1992; Hardt & Forman, 1989; Del Moral *et al*, 1995), (iii) the availability of suitable micro-sites such as crevices (Harper, 1977; Drake, 1992; Del Moral & Bliss, 1993; Del Moral *et al*, 1995) (iv) seed predation and herbivory (Crawley, 1992), (v) and the tolerance of colonists to substrate conditions (Williamson *et al*, 1982; Bradshaw, 1987, 1995; Bradshaw & Johnson, 1992; Borgegard, 1990; Ash, *et al*, 1994).

4.1.1 Aim

This chapter examines (i) the distribution patterns and (ii) survival of plants on bare ground following mining activity in order to reveal the processes controlling early successional patterns. These aims require different forms of investigation. Accordingly, this chapter reports field surveys describing colonisation patterns on mines and prospecting roads abandoned after 10 years and 20 years, and two experiments examining the response of seed germination and survival of primary colonist species to different conditions. The methods and results of each of these studies are presented separately then combined in an overall discussion.

4.2 Colonisation on mine sites and cleared ground

Surveys of colonisation were conducted on bare ground cleared and abandoned about 10 years and 20-30 years previously. The 10 year stage was examined on road sides at Goro, the 20-30 year stage on mines at Prony and Goro.

4.2.1 Colonisation on 10 year old prospecting roads

Surveys of *Gymnostoma deplancheanum* seedling distribution were conducted in 1998 along bulldozed prospecting roads surrounding an open cut nickel mine operation at Goro abandoned in 1988 (Lat: 22°17'; Long: 166°58'; 240 m a.s.l). These bare surfaces range from 10 to 100 m wide. The center of road surfaces consists of a compacted mixture of sub surface clay, iron crust and gravel containing few seedlings. Road edges bordering iron crust vegetation are largely composed of loose iron crust blocks and gravel, and often support abundant plant colonisation.

4.2.2 Methods

Gymnostoma seedling abundance was recorded at ten sites within which two adjacent 1 m^2 quadrats were located at distances of 1, 3, 5, 7 m from the vegetation margin. Soil surface type (clay & gravel; gravel; gravel & iron crust; iron crust), slope (degrees) and aspect of the ground slope were also recorded for each quadrat.

Multiple linear regression (SAS institute software JMP ® version 3) was used to test for effects of boundary distance, soil surface type, slope and aspect on the $\log_{10}$ number of *Gymnostoma* seedlings (+1), treating each site as a replicate.

4.2.3 Results

Regression showed that seedling numbers decline sharply with distance from the vegetation boundary (table 4.1; fig 4.4). The marginally significant aspect effect suggests that seedlings were more abundant on west facing sites. This colonisation pattern may have arisen due to either a dispersal effect from easterly winds or a microclimate effect of colonisation. The regression did not detect significant soil surface or slope effects on seedling distribution.

4.3. Colonisation patterns on 20 year old mine surfaces

4.3.1 Survey areas

Twenty year old abandoned mine surfaces at Prony and Goro in the Plaines des Lacs region were chosen to investigate the patterns of plant colonisation. Both areas were (i) cleared of vegetation and some surface soil using bulldozers and (ii) contain surrounding vegetation which is floristically similar and therefore likely to share colonist species (Section 3.2). In contrast, the bare areas differ in size and extent of iron crust removal.

At Prony (Lat: 22°19'; Long: 155°49'; 150 m a.s.l) a strip mining operation from 1953-1968 removed most of the surface iron crust to a depth of 3 m, along with vegetation and seed banks over an area of 700 ha

Table 4.1: Results of multiple linear regression to test for the effects of boundary distance, slope (°), aspect and soil surface characteristics on the $\log_{10}$ number of *Gymnostoma deplancheanum* seedlings (+1) found on prospecting roads at Goro. Significance (*t* / *F*) is indicated, $p > 0.05$ = ns, $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***.

Whole model test	R^2			*F*	
n = 80	0.63			15.71	***
Term	Estimate	s.e.	*t*	*F*	
Intercept	1.93	0.154	12.51		
Boundary distance (m)	-0.191	0.027	-7.04	49.59	***
Slope (°)	-0.021	0.013	-1.52	2.30	ns
Aspect (1-4)	-	-	-	3.10	*
Soil (1-4)	-	-	-	0.50	ns

Aspect	l.s.m	s.e
1. North	1.028	0.073
2. East	1.023	0.144
3. South	0.961	0.095
4. West	1.267	0.08

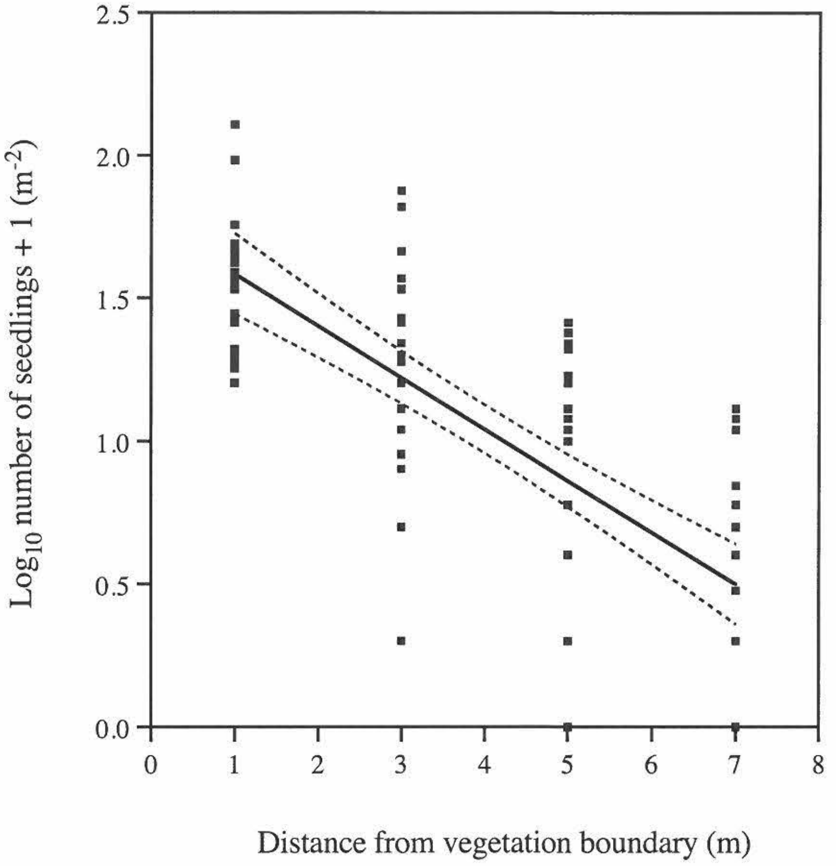


Figure 4.4 The $\log_{10}$ number of *Gymnostoma deplancheanum* seedlings + 1 on prospecting roads at Goro plotted against distance from the forest margin. The fitted splines indicate the mean trend (solid line) and confidence intervals (± 95%).

(Chevalier, 1996). Much of the remaining surface is composed of flat gravel terraces containing isolated pockets of broken iron crust. These bare surfaces are subject to high wind speeds because of their near coastal location and are eroded by sheet flow and gullying on steeper parts. By 1993, these areas supported a sparse cover of primary colonist species.

The site on the Goro plateau (Lat: 22°17'; Long: 166°57'; 300 m a.s.l) (500 m x 100 m) was cleared of vegetation and surface iron crust boulders over an area of 5 ha in 1971. The remaining surface substrate consists of iron crust and gravel pockets which each occupy approximately half of the cleared area. The bare area at Goro experiences less windy conditions than bare ground at Prony because the tall surrounding vegetation provides a wind break.

4.3.2 Methods

4.3.2.1 Dispersal characteristics

Common species neighbouring the survey sites were classified as either (i) animal dispersed (fleshy fruits) or (ii) wind dispersed. Diaspores were further classified as round seeds, winged seeds, plumed seeds, woolly seeds and spores or minute seeds; according to dispersability criteria given by Burrows (1975). Species were ranked by the maximum height of their diaspore release to give an indication of their dispersability from vegetation surrounding the survey areas.

4.3.2.2 Aerial photography

Aerial photographs taken in 1976 and 1992 of the Prony mine were examined to determine the extent of colonisation at Prony. Large trees and shrubs producing more than about 2 m^2 cover were detectable on aerial photographs from both periods and were mapped in order to estimate the rates and pattern of colonisation.

4.3.2.3 Field survey design

Several criteria were established prior to both surveys in order to distinguish primary colonists from secondary colonists. A plant was considered to be a primary colonist if it was the tallest individual providing most of the cover (refer to 3.2.1), otherwise it was classified as a secondary colonist.

Surveys of plant distribution on cleared areas were conducted at Prony in 1994 and at Goro in 1996 along transects at different distances parallel to the vegetation boundary. At Prony, 100 metre transects were placed in an east - west direction at 20 m, 60 m and 120 m parallel to the northern forest boundary. At Goro, 100 hundred metre transects were placed at 5 m, 15 m and 25 m parallel to the eastern forest boundary. Surveys aimed to reveal whether (i) distance to the boundary, and (ii) substrate had an effect on colonisation. Seedling distribution patterns were examined for primary and secondary colonists on bare ground and underneath primary colonists to determine the impact these plants have on colonisation.

A preliminary investigation along transects at Goro indicated that colonist vegetation was abundant. Sampling was conducted at 1 m intervals along transects and primary colonists were recorded if their canopy overlapped the transect line at measured intervals. In contrast, colonist vegetation at Prony was sparse and consisted of isolated individuals. All primary colonists were therefore examined within 20 m either side of the transects at Prony.

Three different measures were made at each primary colonist site.

(i) Records were made of primary colonist height, stem diametre (at 10 cm above the ground), the area of litter (cm^2) and the underlying soil surface characteristics (iron crust, gravel).

(ii) Secondary colonists were identified underneath primary colonists and recorded in terms of their distance (< 10 cm, 10-25 cm, 25-50 cm and 50-100 cm) from the trunk, their occurrence in litter or on bare ground and the soil surface characteristics (continuous iron crust, broken iron crust, iron crust blocks within gravel, gravel). Seedlings belonging to primary colonists were also included in secondary colonists records.

(iii) A 1 m radius plot was examined two metres away from each and any other primary colonist to determine secondary colonisation on adjacent surfaces not influenced by primary colonist presence.

The vector of each species was assessed (refer to 4.2.2.1).

A primary colonist index (C_i) was calculated for each species from records of all colonists at Goro and Prony using the following formula.

$$C_i = \frac{P_i}{T_i}$$

where P_i = proportion of species$_i$ as primary colonists.

T_i = proportion of species$_i$ as primary and secondary colonists.

4.3.2.4 Statistical analysis

Logistic regression (SAS institute software JMP ® version 3) was used to test for effects of distance to boundary, soil surface type and vector type on the presence/absence of primary colonists. Multiple linear regression (SAS institute software JMP ® version 3) was used to test for effects of distance to boundary, soil surface type, vector type, primary colonist litter area and primary colonist species on the number of secondary colonists, and seedling density underneath primary colonists. Common log transformation ($\log_{10}$ + 1) of seedling counts was used to obtain normal residuals and homogenise the variance.

4.3.3 Results

4.3.3.1 Dispersal

Figure 4.5 illustrates the dispersability of common species found at the vegetation boundary in wind. Ferns and orchids produce minute spores which are highly dispersed. High dispersability may also result from a combination of height of the diaspore release and the aerodynamic properties of the diaspore. Such characteristics were observed in shrubs and trees with plumed diaspores (*Codia montana* and *Pancheria veillardii*) and winged diaspores (*Gymnostoma deplancheanum, Tristaniopsis guillanii* and *Myodocarpus fraxinifolius*) that may aerodynamically assist lifting (Burrows, 1986). Aerodynamically neutral diaspores produced by *Arillastrum gummiferum* and *Metrosideros nitida* may also be well dispersed for short distances by wind because of their tall stature at maturity and small seed size.

4.3.3.2 Aerial photograph interpretation

Shrub and tree distribution patterns on the mine site at Prony illustrated in figure 4.6 suggest that less than 10% of the total cleared surface

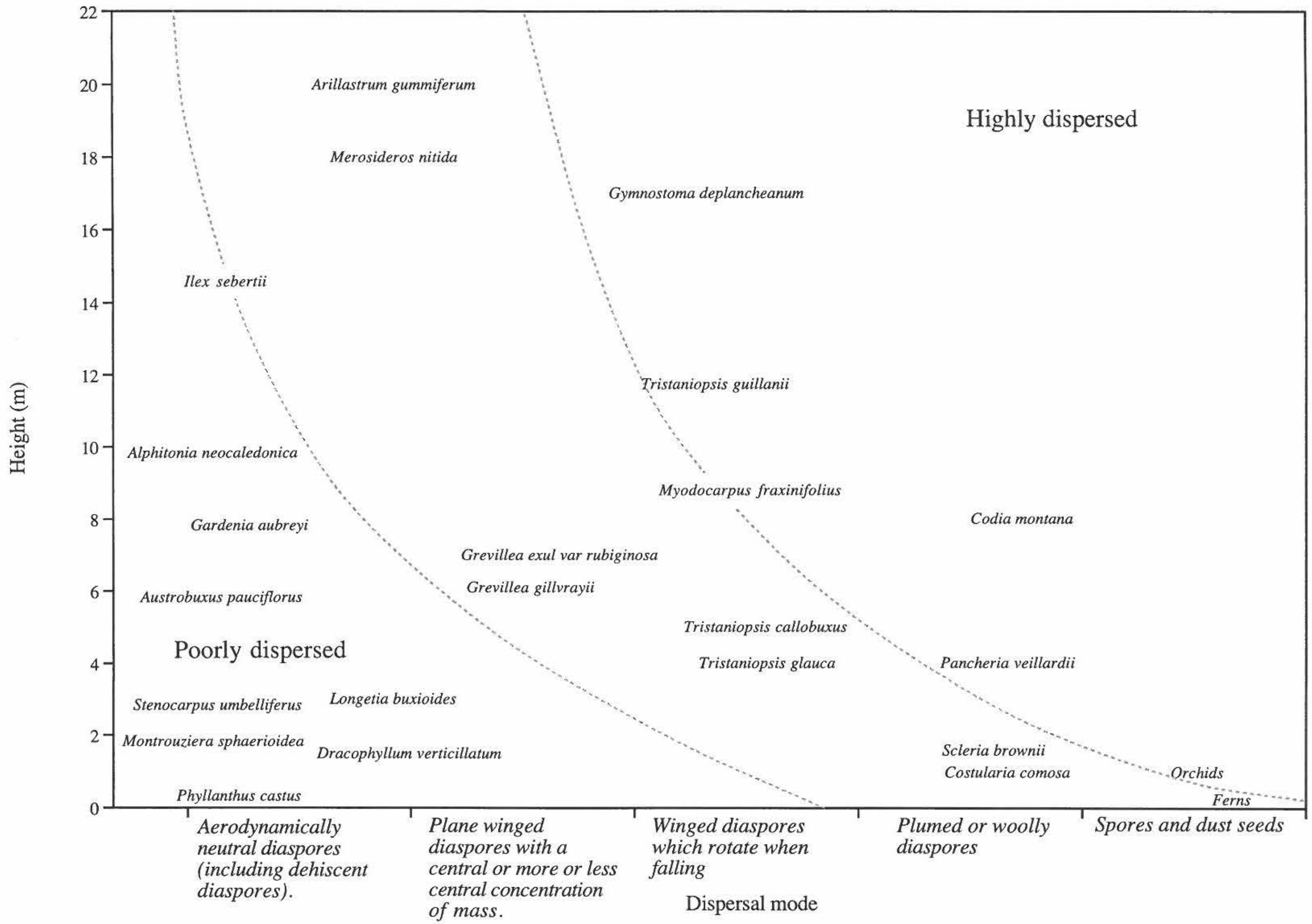


Figure 4.5 Dispersability by wind of common species found in vegetation surrounding bare iron crust sites at Prony and Goro. The ranking of dispersal mode uses criteria proposed by Burrows (1975) for wind dispersed species which are based on the aerodynamic potential of diaspore size. The height at which diaspores are typically released in mature individuals is also indicated. The dotted lines suggest similar dispersability for species groups from poorly dispersed to highly dispersed, taking maximum height of the species into account.

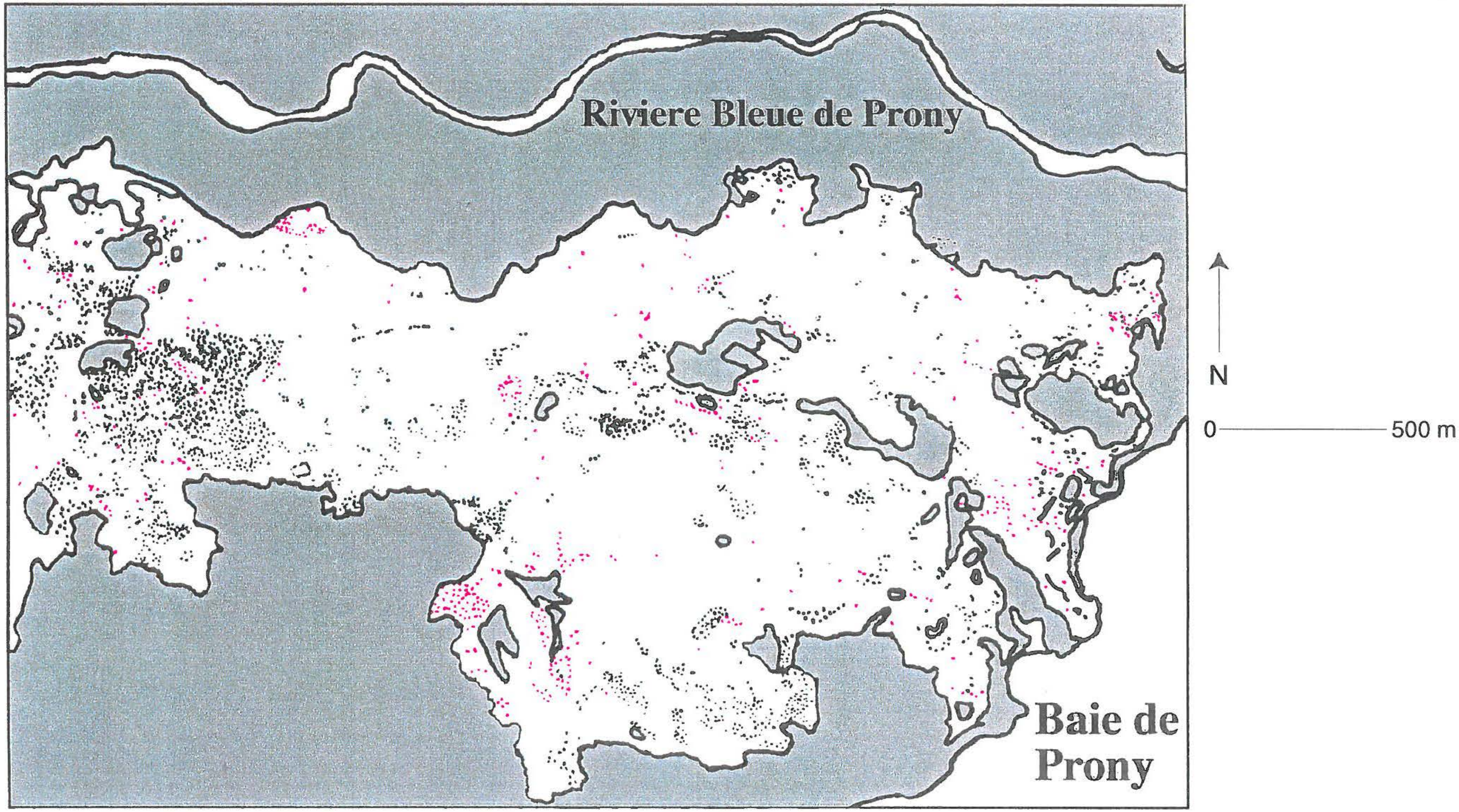


Figure 4.6 Vegetation establishment on the mine surface at Prony between abandonment (1952-1968) and 1976 (black dots) and between 1976 and 1992 (red dots). Dots indicate individual trees or shrubs visible (2 m sq.) on aerial photographs taken in 1976 and 1992.

had a cover of colonist vegetation by 1992. Much of the colonisation prior to 1976 appears to have been limited to the vicinity of forest on southern slopes, along drainage lines and remnant areas of iron crust. Colonisation may have occurred progressively as areas were abandoned after iron crust had been removed between 1953 and 1968. Aerial photographs from 1992 indicate that there was a slight increase in shrubs and tree establishment on the mine since 1976 (red dots). This colonisation appears to have occurred mainly on south facing slopes that contained no visible vegetation in 1976. The absence of more recent establishment within pre 1976 shrub patches was particularly apparent on areas of remnant iron crust.

4.3.3.3 Colonisation patterns on mine surfaces

The surveys of mine sites at Goro and Prony show considerable variation in the number and abundance of primary and secondary colonist species (table 4.2). Colonist vegetation at Goro was abundant and covered approximately 46% of the cleared area surveyed. This vegetation consisted of 33 species of primary colonist shrub and tree and 53 species of secondary colonist. In contrast, only about 13% of the cleared area surveyed at Prony contained colonist vegetation. This vegetation consisted of 9 primary colonist species and 33 secondary colonist species. Species found at early stages of the iron crust succession (I<4.3) were more abundant as primary colonists than late successional species at both sites.

The primary colonist index constructed from total plant number at both sites indicates that *Gymnostoma deplancheanum, Longetia buxioides, Grevillea exul, Babingtonia leratti* and *Alphitonia neocaledonica* were well represented as both primary and secondary colonist seedlings possibly originating from either the vegetation boundary or established plants from seed banks. Goro also supported species normally found at later successional forest stages (eg: *Hugonia penicillanthemum, Austromyrtus stricta*) as isolated primary colonists containing no regeneration.

Primary colonists

Results presented in table 4.3 show that soil surface type is strongly correlated with primary colonist abundance at Prony and Goro. This suggests that primary colonists are found more frequently on iron crust than on gravel. Logistic regression also showed that there was a significant difference between vertebrate and wind dispersed primary colonist species abundance, with animal dispersed species more common at both mine sites.

Table 4.2: The number of colonists recorded along transects at Goro and Prony Species are placed in successional order based on the index I derived in chapter "W" indicates species posessing wind dispersed diaspores. The Pioneer index (Ci indicates the relative abundance of each species as a primary colonist.

				Goro		**Prony**		
Family	**Species**	Disp	I	Primary	Secondary	Primary	Secondary	C_i
Cyp.	*Costularia comosa*	W	2.18	2			2	6.7
Myrt.	*Xanthostemon aurantiacum*	W	2.20	2				13.4
Myrt.	*Babingtonia leratti*	W	2.32	20	65	2	13	3.0
Prot.	*Grevillea gillvrayi*	W	2.54	1	5	7	26	2.8
Cyp.	*Costularia arundinacea*	W	2.59				1	0.0
Orch.	*Dendrobium steatoglossum*	W	2.62		14		2	0.0
Cun.	*Pancheria veillardii*	W	2.64	4	7			4.9
Denn.	*Pteridium esculentum*	W	2.65		22		12	0.0
Orch.	*Eriaxis rigida*	W	2.68	3	91		18	0.4
Cyp.	*Costularia nervosa*	W	2.74		42		36	0.0
Rham.	*Alphitonia neocaledonica*		2.76	27	237	18	93	1.6
Good.	*Scaevola beckii*		2.79	1	61		7	0.2
Prot.	*Stenocarpos comptonii*		2.86				1	0.0
Celas.	*Geniostoma celastrenium*		2.87		18		1	0.0
Epac.	*Dracophyllum verticillatum*	W	2.90	1	10		1	1.1
Prot.	*Stenocarpus umbelliferus*		2.92	2	4		7	2.1
Dill.	*Hibbertia lucens*		2.97	1	2	2	3	5.0
Myrt.	*Uromyrtus emarginatus*		3.22	6	67		2	1.1
Euph.	*Longetia buxoides*	W	3.23	25	585	2	46	0.6
Epac.	*Dracophyllum ramosum*	W	3.33		3		1	0.0
Flag.	*Flagellaria neocaledonica*		3.41		3		3	0.0
Gutt.	*Montrouziera sphaerioides*		3.45	4	22			2.1
Myrt.	*Tristaniopsis guillainii*	W	3.45		11	1	16	0.5
Aral.	*Polycias pancheri*		3.49	11	196		5	0.7
Cyp.	*Lepidosperma perteres*	W	3.61		1			0.0
Smi.	*Smilax* sp.		3.93		5			0.0
Sapin.	*Gioua glauca*		3.95	2	22		2	1.0
Podo.	*Dacridium araucarioides*		3.95	1	3			3.4
Epac.	*Styphelia veillonii*		3.99	6	37	1	13	1.6
Cas.	*Gymnostoma deplancheanum*	W	4.02	20	69	11	54	2.7
Dill.	*Hibbertia pancheri*		4.05	18	28	5	10	5.1
Rub.	*Gardenia aubryi*		4.12		4			0.0
Xanth.	*Lomandra insularis*	W	4.16	1	59		1	0.2
Lil.	*Dianella intermedia*		4.19		10			0.0
Rubi.	*Ixora francii*		4.23		12			0.0
Apoc.	*Parsonsia carnea*		4.28		7			0.0
Thym.	*Solmsia calophylla*		4.29		1			0.0
Cun.	*Codia montana*	W	4.29	4	18			2.4
Elae.	*Elaeocarpos alaternoides*		4.37	2	2			6.7
Orch.	*Dendrobium verruciferum*	W	4.39		4			0.0
Dill.	*Hibbertia veillardii*		4.43		6			0.0
Euph.	*Phyllanthus francii*		4.48		8			0.0
Schi.	*Schizaea laevigata*	W	4.57		560		92	0.0
Myrt.	*Austromyrtus stricta*		4.63	5				13.4
Aral.	*Mydocarpos lanceolata*		4.68		2			0.0
Myrs.	*Rapanea diminuta*		4.69		1		1	0.0
Apo.	*Alstonia coriaceae*		4.70	2	10			2.2
Apoc.	*Rauvolfia semperflorens*		4.71				2	0.0
Sapot.	*Beccariella baueri*		4.80	4	9			4.1
Celas.	*Maytenus fournieri*		4.94		7			0.0
Gutt.	*Garcinia neglecta*		4.94		3			0.0
Rub.	*Psychotria rupicola*		4.95		1			0.0
Orch.	*Liparis chalendei*	W	4.96		1		3	0.0
Join.	*Joinvillea plicata*		4.96	1				13.4
Lin.	*Hugonia penicillanthemum*		4.98	4	1			10.7
Aral.	*Mydocarpos fraxinifolius*	W	5.01		1		1	0.0
Rut.	*Comptonella drupacea*		5.19		1		2	0.0
Flac.	*Casearia silvana*		5.23				1	0.0
Pitt.	*Pittosporum haematomallum*		5.29		1			0.0
Orch.	*Malaxis torena*	W	5.44		8			0.0
	Total number of plants			180	2367	49	478	
	Total number of species			28	52	9	33	

Table 4.3: Results of logistic regression indicating the probability that primary colonists are absent in terms of vector type, boundary distance and soil surface characteristics. Estimatres of soil effects are for a particular combination of vector and distance effects. Significance of the deviance change is indicated, $p > 0.05$ = ns, $p < 0.01$ = **, $p < 0.001$ = ***.

Prony

Whole model test			*deviance change*	
n = 301			65.82	***

Term	Estimate	s.e.	*deviance change*	
Intercept	2.689	0.298	81.35	***
Vector (wind dispersed vs animal dispersed)	-0.739	0.194	14.47	***
Boundary distance (m)	-0.003	0.004	0.65	ns
Soil (Gravel vs Iron crust)	1.077	0.165	42.34	***

Proportion of sites sampled along transects where primary colonists are absent

Soil	mean	upper 95 %	lower 95 %
1. Gravel	0.96	0.97	0.95
2. Iron crust	0.77	0.82	0.71

Goro

Whole model test			*deviance change*	
n = 301			25.57	***

Term	Estimate	s.e.	*deviance change*	
Intercept	0.275	0.200	0.655	ns
Vector (wind dispersed vs animal dispersed)	-0.263	0.088	8.81	**
Boundary distance (m)	0.010	0.013	0.79	ns
Soil (Gravel vs Iron crust)	-0.372	0.102	13.36	***

Proportion of sites sampled along transects where primary colonists are absent

Soil	mean	upper 95 %	lower 95 %
1. Gravel	0.72	0.79	0.64
2. Iron crust	0.36	0.45	0.27

However, there appears to be no decline in primary colonist abundance with increasing distance from the vegetation boundary.

Secondary colonists

Litter area was chosen instead as a measure to investigate primary colonist effects on secondary colonists because it indicates both the size of the primary colonist and may be a direct measure of its influence on substrate conditions.

Results presented in table 4.4 show that (i) the number of secondary colonists at both mines increase significantly with increasing litter area. (ii) Wind dispersed species are significantly more frequent than animal dispersed species. (iii) The number of secondary colonists also shows a marginally significant correlation with distance to the vegetation boundary at Prony and Goro. At Prony, the number secondary colonists show a decline with distance from the vegetation boundary. In contrast, the number of secondary colonist seedlings appears to increase with distance from the vegetation boundary at Goro (fig. 4.7). Multiple linear regression did not show effects of soil surface type.

Number of species of secondary colonists

Results of the multiple linear regression (table 4.5) show that with increasing litter area there are slightly more secondary colonist species. Soil surface has a significant effect on secondary colonist diversity at Goro but not at Prony. This suggests that there are more secondary colonist species found on iron crust than on gravel. Furthermore, boundary distance had a marginally significant effect on secondary colonist species diversity at Prony but not at Goro and suggests that fewer species are found further from the boundary.

Spatial distribution of secondary colonists

Figure 4.8 shows the distribution of secondary colonists with distance from the trunk of the primary colonist. In both areas, there is a strong tendency for secondary colonists to establish near the trunk of primary colonists. The number of secondary colonists shows a sudden decline away from the trunk and are nearly absent 1 m away from primary colonists. These patterns are significantly different (χ^2, $p < 0.001$) from the pattern

Table 4.4: Results of multiple linear regression to test for the effects of boundary distance, litter area, soil surface characteristics and vector type on the $\log_{10}$ number of secondary colonists under primary colonists at Goro and Prony. Seedlings of primary colonists underneath the same species are omitted from the analysis. Significance (*t* / *F*) is indicated, $p > 0.05$ = ns, $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***.

Prony

Whole model test	R^2	*F*	
n = 50	0.27	5.73	***

Term	Estimate	s.e.	*t*		*F*	
Intercept	0.631	0.077	8.13			
Litter area (m^2)	0.0006	0.00032	2.01	*	4.02	*
Boundary distance (m)	-0.00205	0.0011	-2.03	*	4.16	*
Soil (1-2)	-	-	-		2.53	ns
Vector (1-2))	-	-	-		13.1	***

Soil	l.s.m.	s.e.
1. Iron crust	0.667	0.071
2. Gravel	0.514	0.063

Vector	l.s.m.	s.e.
1. Wind dispersed	0.764	0.064
2. Animal dispersed	0.417	0.070

Goro

Whole model test	R^2	*F*	
n = 301	0.38	21.66	***

Term	Estimate	s.e.	*t*		*F*	
Intercept	0.4430	0.033	13.10			
Litter area (m^2)	0.0037	0.00037	10.13	***	102.62	***
Boundary distance (m)	0.0930	0.032	2.85	*	4.55	*
Soil (1-4)	-	-	-		1.40	ns
Vector (1-2))	-	-	-		24.26	***

Soil	l.s.m.	s.e.
1. Smooth iron crust	0.692	0.052
2. Blocky iron crust	0.691	0.053
3. Blocks + gravel	0.707	0.041
4. Gravel	0.572	0.058

Vector	l.s.m	s.e.
1. Wind dispersed	0.778	0.033
2. Animal dispersed	0.553	0.035

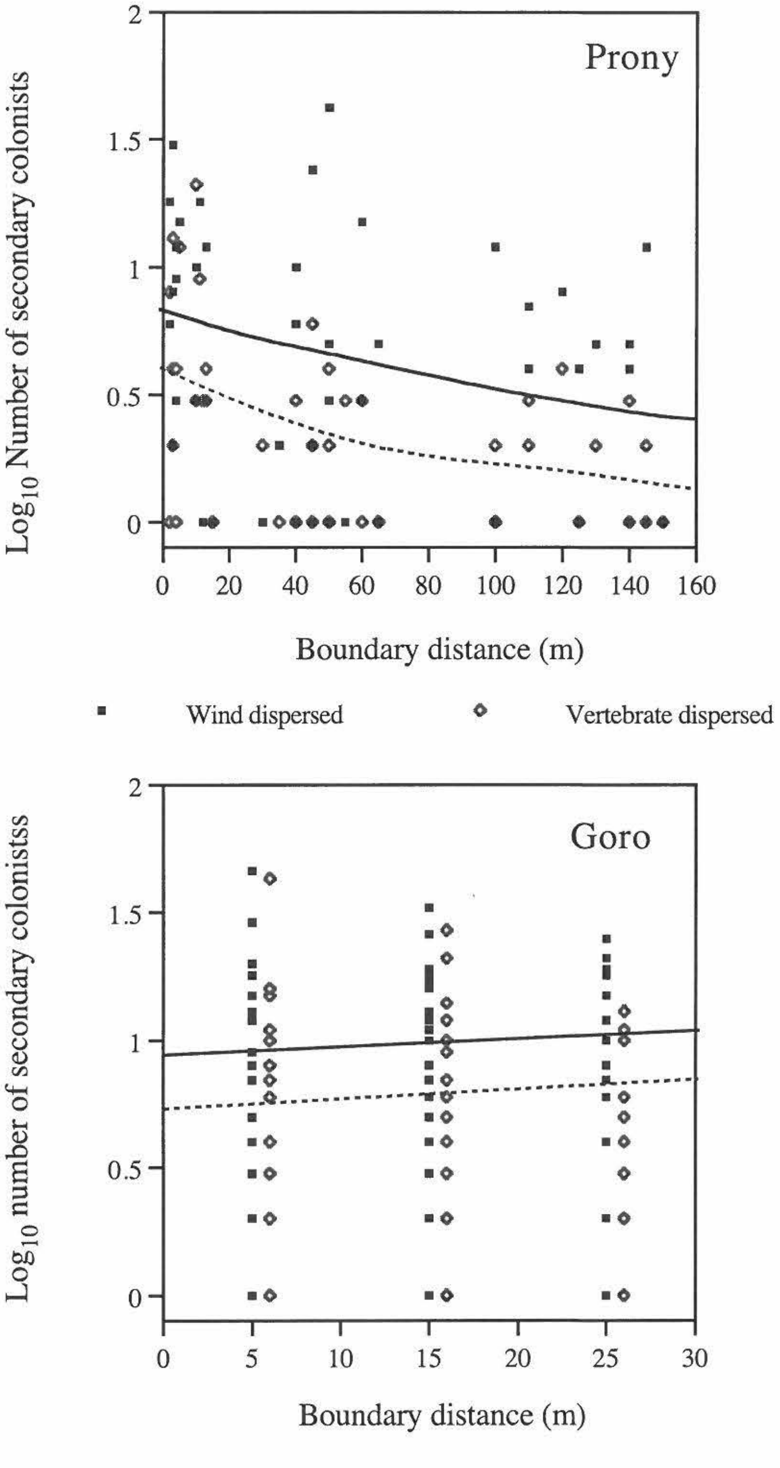


Figure 4.7 Log$_{10}$ number of secondary colonists dispersed by wind or by animals underneath pioneers at Prony and Goro plotted against distance from the vegetation boundary. Spline lines give trends for wind dispersed (solid line) and animal dispersed (dotted line) secondary colonists.

Table 4.5: Results of multiple linear regression to test for the effects of boundary distance, litter area and soil surface characteristics on the number of secondary colonist species at Prony and Goro. Seedling species belonging to the parent primary colonist were omitted from the analysis. Significance (*t* / *F*) is indicated, $p > 0.05$ = ns, $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***.

Prony

Whole model test		R^2				*F*	
	n = 50	0.39				9.9	***

Term	Estimate	s.e.	*t*		*F*	
Intercept	3.2580	0.5538	5.88			
Litter area (cm^2)	0.0126	0.0032	3.93	***	15.42	***
Boundary distance (m)	-0.0140	0.0060	-2.11	*	4.44	*
Soil surface (1-2)	-	-	-		3.10	ns

Soil surface	l.s.m	s.e.
1. Blocks + gravel	3.65	0.50
2. Gravel	2.47	0.43

Goro

Whole model test		R^2				*F*	
	n = 301	0.64				104.6	***

Term	Estimate	s.e.	*t*		*F*	
Intercept	1.2280	0.2690	4.56			
Litter area (cm^2)	0.0477	0.0023	19.97	***	398.72	***
Boundary distance (m)	0.0109	0.0163	0.62		0.38	ns
Soil surface (1-4)	-	-	-		6.17	**

Soil surface	l.s.m	s.e.
1. Smooth iron crust	2.46	0.28
2. Blocky iron crust	3.13	0.30
3. Blocks + gravel	2.97	0.23
4. Gravel	1.81	0.19

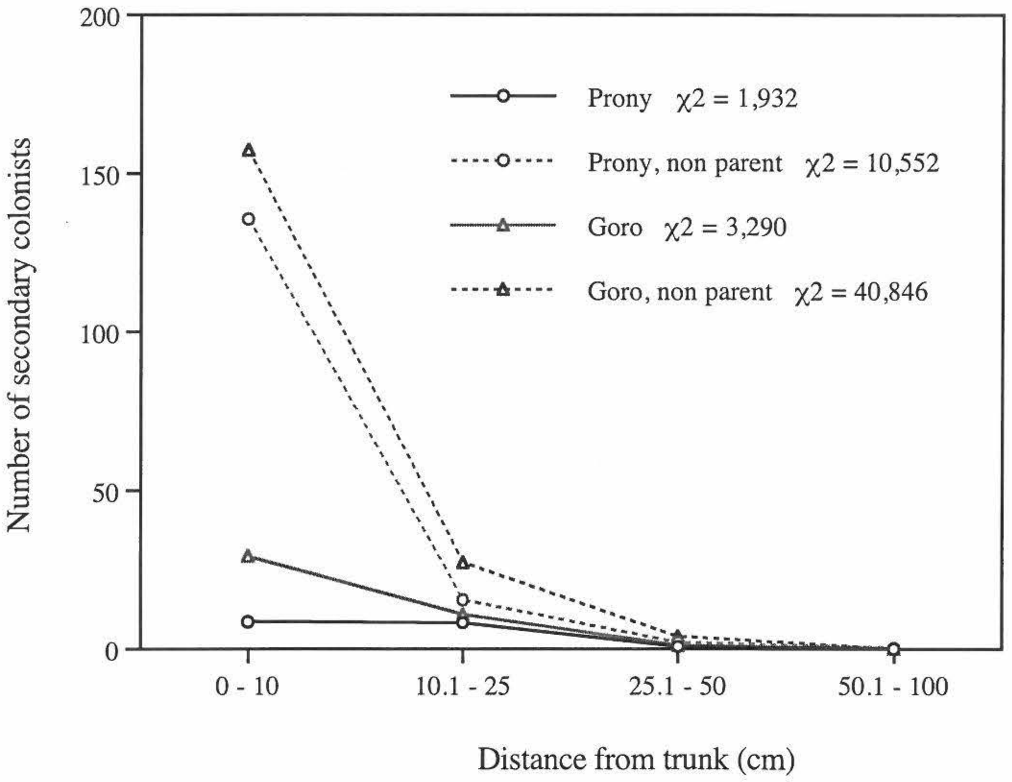


Figure 4.8 The distribution of secondary colonists with distance from the trunk of the 43 primary colonists at Prony and 142 at Goro. Hollow symbols indicate the number of seedlings belonging to primary colonists. Solid symbols indicate seedlings belonging to species other than the primary colonist. Secondary colonists are rare beyond 100 cm from primary colonists at both areas. Chi-square values were calculated for the observed versus the predicted number of seedlings if they were randomly distributed out to 1 metre. All values are highly significant ($p < 0.0001$).

expected by chance. Seedling colonisation near a primary colonist of the same species exhibits a similar pattern to that of secondary colonist, except that primary colonist seedling numbers are much lower.

Surveys at Prony indicate that no plants were found at a distance of 2 m away from primary colonists. At Goro, eleven seedlings were found 2 m away from primary colonists, primarily in iron crust crevices.

Effect of litter and primary colonist species

Multiple linear regression showed that secondary colonists densities (table 4.6) were not influenced by the identity of the primary colonist species, but were 10-15 times higher when litter was present.

4.4 Germination of primary colonist species

4.4.1 Methods

An experiment was conducted at Prony to examine the germination and survival of local maquis species under eight different habitat conditions found on or adjacent to the mine (table 4.7). These environments were different types and combinations of soil, litter and shade. Six maquis species were selected to include a range of seed sizes and dispersal mechanisms (table 4.8).

The experiment was conducted from April to October of 1994 using seed collected in January 1994 for *Gymnostoma deplancheanum*, *Beccariella baueri*, *Grevillea exul* var. *rubiginosa* and *Alphitonia neocaledonica*, and in 1993 for *Tristaniopsis glauca* and *Costularia comosa*. Seeds of *Grevillea*, *Gymnostoma* and *Tristaniopsis* were released from dehiscent fruits using heat from infrared lamps. A wet/dry scarification technique (Jaffré & Rigault, 1990) was used to separate the woody exocarp from the seed of *Alphitonia*. Seeds of *Beccariella* were removed from the fleshy fruit.

4.4.1.2 Experimental design

The experiment consisted of 40 plots (60 cm x 20 cm) subdivided into 6 subplots each containing 40 seed of one species. Species were randomly allocated to subplots. The experiment was established in five areas of the mine 1 to 3 km apart. Each area contained one plot in six of the contrasting

Table 4.6: Results of multiple linear regression to test the effect of the presence/absence of litter and primary colonist tree species on the $\log_{10}$ seedling density (m^{-2}) underneath primary colonists at Prony and Goro. Significance (t / F) is indicated, $p > 0.05$ = ns, $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***.

Prony

Whole model test	R^2				F	
n = 50	0.51				10.42	***

Term	Estimate	s.e.	t		F	
Intercept	1.802	0.121	14.89			
Litter cover (0-1)	-0.726	0.085	-8.75	***	76.56	***
Primary colonist species	-	-	-		1.91	ns

$\log_{10}$ seedlings m^{-2}	l.s.m	s.e.
0. No litter	1.07	0.14
1. Litter	2.53	0.15

Goro

Whole model test	R^2				F	
n = 301	0.42				9.63	***

Term	Estimate	s.e.	t		F	
Intercept	1.405	0.079	17.6			
Litter cover (0-1)	-0.580	0.044	-13.03	***	169.73	***
Primary colonist species	-	-	-		1.41	ns

$\log_{10}$ seedlings m^{-2}	l.s.m	s.e.
0. No litter	0.82	0.084
1. Litter	1.98	0.097

environmental conditions (table 4.7). Plots were positioned so that they were within 10 metres of each other so as to reduce mesoscale site effects. No recently burnt sites or woody sedge maquis were found in the vicinity of the mine. These plots were established at 50 m intervals on either side of a road in burnt (December 1993) and unburnt woody sedge maquis 3 km south west of the mine. Seed from each species was also germinated under a daily watering regime in a glasshouse at Nouméa.

All plots at Prony were located on level ground to minimise seed removal by surface run-off. In plots containing litter, seeds were placed on the underlying substrate then recovered with the litter. Bare mine and burnt plots experienced windy conditions, and seed was covered with a thin layer of soil (< 2 mm) to ensure that seed remained in the sub plots. Monthly observations were made of seedling emergence and seedling death. The causes of seed and seedling mortality such as unsuitable microhabitats, predation, herbivory and fungal attack are likely to influence colonisation patterns but were not directly analysed because of the difficulty in determining the cause of death.

4.4.1.3 Statistical analysis

The proportion of seed germinated was examined for environmental effects using logistic regression analysis (Genstat 5). All replicates were pooled for the statistical analysis due to the low rates of germination.

4.4.2 Results

Logistic regression showed no significant differences in germination of the test species between the 8 habitats possibly because of low germination. Low germination was recorded for all species and may have arisen for several reasons. (i) Seed of certain species suffered heavy predation by crickets (eg: *Beccariella, Grevillea, Alphitonia*) and fungal pathogen attack (eg: *Gymnostoma*) in habitats containing litter. (ii) Measures taken to reduce seed loss by wind (soil covering) on bare ground were ineffective and allowed the disappearance of seed (eg: *Costularia, Gymnostoma*). (iii) Rainfall was lower than average over the experimental period and may have reduced germination rates for species requiring humid conditions to break dormancy.

Table 4.7: Environmental conditions used in the germination experiment at Prony.

Environmental condition	Litter depth (cm)	Shade (%)	Soil
1. *Arillastrum* forest	3-6	90	Iron crust
2. Isolated *Arillastrum* trees	1-3	75	Iron crust
3. *Gymnostoma* forest	5-7	93	Iron crust
4. Isolated *Gymnostoma* trees	1-3	45	Iron crust + gravel
5. Burnt woody sedge maquis	0	no shade	Ash bed + gravel
6. Woody sedge maquis	< 0.5	no shade	Eroded oxisol
7. Broken iron crust (Prony mine)	0	no shade	Iron crust + gravel
8. Gravel (Prony mine)	0	no shade	Gravel

Table 4.8: Primary colonist species used in the germination experiment at Prony. All of these species are found in vegetation surrounding the mine. Mean seed weight and area (length by breadth) indicate the dispersability and microsite size requirements of species. Species index (I) successional scores are defined in chapter 3.

Species	Seed weight (mg)	Seed area (mm^2)	Period of fruit/seed production	Seed dispersal mechanism	Viability (Year)	Species index (I) ref. ch. 3
Gymnostoma deplancheanum	0.5	12	Dec- Feb	Rotating winged - wind	0.3-0.4	4.02
Grevillea exul var. rubiginosa	1.5	64	Jan- Feb	Plane winged - wind	< 1	-
Alphitonia neocaledonica	2.7	10	Jan-April	Round - wind	< 1	2.76
Costularia comosa	0.13	2	Oct-Dec	Plumed - wind	< 2	2.18
Beccariella baueri	6.9	12	Dec-Jan	Round - vertebrate	0.2-0.3	4.80
Tristaniopsis glauca	0.034	1	April-June	Rotating winged - wind	< 1 year	-

Figure 4.9 illustrates the amount of seed germination and germinants surviving for each species in the eight habitats at the end of the experiment. *Grevillea* seedlings exhibited the highest rate of germination and survival followed by *Costularia*. Woody-sedge maquis contained the highest number of germinations; followed by open *Arillastrum* formations with partial sun and litter, then broken iron crust and gravel substrates on the Prony mine.

4.5 *Gymnostoma* seedling survival

4.5.1 Methods

Gymnostoma seedling survival was monitored at Creek Pernod in the Plaines des Lacs region and on a serpentinite outcrop at Kouaoua. At Creek Pernod, 100 *G. deplancheanum* seedlings were monitored on open bare gravel and broken iron crust on an abandoned prospecting road created in 1968, and 100 *G. deplancheanum* seedlings were monitored in adjacent tall maquis. At Kouaoua, 100 *Gymnostoma chamaecyparis* seedlings were monitored on open rocky landslips and 100 *G. chamaecyparis* seedlings were monitored underneath the canopy of tall maquis on hypermagnesian soil.

Seedlings were tagged in January 1994 and monitored every 3 months over a period of 11 months. All seedlings were initially < 2 cm tall and still possessed their cotyledon leaves which suggests that they were recent germinants. The aluminium tags around seedlings were fixed to the substrate with stones to avoid damage to seedlings.

4.5.2. Results

4.5.2.1 Seedling survival

Figure 4.10 shows the total number of seedlings surviving plotted against time. Overall, *Gymnostoma* seedlings at Creek Pernod exhibit much higher survival rates than on serpentinite outcrops. *Gymnostoma chamaecyparis* seedlings remained much smaller (≈ 1 cm tall) than *G. deplancheanum* seedlings and exhibited higher rates of mortality. Bare sites at both areas show the lowest rate of seedling survival. Seedling survival in crevices at Creek Pernod is slightly higher than on bare gravel sites. Seedlings monitored under the canopy of tall maquis at both areas had higher rates of survival than on exposed sites.

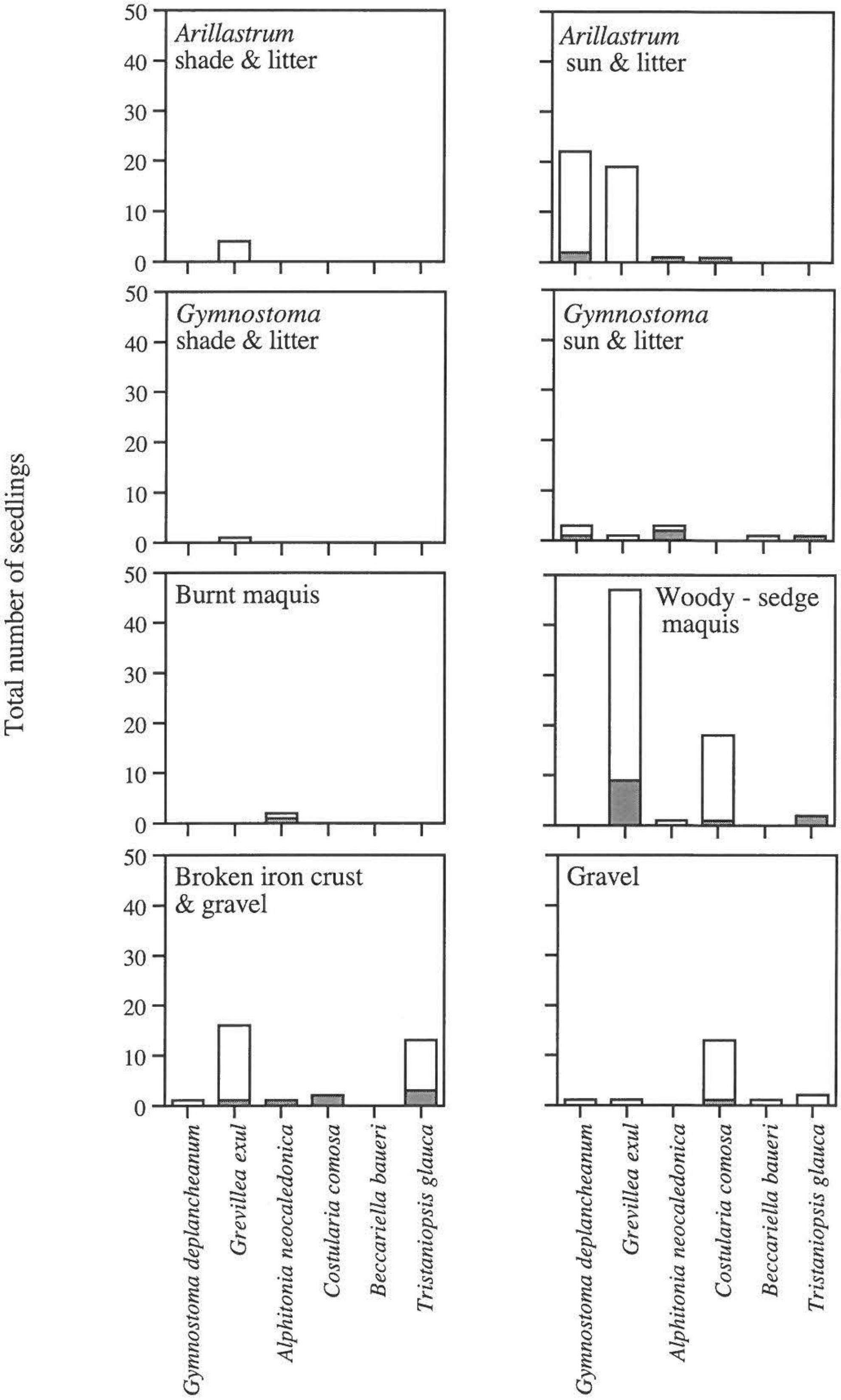


Figure 4.9 Total number of germinations (white) and surviving seedlings (grey) of the 200 seeds per treatment after 4 months under eight different environmental conditions.

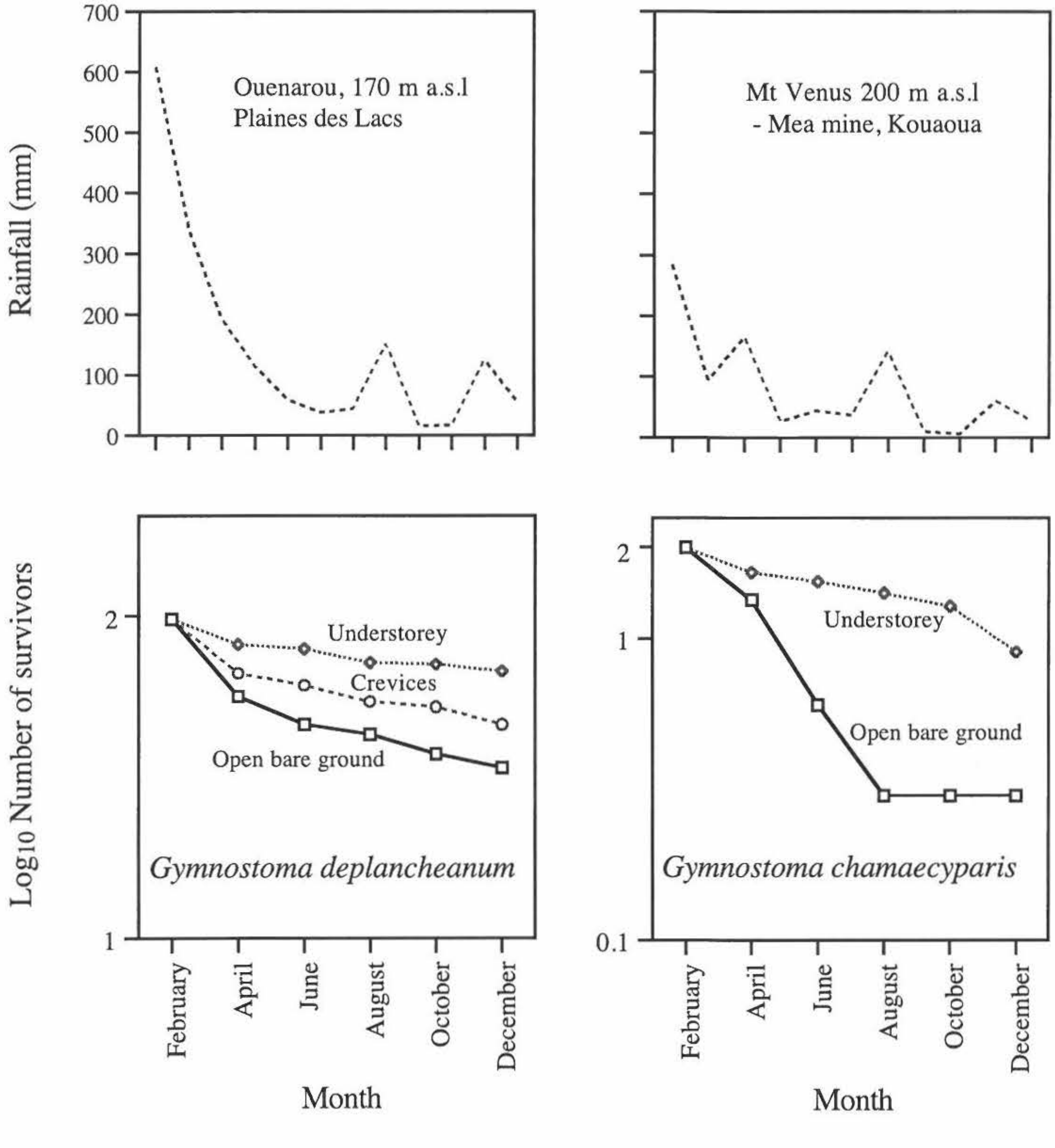


Figure 4.10 Monthly rainfall and survivorship of naturally occurring *Gymnostoma* seedlings during 1994. *Gymnostoma deplancheanum* seedlings were monitored at Creek Pernod at Plaines des Lacs and *G. chamaecyparis* was monitored at Kouaoua.

4.6 General discussion

4.6.1 What is influencing primary colonist establishment?

Spread of a species will depend on the type of vector and the abundance of seed production (Burrows, 1986; Willson, 1992). For wind dispersed species, the height of the seed release will also influence the spread of the species (Burrows, 1986). Many common plants found at the periphery of mines at Goro and Prony are tall trees, shrubs or sedges that produce wind dispersed seed (*Gymnostoma, Tristaniopsis, Grevillea, Codia, Costularia*) that could be spread over large areas by wind (fig. 4.5). However, measures of colonisation along prospecting roads abandoned 10 years previously indicate that *Gymnostoma deplancheanum* seedling numbers sharply decline with distance from the vegetation boundary (fig. 4.4). Localised micro-climatic variations produced by aspect also appear to influence *Gymnostoma* seedling abundance, but this effect is minor. Colonisation of bare sites by species possessing winged seed such as *Gymnostoma* may be therefore limited to the vicinity of the seed source, with only about 1% of seed reaching 10 m. This pattern is consistent with studies on lava flows (Del Moral & Bliss, 1993; Del Moral *et al*, 1995) and on mine sites (McClanahan, 1986; Hardt & Forman, 1992; Ausperger & Kitajima, 1992; Ash *et al*, 1994) which show that few species establish far from the vegetation boundary.

Measures of plant colonisation on mine surfaces at Goro and Prony failed to show a decline in primary colonist abundance with distance from vegetation margins. One possible explanation for this pattern is that transects at Prony and Goro were placed too far from the vegetation boundary to pick up primary colonist edge effect patterns as observed along prospecting roads. Instead transects on mines detected populations of primary colonists that may have arisen at early stages of the mine and then become isolated from seed invasions by the progressive clearance of vegetation. This boundary distance pattern is also likely to have confounded by the suitability of the substrate for colonisation.

Iron crust is a hard, nutrient poor, porous surface which may experience high temperatures (refer to 7.3.2) and evaporation that generate frequent water stress which may be unsuitable for plant survival. However, iron crust blocks are separated by crevices (fig. 4.1) that may improve colonisation rates by acting as (i) seed traps and (ii) by generating micro-environmental "safe sites" (Harper, 1977). In contrast, gravel pockets separating iron crust patches are composed of loose porous material containing few crevices. Mueller-Dumbois (1997) remarked that iron crust surfaces physically resemble *pahoehoe* lava. Seedlings in iron crust might therefore benefit from similar micro-environmental conditions of lava crevices which generate shade and micro watershed effects by funneling nutrients and water from the surrounding surface (Aplet *et al*, 1998).

Iron crust was removed from an extensive area at Prony, and left only as isolated pockets in the center of the mine and along the forest margin. Removal of iron crust had two major impacts on colonisation. (i) It eliminated potential seed banks over a large area, and (ii) reduced the abundance of suitable crevices by changing the substrate from an extensive iron crust containing numerous large crevices to a gravel plain containing few crevices. Vegetation surveys at Prony show that remnant iron crust supports a higher proportion of primary colonists than gravel (table 4.3), and that much of this primary colonist cover is largely composed of poorly dispersed primary colonists such as *Alphitonia* and *Hibbertia*. Colonisation on remnant iron crust appears to have arisen soon after the abandonment of the mine and impacted on subsequent primary colonist establishment. Aerial photos of Prony (fig. 4.6) show that remnant iron crust areas contained many trees and shrubs by 1976. However colonisation of iron crust after 1976 was very limited. Such a pattern suggests several possible scenarios.

(i) Available habitat for primary colonist establishment in iron crust crevices was saturated within 8-24 years by species arising from residual seed banks.

(ii) As the mine expanded, remnant iron crust in the center became progressively isolated from potential sources of primary colonist seed invasion in surrounding vegetation. A possible explanation for the absence of colonisation beyond remnant iron crust may be because many of the well dispersed primary colonist species posses aerodynamic seeds (eg : *Grevillea, Gymnostoma,*) that under windy conditions, are unlikely to remain on gravel surfaces because of the limited availability of suitable crevice seed traps.

Plant colonisation at Goro appears to have been more abundant and diverse than at Prony because much of the iron crust clearance was left intact. Several sources of evidence suggest that Goro has a colonisation pattern similar to post-fire succession on iron crust. Floristic records show that most primary colonist species at Goro are found in early post-fire maquis disturbed at approximately the same time. Moreover, they both contain occasional late successional species that are often poorly dispersed which suggests that seed banks were left intact at Goro. Part of the initial colonisation at Goro is therefore likely to have arisen from residual seed banks or from shrubs (*Babingtonia*) that resprouted after partial iron crust clearance. However, the presence of colonist seedlings in iron crust crevices away from primary colonists suggest that suitable microhabitats are still present on bare surfaces at Goro. In contrast, gravel pockets support fewer primary colonists than iron crust possibly because the conditions are unsuitable for establishment. Alternatively gravel substrates were devoid of a seed bank.

Results of the germination experiment and *Gymnostoma deplancheanum* seedling monitoring show that seedlings which do establish on bare gravel substrates suffer higher levels of mortality than in broken iron crust crevices. *G. chamaecyparis* seedling mortality at Kouaoua was particularly high on open bare ground, and may have arisen because exceptionally low rainfall during the dry season in 1994 (Fig. 4.10).

Patterns of primary colonist colonisation along prospecting roads and on mine sites have similarities with patterns observed on lava flows. Drake (1992) found that all primary colonist seedling colonisation by *Metrosideros polymorpha* on lava flows in Hawaii occurred in blocky lava crevices. These crevice sites became rapidly saturated by primary colonists, especially along vegetation boundaries, and generated islands of vegetation surrounded by smooth lava or ash deposits that remained bare for long periods of time (Drake, 1992; Del Moral & Bliss, 1993; Del Moral *et al*, 1995; Aplet *et al*, 1998). A difference between patterns on lava flows and on mine sites at Goro and Prony is that primary colonist establishment may have arisen partly from residual seed banks.

4.6.2 What is influencing secondary colonisation?

After 20-30 years, the general pattern of plant colonisation at Goro and Prony consisted of a primary colonist cover which had reached small tree size. Results indicate that secondary colonist distribution around primary colonists is not random and shows a steep decline away from the trunk of the primary colonist, and seedlings are rare or absent on bare ground surrounding primary colonists (fig. 4.8). In addition, primary colonists which have accumulated litter support more secondary colonists species than primary colonists which do not (table 4.5). *Gymnostoma* seedling monitoring at Plaines des Lacs and Kouaoua show that *Gymnostoma* seedlings in habitats influenced by a tree canopy showed a higher rate of survival than seedlings on bare substrates. Such a pattern clearly demonstrates both the importance of primary colonists as suitable habitats and the harshness of bare iron crust and gravel environments. Primary colonists may ameliorate the survivorship of seedlings by acting as a large microsite providing litter and shade.

Multiple linear regression did not detect a significant difference in secondary colonist abundance underneath primary colonists between iron crust and gravel sites which suggests that primary colonists can overcome most soil effects.

Distance from possible seed sources at the boundary is influencing the abundance of secondary colonist seedlings underneath primary colonists, but these patterns are confounded and overridden by direct primary colonist effects. Seedlings beneath primary colonists show different patterns of abundance with distance from the boundary at Prony and Goro for several reasons. (i) The areas of bare ground vary in size and (ii) support different amounts of suitable primary colonist habitat. (iii) Sampling at Prony was conducted further from the vegetation boundary than at Goro and possibly failed to pick up many of the late successional secondary colonists recorded at Goro because of their dispersability and small primary colonist sample size.

Vegetation surveys at Prony show that iron crust areas along the forest margin contain similar amounts of animal and wind dispersed species (fig. 4.7). On central parts of the mine, wind dispersed species show a slight decline suggestive that distance from seed sources is limiting secondary colonisation. Animal dispersed secondary colonists are nearly absent underneath primary colonists on central parts of the Prony mine. Central areas of the mine support a sparse cover of *Alphitonia* and *Grevillea* shrubs, and *Costularia* sedge land that is unlikely to present a suitable habitat for frequent use by frugivorous birds (eg: Silver eye: *Zosterops neocaledonica* and pigeons: *Chalcophaps indica chrysochlora, Drepanoptila holoserica*) or bats. Ants: *Anoplepis longipes* and *Polyrhachis guerini* are abundant on bare ground, but are unlikely to act as major seed vectors because they feed on insects, and were not observed to harvest seed from the germination experiment. An alternative explanation for the near absence of animal dispersed secondary colonist seedlings underneath primary colonists may be that suitable habitat underneath primary colonists is either (i) limited because of their small size or has been saturated by (ii) wind dispersed or (iii) seed banks in iron crust crevices.

At Goro, there is a slight increase in the number of secondary colonists plants and species underneath primary colonist with increasing distance from the forest boundary (Fig. 4.7). This pattern is difficult to interpret because primary colonists are just as abundant on central parts of the mine as they are along the vegetation margin and are therefore likely to provide similar habitats for secondary colonists. A possible explanation for the increase in abundance of secondary colonists with distance may be that the spatial extent of the narrow iron crust strip is small enough to have little impact on seedlings establishing from surrounding vegetation by either wind dispersal or vertebrate vector means.

4.7 Conclusion

In summary, surveys indicate that colonisation of bare ground following mining disturbance at Prony and Goro is largely dependent on (i) existing seed banks (ii) species dispersability, (iii) the availability of suitable microsites and (iv) primary colonists which create habitats suitable for subsequent colonists. Initial establishment occurs from seed banks in crevices. Primary colonists seedlings such as *Gymnostoma* show higher survival rates in crevices and eventually develop into trees and shrubs that modify environmental conditions such as litter and shade. The establishment of secondary colonists is greatly increased underneath primary colonists which suggests that litter and shade may potentially be important in seedling survival. However, both of these factors are confounded underneath pioneers so it is difficult to determine which is important for seedling survival. Light and litter effects on plants and successional development will be examined in chapter 5 and 6, and then tested experimentally in chapter 7.

Chapter 5

Effects of light on succession

5.1 Introduction

Successional development of vegetation causes changes in environmental conditions which may facilitate or exclude species. The most obvious early successional pattern is an increase in vegetation cover. Changes to vegetation cover strongly impact on understorey light levels, which in turn will directly influence the establishment, growth and population dynamics of species. Canopy shade causes a variety of effects on plants. It may have a direct affect on plant development in the understorey by altering the spectral quality of solar radiation available for photosynthetic carbon fixation (Lee & Graham, 1986). Canopy shade also has indirect effects on plants by reducing temperature and evaporation effects of infrared radiation in the understorey (Bjorkman *et al,* 1984; Attridge, 1990).

Recent research has been conducted on the relationship between plant stress and photoinhibition by measuring chlorophyll fluorescence (Ball *et al,* 1991; Krause & Weiss, 1991; Lovelock *et al,* 1994; Ball *et al,* 1994). Chlorophyll fluorescence can provide a non-destructive measure of the performance of the photosystem II pathway in plants (Ball *et al,* 1994). This photosynthetic pathway is sensitive to environmental conditions and will utilise available light for photosynthesis depending on the degree to which photosynthetic carbon metabolism is unaffected by unfavourable environmental conditions (Osborn, 1994). Plants may absorb more light energy than they can use in photosynthesis resulting in damage to photosystem II evident as a decline in photosynthetic efficiency (ie. mol CO_2 fixed or mol of O_2 evolved per mol photons absorbed), termed photoinhibition (Osmond, 1981; Osborn, 1994). Reduced photosynthetic efficiency may arise through direct photodamage or photoprotection (Raven, 1995).

Plants differ in their reception of light levels through differences in albedo and leaf orientation, which will alter their levels of photoinhibition (Attridge, 1990; Lovelock *et al,* 1994; Osmond, 1994). While high light intensity alone is sufficient to cause photoinhibition, any environmental factor that may affect the performance of photosystem II can also induce photoinhibition in combination with high light. These factors may be chronic deficiencies in nutrients, water supply, chronic toxicity, or acute climatic factors such as extremely high or low temperatures (Bjorkman *et al,* 1984; Ball *et al,* 1991; Ball *et al,* 1994; Lovelock *et al,* 1994). Whereas persistent limitations to growth create chronic levels of photoinhibition, acute environmental stresses cause transient photoinhibition which may be overcome within hours or days (Lovelock *et al,* 1994).

Photoinhibition is a potentially an important process in colonisation and succession patterns of maquis and forest communities at Kouaoua and Plaines des Lacs because species experience high light levels and nutrient limitations from ultramafic soils. The very strong association of colonists with shade and litter and the lower survival of colonists in the open strongly suggests that photoinhibition may be involved (chapter 4). Furthermore, foliage in the open is often yellow or purple in contrast to deep green in shade, suggesting major differences in leaf pigments.

5.1.1 Aims

This chapter addresses several questions concerning the light environment. How do light regimes change across the succession sequence? Does the photosynthetic apparatus of plant species found at different successional stages respond differently to high solar radiation environments of bare ground and shade of a continuous canopy? What mechanisms do maquis plants use to overcome the environmental stress associated with high light environments? These questions require different methods of investigations. This chapter describes field measurements of light in different *Gymnostoma* communities and reports chlorophyll fluorescence measures of common plant species. Leaf orientation was also examined for these species. The methods and results of each of these studies are presented separately then combined in an overall discussion.

5.2 Light regimes across succession

5.2.1 Methods

Light regimes were characterised in open maquis, tall maquis and forest on iron crust oxisols at Plaines des Lacs and on hypermagnesian soil at Kouaoua using a portable photometer with a quantum sensor (Li-Cor: LI 190SA). This sensor measures the photon flux (μmol s^{-1} m^{-2}) within the waveband of 400-700 nm, termed photosynthetically active radiation (PAR) (Lee & Graham, 1986). This gives a rapid estimation of the amount of light available for the photosynthesis.

Photometer readings were taken from mid-morning to mid-afternoon during overcast days with diffuse solar radiation. All measures were taken at ground level at 50 sites in each vegetation type. Readings in each vegetation type were taken at 5 m intervals and averaged over a two minute period.

5.2.2 Results

Figure 5.1 describes the light regime along the succession sequence of *Gymnostoma* communities found on iron crust oxisols at Plaines des Lacs. PAR values show considerable variation in open maquis because of variability in canopy conditions ranging from no canopy to isolated tree cover. In tall maquis, forest and rainforest, little PAR reaches the ground surface because of the dense canopy produced by an abundant understorey of broad- leafed species. *Gymnostoma intermedium* forest was not sampled, but potentially possessed understorey light levels that were similar to forest on iron crust oxisol. Light regimes show a decrease in PAR with increasing vegetation cover on hypermagnesian soils (fig. 5.2), but *G. chamaecyparis* trees are sparse on hypermagnesian soils, resulting in large canopy gaps which allow light levels to remain high and variable in tall maquis and forest.

5.3 Photoinhibition in ultramafic maquis

5.3.1 Methods

5.3.1.1 The principle of chlorophyll fluorescence measurement

Photoinhibition was assessed using a portable chlorophyll *a* fluorescence measuring system [Plant Efficiency Analyser (PEA meter), Hansatech Instruments Ltd., Kings Lynn, Norfolk, UK]. Plants absorb light within a narrow range of wavelengths for photosynthesis. Excess light energy is re-emitted or fluoresces from plant leaves (Osborn, 1994). Measures of fluorescence with a PEA meter involve dark adapting plant leaves to reduce the activity of the photosynthetic apparatus. The leaf is then illuminated by the instruments far infra-red light source for 0.3 seconds which causes the fluorescence to rises from a steady state, termed

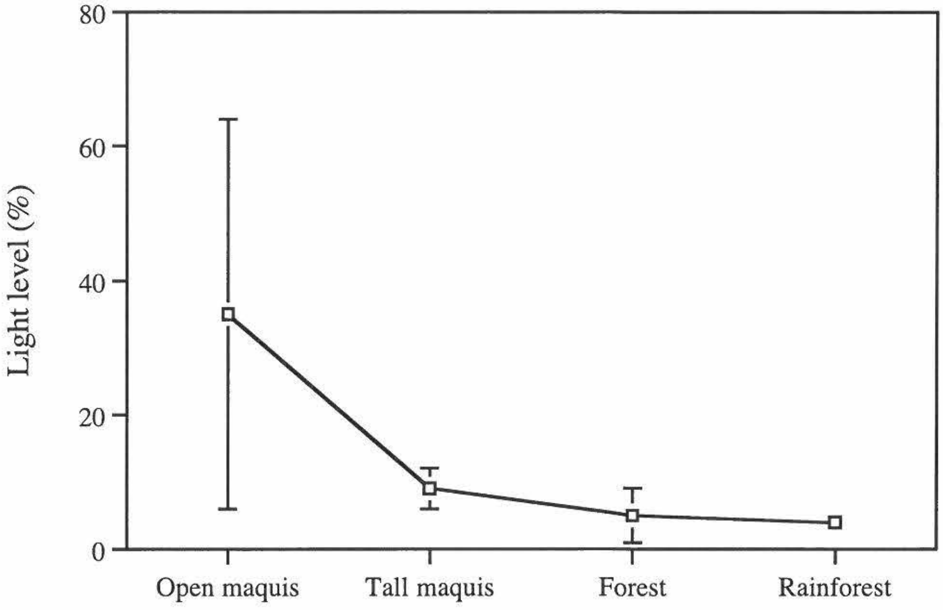


Figure 5.1 Mean light level (%) ± 1 s.d at ground level in different iron crust vegetation communities and rainforest on eroded oxisol at Plaines des Lacs.

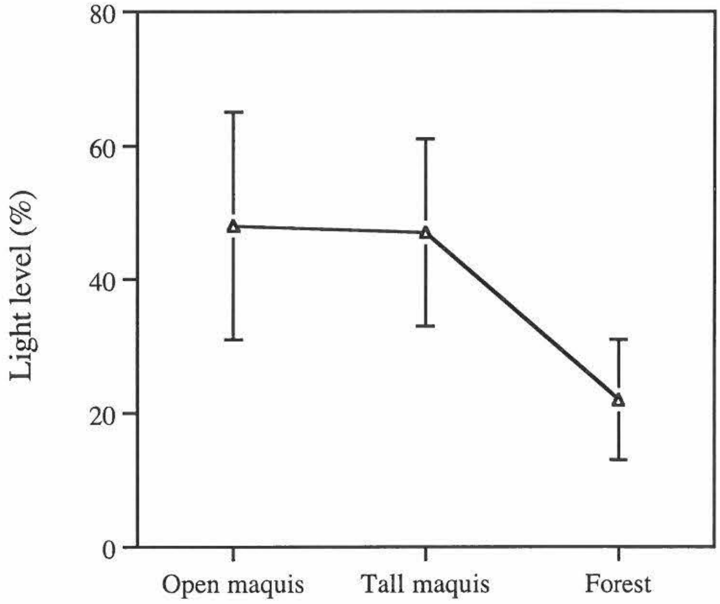


Figure 5.2 Mean light level (%) ± 1 s.d at ground level in different vegetation types found on hypermagnesian soil at Kouaoua.

Fo, to a maximum fluorescence yield, termed *Fm*, and then decline back to a steady state. The difference between the maximal fluorescence signal (*Fm*) and the low level fluorescence signal (*Fo*) represents the variable fluorescence *Fv* (Anon, 1990) (Fig. 5.3). The ratio of *Fv/Fm* is a measure of the potential maximum quantum efficiency of the photosystem II pathway (Ball *et al*, 1994). Changes to the *Fv/Fm* ratio are highly correlated with CO_2 fixation or O_2 evolution and therefore give a good indication of the state of the photosynthetic apparatus of leaves (Lovelock *et al*, 1994; Ball *et al*, 1994). Non-photoinhibited leaves will tend to have high *Fv/Fm* ratios between 0.8 and 0.83 (Ball *et al*, 1994). Conversely photoinhibited leaves have *Fv/Fm* values less than 0.8. *Fo* is affected by any environmental stress that causes structural alterations at the photosystem II pigment level. Thermal damage to photosystem II is characterised by an increase in *Fo* (Anon, 1990).

5.3.1.2 Field measurement of photoinhibition

The objective of the chlorophyll fluorescence survey was to give an indication of the level of stress experienced by the photosynthetic apparatus of maquis species under different environments by measuring both the *Fv/Fm* ratio and the steady state fluorescence *Fo*. Three contrasting aspects of leaf position and age were investigated for common ultramafic species at Plaines des Lacs and Kouaoua. (i) A comparison was made between upper leaves of plants in either full sun or in shade. (ii) Newly expanded leaves and old leaves were compared on plants in full sunlight for (a) plants of similar height and (b) plants of differing height.

Fluorescence measures were recorded between mid-morning to mid-afternoon on sunny days in December 1994, when radiation levels are at their maximum (fig. 1.5). Fluorescence measures were recorded for at least six individuals of each species. All leaves or cladodes were dark adapted for 15 minutes using leaf clips. Several cladodes were placed within clips for *Gymnostoma* spp. to ensure that the entire surface of the plant clip/sensor interface was covered. Fluorescence measurements were made at full light intensity (100%: 1000 μmol quanta m^{-2} s^{-1}) because initial tests of light intensity effects on the *Fv/Fm* ratio response of plant leaves showed a slight variation at lower levels.

5.3.1.3 Statistical analysis

Fv/Fm ratios were transformed by taking $\log_{10}$ (0.96 - *Fv/Fm*) to derive a statistic with a normal error distribution and homogenise variance.

An ANOVA (SAS institute software JMP version 3) was used to determine the effects of (i) shading, (ii) leaf age and (iii) plant height or age on the *Fv/Fm* ratio of select maquis species.

5.3.1.4 Census of leaf orientation

This survey examined foliage orientation in sun and shade of plant species examined in chlorophyll fluorescence surveys.

5.3.2 Results

5.3.2.1 Fluorescence measures of photoinhibition

Photoinhibition under full sun and shade for different species

Mean *Fv/Fm* values of species under full sun and shade are given in fig. 5.4 for iron crust oxisol communities, in fig. 5.5 for eroded oxisol communities and in fig. 5.6 for hypermagnesian communities. Measures of *Fv/Fm* taken on established individuals under canopy shade, showed that all species within a community had similar *Fv/Fm* ratios, averaging about 0.8 on oxisols and 0.75 on hypermagnesian soils. In contrast, in full sun, all species in all communities had lower *Fv/Fm* values, suggesting that the photosynthetic apparatus of plants is photoinhibited by the high light conditions. Species normally found in open maquis generally had high *Fv/Fm* ratios which suggests that maquis species may possess adaptations to overcome stress associated with high light. Later successional species generally had much lower *Fv/Fm* values than maquis species in full sun. This suggests that full sun is causing greater photoinhibitive damage to forest species than open maquis species.

Mean *Fo* values for leaves experiencing full sun and shade are given in fig 5.7 for iron crust oxisol species, in fig. 5.8 for eroded oxisol species and in fig. 5.9 for hypermagnesian species. There is a general pattern across all soil types for leaves of most species to have higher *Fo* values under full sun which suggests the photosystem II pathway had been damaged by high radiation. The lower *Fo* values for plant leaves under shade is particularly apparent for late successional species found on eroded oxisol (fig. 5.8: *Lomandra insularis, Styphelia cymbulae* & *Nepenthes veillardii*) suggesting that high light levels of open sites may damage the photosystem II pathway of species more often found under forest conditions.

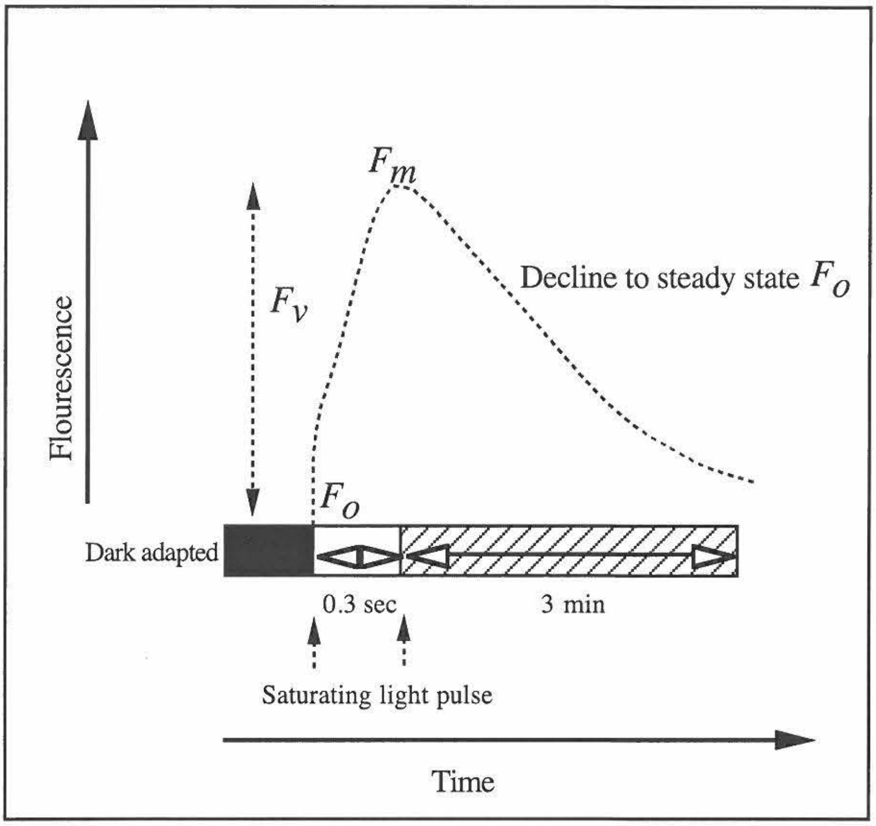


Figure 5.3 Schematic representation of a chorophyll fluoroscence trace showing parameters measured by the PEA meter (Adapted from, Anon,1990). Hollow arrows indicate duration of light pulse and lapse time of *Fo* decline to a steady state.

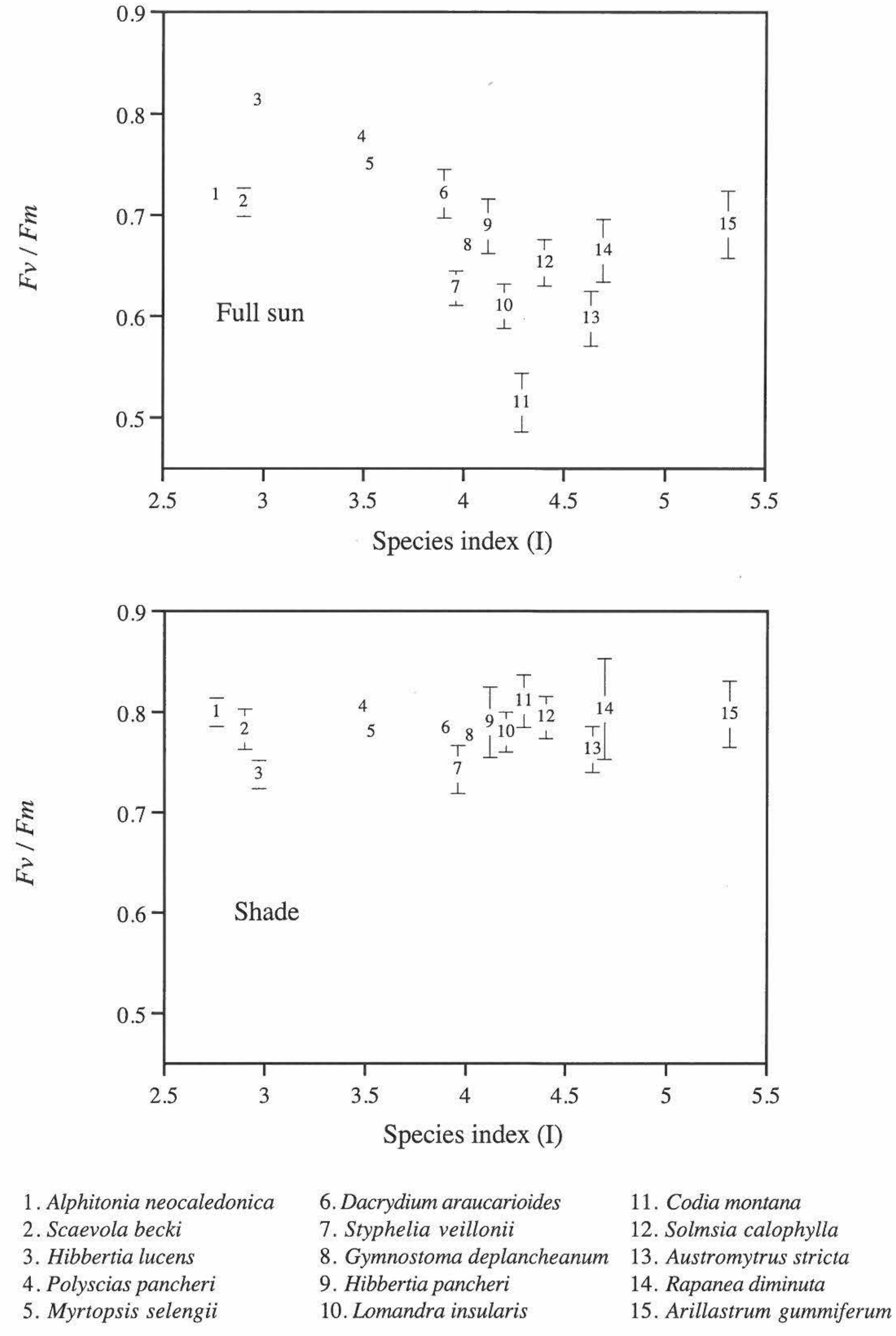
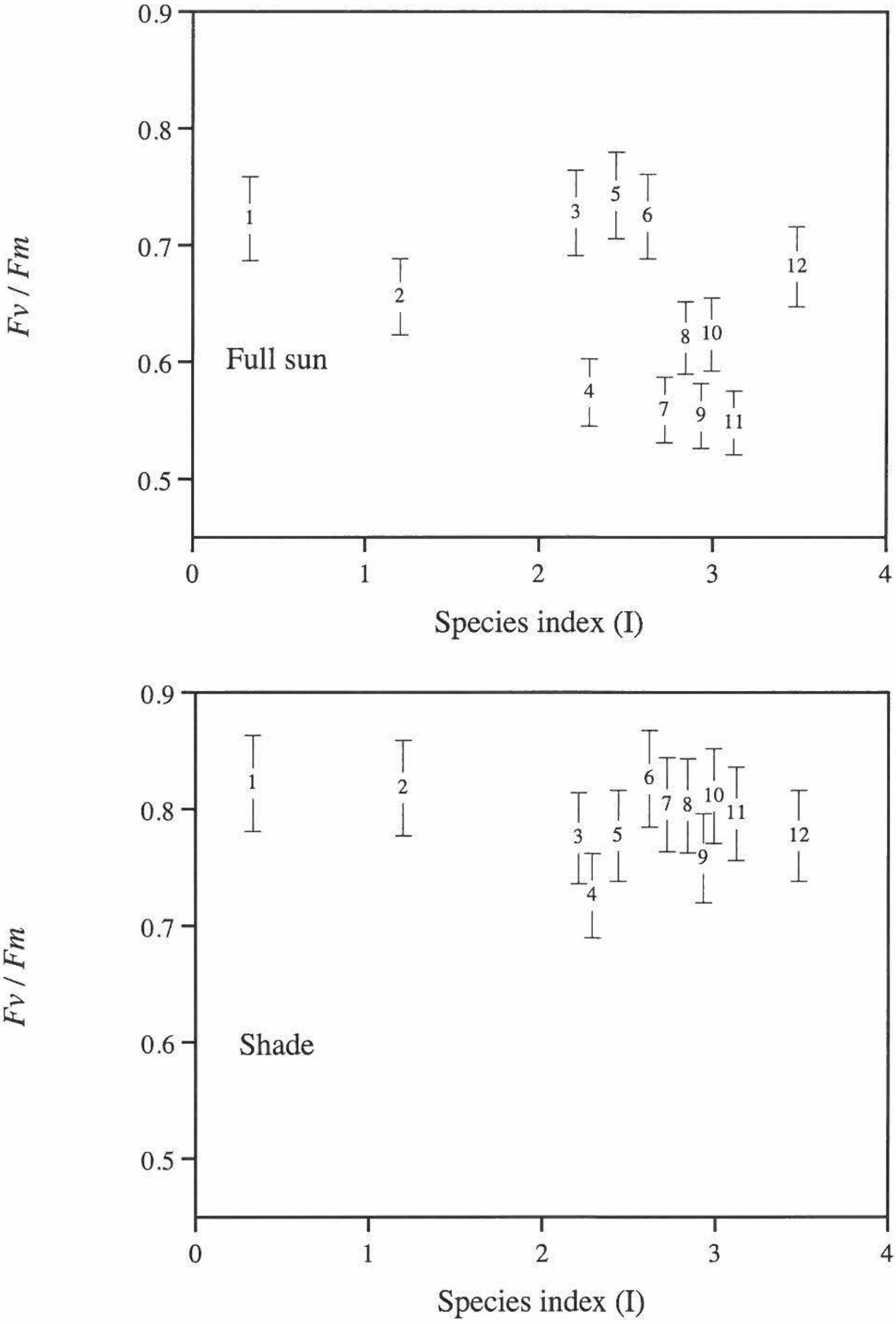


Figure 5.4 Mean *Fv/Fm* values ± 1 s.d. for leaves of species found in full sun and shade plotted against their species index (I) position in the iron crust oxisol succession sequence.



1. *Costularia nervosa*
2. *Dracophyllum verticillatum*
3. *Longetia buxioides*
4. *Codia montana*
5. *Hibbertia pancheri*
6. *Carpolepis laurifolia*
7. *Lomandra insularis*
8. *Styphelia cymbulae*
9. *Gymnostoma intermedium*
10. *Nepenthes veillardii*
11. *Rapanea assymetrica*
12. *Xanthomyrtus heighenensis*

Figure 5.5 Mean *Fv/Fm* values ± 1 s.d. for leaves of species found in full sun and shade plotted against their species index (I) position in the eroded oxisol succession sequence.

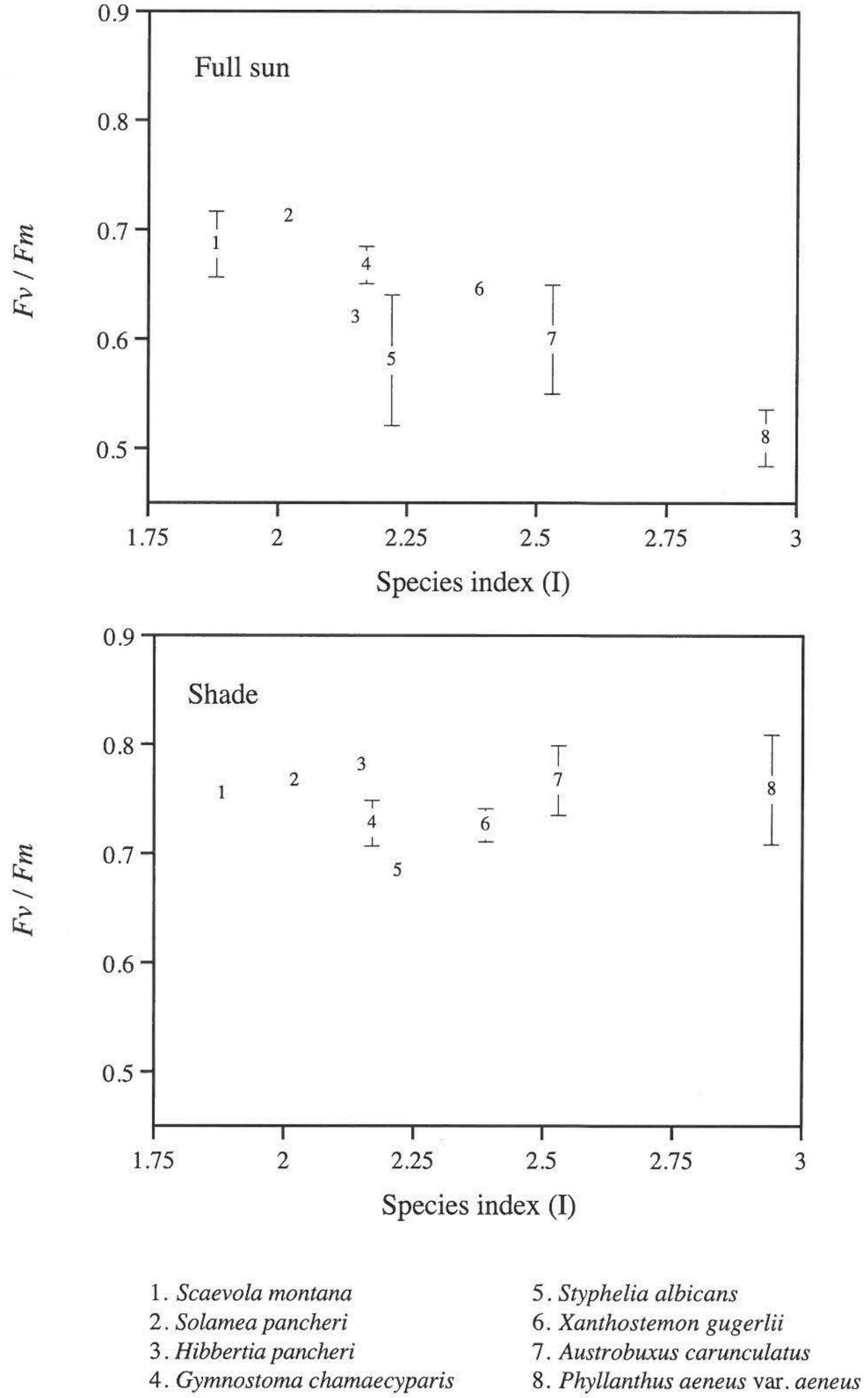


Figure 5.6 Mean *Fv/Fm* values ± 1 s.d. for leaves of species found in full sun and shade plotted against their species index (I) position in the hypermagnesian soil succession sequence.

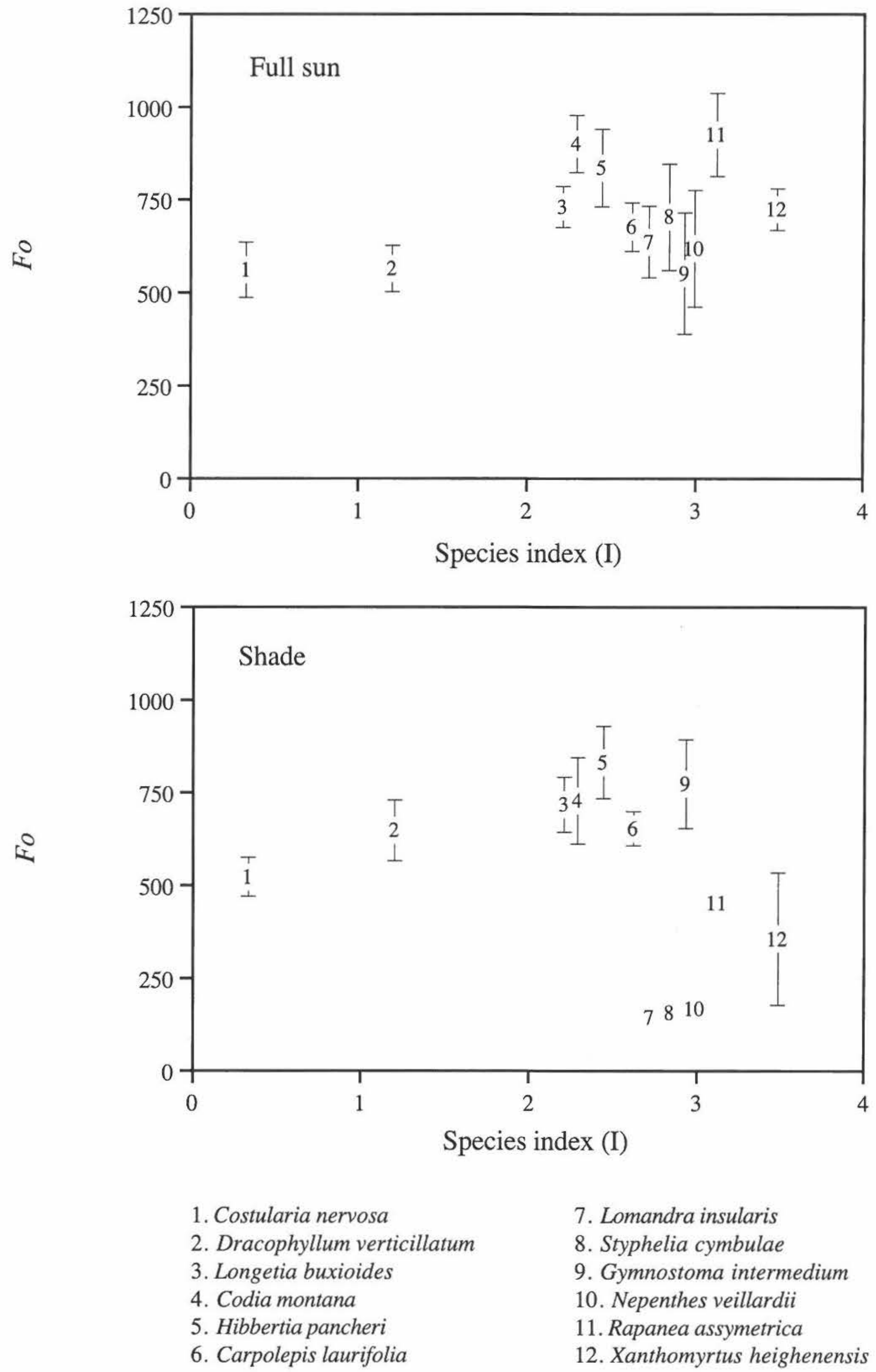


Figure 5.8 Mean *Fo* values ± 1 s.d. for leaves of species found in full sun and shade plotted against their species index (I) position in the eroded oxisol succession sequence.

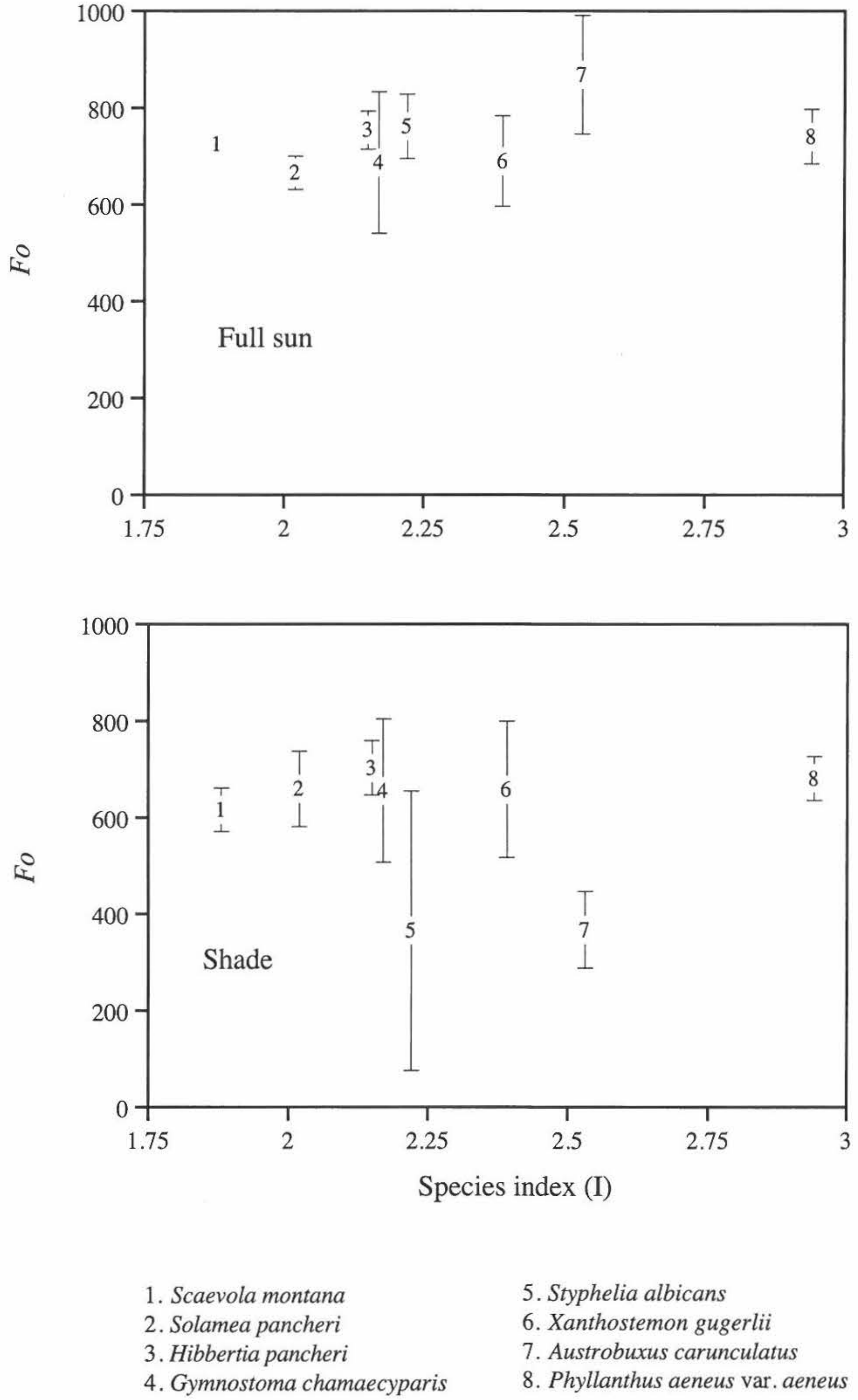


Figure 5.9 Mean *Fo* values ± 1 s.d. for leaves of species found on full sun and shade plotted against their species index (I) position in the hypermagnesian soil succession sequence.

Photoinhibition of young and old leaves

The ANOVA of transformed *Fv/Fm* ratios for newly emerged and older leaves of select maquis species showed that *Styphelia veillonii* and *Codia montana* have lower *Fv/Fm* values in young leaves under full sun. This suggests that new growth may experience photodamage under full sun, but eventually becomes tolerant of high light with age (fig. 5.10). In part, age is correlated with a lower *Fv/Fm* ratio as leaves become more shaded.

Differences in plant photoinhibition with height

The *Fv/Fm* ratios of upper foliage of seedlings, saplings and mature individuals of maquis species found in full sun and shade are given in fig. 5.11. All species show an increase in *Fv/Fm* values with increasing height suggesting that plants experience less photoinhibitive effects as they grow older and taller. Plants found in full sun have lower *Fv/Fm* values than under shade.

5.3.2.2 Plant leaf orientation under high light and shade

A census of plant leaf orientation examined under full sun and partial shade is given in table 5.1. New leaf growth of many species is nearly vertical which may reduce the impact of peak radiation levels around midday. Cladodes on *Gymnostoma* seedlings and saplings also have a vertical orientation under full sun. In contrast, the cladodes of *Gymnostoma* seedlings and saplings found under deep shade are often horizontal possibly in response to forest understorey light levels.

5.4 Discussion

5.4.1 The effects of light on colonisation and succession on ultramafic communities

Light levels across the succession at Plaines des Lacs and Kouaoua show a decline in both mean and variance as the vegetation cover increases (figs. 5.1 & 5.2). Light levels in open maquis are highly variable because of the presence of mature pioneer trees which provide shaded conditions similar to forest. As canopy trees become more abundant, light levels on the forest floor are reduced to sun flecks and canopy gaps.

Light regimes in open maquis reflect the patchiness of vegetation and range from 10% to 100% in iron crust communities, and from 30% to 65% in

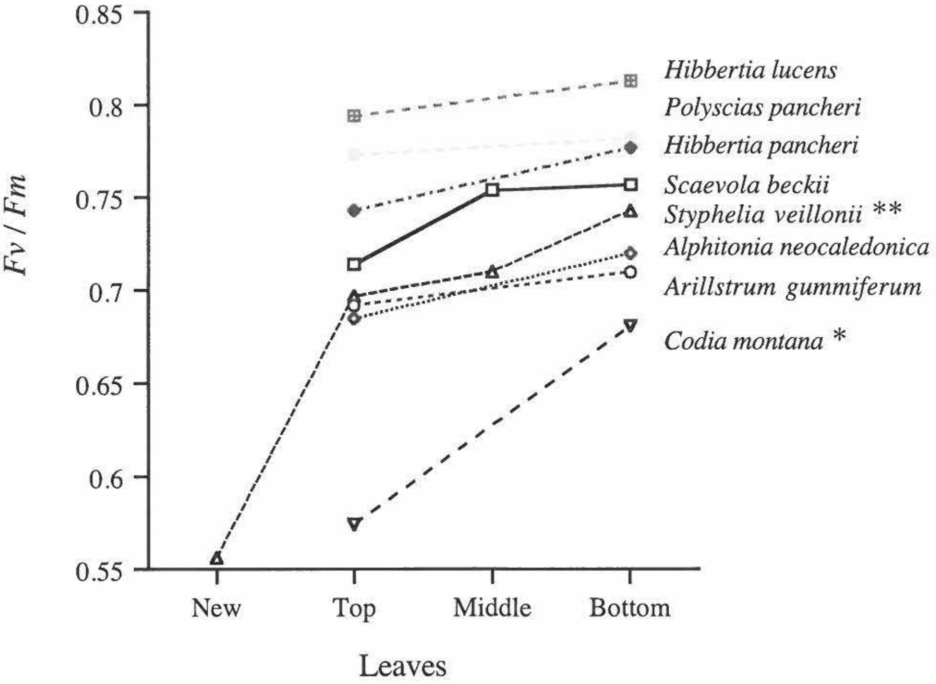


Figure 5.10 Mean *Fv/Fm* values for new, top, middle and bottom leaves corresponding to increasing age of maquis species experiencing full sunlight. Significant differences between leaves are indicated by * for F-prob < 0.05 and by ** for F-prob < 0.01. For species with top and bottom leaf samples only, leaf ages were thought to be ≤ 1 year and > 1 to < 3 years. For *Scaevola beckii*, the top, middle and bottom leaves probably represent ≤ 1, 2 and 3 yr. For *Styphelia veillonii*, new, top, middle and bottom leaves represent < 0.1, 1, 2 and 3 years.

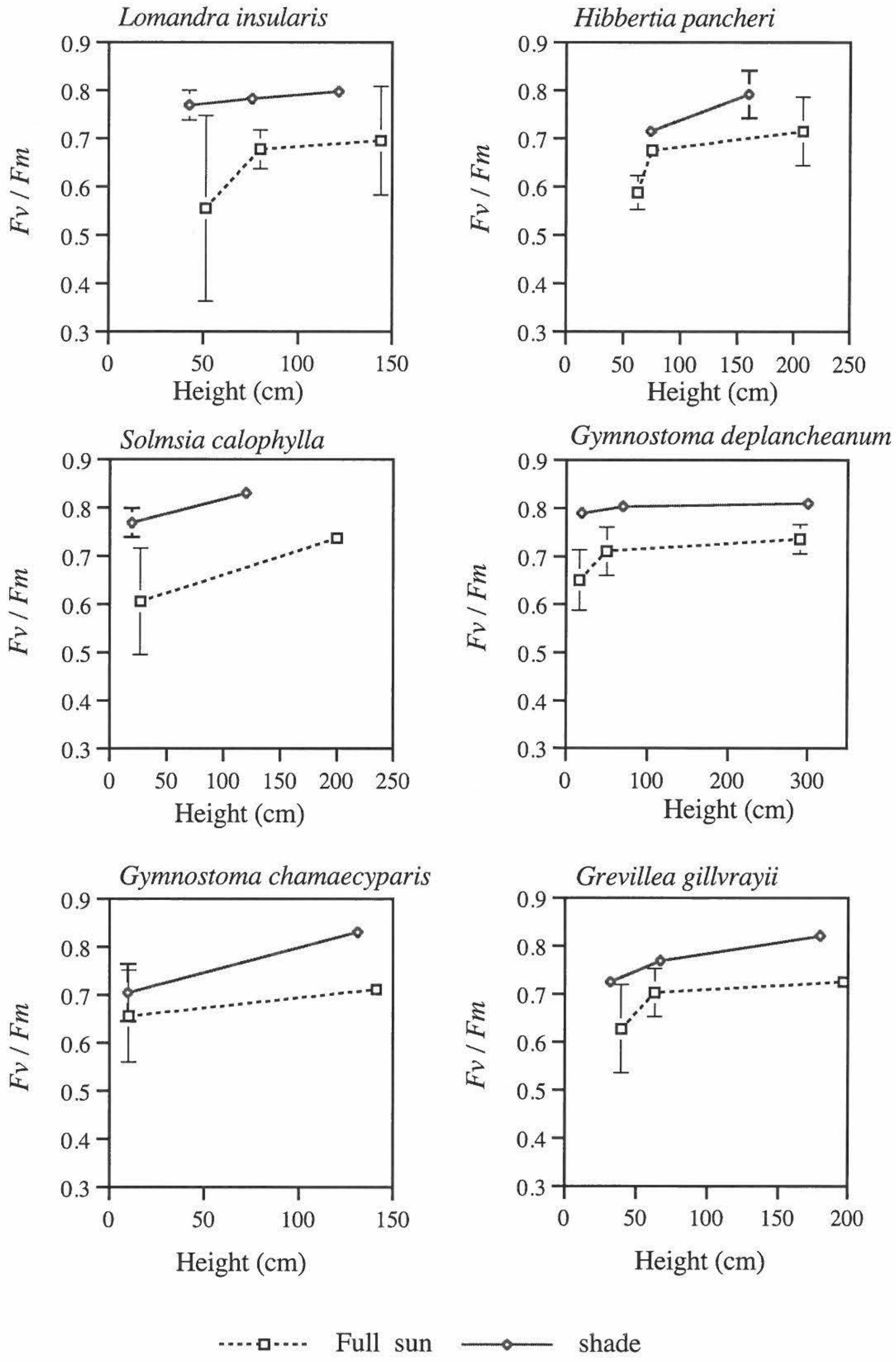


Figure 5.11 Mean *Fv/Fm* values ± 1 s.d. for top fully expanded leaves or cladodes of maquis species found under full sun and shade plotted against average height for seedlings saplings and mature individuals.

Table 5.1: Leaf and cladode orientation of ultramafic species examined under full sun and shade. ** indicates that leaves are >75° vertical, * indicates that leaves are often <75°.

	Full sun	Shade	Trend
Iron crust oxisols			
Alphitonia neocaledonica	**	**	same
Scaevola beckii			none
Hibbertia lucens	**	*	slight decline in shade
Polyscias pancheri			none
Myrtopsis selengii	**	**	same
Dacrydium araucarioides			none
Styphelia veillonii	**		strong decline in shade
Gymnostoma deplancheanum	**	*	slight decline in shade
Hibbertia pancheri	**	**	same
Lomandra insularis	**	*	slight decline in shade
Codia montana	*	*	same
Solmsia calophylla	**	**	same
Austromyrtus stricta			none
Rapanea diminuta	**	*	slight decline in shade
Arillastrum gummiferum	*	*	same
Eroded oxisol			
Costularia nervosa			
Dracophyllum verticillatum	*	*	same
Longetia buxioides	*	*	same
Carpolepis laurifolia	**	*	slight decline in shade
Styphelia cymbulae	**	**	same
Gymnostoma intermedium	**	*	slight decline in shade
Nepenthes veillardii	*		slight decline in shade
Rapanea assymetrica	**	**	same
Xanthomyrtus heighenensis	*		slight decline in shade
Hypermagnesian soil			
Scaevola montana			none
Soulamea pancheri	**	**	same
Gymnostoma chamaecyparis	*	*	same
Styphelia albicans	**	**	same
Xanthostemon gugerlii			none
Austrobuxus carunculatus	*		slight decline in shade
Phyllanthus aeneus var. aeneus	*		slight decline in shade

hypermagnesian communities. Growth and survival of plant species in these environments will depend on their ability to not only efficiently utilise the spectra available for photosynthesis (Lee & Graham, 1986) but also to tolerate various stresses at an early stage. Photoinhibition appears to be most acute for seedlings colonising bare ground evident as very low *Fv/Fm* ratios (fig. 5.11). Stress to the photosynthetic apparatus is probably high in seedlings as their initial root development is unlikely to sustain nutrient and moisture supply on bare ground that frequently experiences high temperatures (fig. 7.5) and evaporation, and contains limited nutrient sources. Such conditions may explain the higher rates of mortality of *Gymnostoma* seedlings on bare ground compared to rock crevices (chapter 4). Furthermore, plant stress that arises from a combination of high light effects and unfavourable substrate conditions on bare ground may also explain the observed pattern of secondary colonists seedlings which are restricted to underneath the primary colonist canopy (chapter 4). This area contains litter and shade at mid-day which may reduce the deleterious effects of high solar radiation on seedling leaves.

Chlorophyll fluorescence measurements at Plaines des Lacs and Kouaoua indicate that larger plants have higher *Fv/Fm* ratios than seedlings. This suggests that plants become less photoinhibited by bare ground environments once they attain a certain height and develop a root systems that is sufficiently extensive to overcome the potential stress of moisture and nutrient deficiencies. However chlorophyll fluorescence measures also indicate that photosynthetic efficiency varies between early and late successional species. Late successional species generally have lower *Fv/Fm* ratios and slightly higher *Fo* values under full sun than open maquis species. This suggests that the photosynthetic apparatus of late successional species is either damaged at high radiation or possesses photoprotective mechanisms (figs. 5.4-5.9). It also infers that early successional species are more efficient at utilising full sun for photosynthesis than late successional species by being able to tolerate high solar radiation and (ii) avoid photodamage. Early successional species are probably similar to most sun tolerant plants which have higher light compensation points than shade tolerant plants and a photosaturation that is achieved close to full sun light (Attridge, 1990).

Plants generally overcome or avoid damage from high light effects through various mechanisms. High leaf temperatures are overcome by dissipating heat through increased respiration and transpiration, and decreasing the amount available chlorophyll moisture per chloroplast (Attridge, 1990). This lowering of foliar chlorophyll content is common in sun tolerant plants and may result in a reduced photosynthetic efficiency (Attridge, 1990; Osborn, 1994). However, reduced photosynthetic efficiency is unlikely to affect photosynthetic rates under high light environments. Furthermore, chlorophyll fluorescence measures indicate that open maquis species have *Fo* values which are only slightly lower than late successional species. This suggests that photosynthetic activity in chloroplasts remains high in open maquis species despite containing less chlorophyll.

Sun tolerant plants reduce high light effects by producing shiny leaves which dissipate excess light and heat (Bjorkman *et al*, 1984). They may also produce small leaves or vertically orientated foliage which reduce the surface area of solar radiation contact (Attridge, 1990). A census of species found at Kouaoua and Plaines des Lacs indicates that *Alphitonia neocaledonica, Longetia buxioides, Hibbertia pancheri, Codia montana* and *Solmsia calophylla* produce new leaf growth that has a near vertical leaf orientation. Vertical orientation of leaves is prominent in *Gymnostoma* and occurs over the entire plant. Such a leaf architectural arrangement may serve to reduce both the photoinhibitive effects of full sun and higher levels of evaporation experienced under open conditions.

Light levels are altered in late successional stages by a tree canopy which reduces the effects of solar radiation penetration to the understorey. Reduced light penetration results in a lowering of temperatures and evaporation which potentially cause less photoinhibitive damage. Measures of chlorophyll fluorescence indicate that all species possess similar *Fv/Fm* ratios under this shaded environment. This suggests that the inhibiting effects of light are less under shade. Studies elsewhere have shown that early successional species are generally less efficient at utilising forest shade than late successional species which respond to the lower range of solar spectra in the understorey by maintaining a higher photosynthetic induction state (Kuppers *et al*, 1996). Furthermore early successional species often maintain sun tolerant leaf adaptations (small leaf size) which may reduce the amount of light intercepted (Kuppers *et al*, 1996).

5.5 Conclusion

In summary, PAR declines with increasing vegetation cover from maquis to rainforest. In open maquis, bare ground and colonist vegetation provide a mixture of light regimes from high light to deep shade. Seedlings exhibit acute photoinhibition on bare ground from a combination of high light effects and low nutrient availability. This potentially reduces survival rates of plant survival and growth until they attain a certain height at which plants are able to overcome photoinhibition. Many maquis species produce near vertical foliage which may reduce light effects on photosynthetic mechanisms. Furthermore, chlorophyll fluorescence measures suggest that they are more efficient at utilising full sun for photosynthesis. Late successional species have lower Fv/Fm ratios and higher Fo than open maquis species indicating that high light may damage the photosynthetic apparatus of leaves and potentially reduce the growth and survival of these species. Plants have higher Fv/Fm ratios in shade than in full sun indicating that the development of a continuous tree canopy at later successional stages favours plant growth and survival by reducing high light effects. However open maquis species are potentially less efficient at utilising light in understorey shade than late successional species because of their reduced leaf area.

Chapter 6

Effects of litter on ultramafic succession

6.1 Introduction

In chapter 4, it was shown that colonisation of bare oxisol and hypermagnesian sites may be severely restricted by unfavourable microhabitat, and that shade and litter are strongly correlated with colonisation success. In chapter 5, it was shown that high light levels may photoinhibit plants in open habitats, especially seedlings on bare ground. This chapter reports successional changes in biomass and litter and explores how these may influence plant establishment. Litter potentially has several physical effects both on the micro-environment of plant communities by modifying albedo, shade, temperature and soil moisture, but also on seedling establishment in terms of seed burial (Ahlgren & Ahlgren, 1981; Hopkins & Graham, 1987; Molofsky & Augsperger, 1992; Parrotta; 1995). Litter may also have chemical effects on plant communities by providing nutrients and allelochemicals through leaching or decay by micro-organisms (Swift *et al*, 1979; Vitousek, 1984; Vitousek & Sanford, 1986; Attiwill & Leeper, 1987; Brown & Lugo, 1990; Bruijnzeel, 1991).

6.1.1 Aim

This chapter examines the productivity and nutrient dynamics of ultramafic communities, the impact of changes in litter and soil nutrients on successional processes, and especially, the role of *Gymnostoma*. The first part of this chapter reports surveys of standing biomass, fine litter biomass, litter and soil nutrient content, and litterfall for maquis and forest communities, and the breakdown of *Gymnostoma deplancheanum* cladodes and *Arillastrum gummiferum* leaves. These measures are used to generate simple models of the productivity and nitrogen balance of iron crust communities. The second part reports a survey comparing mature plant and seedling abundance with seedfall of select maquis and forest species. The third part reports the results of two glasshouse experiments examining (a) the effect of *Gymnostoma* litter leachates on maquis seedling growth and (b) the effect of *Gymnostoma* litter on seed germination and seedling survival of maquis species.

6.2 Biomass and nutrients of successional communities

6.2.1 Methods

6.2.1.1 Standing biomass

The standing biomass of stems > 2 cm d.b.h in open maquis, tall maquis, forest on iron crust oxisol and rainforest on eroded oxisol at Plaines des Lacs, and in open and tall maquis on hypermagnesian soil at Kouaoua was estimated for several plots (outlined in 3.2.1.2. and 3.4.3.2). Several widely adopted (Whittaker & Mark, 1975) simplifying assumptions were made when calculating biomass because of the lack of species specific information on wood density, foliage biomass and the height of understorey saplings and shrubs.

Tree height (h, m) was estimated from trunk diametre (d, m) with reference to stand canopy height (H, m).

If $100d \geq H$, $h = H$
If $100d < H$, $h = 100d$

Individual tree biomass (T_b, t ha^{-1}) was estimated as

$$\boxed{T_b = \left(\frac{2}{3}\right) h\, \pi \left(\frac{d}{2}\right)^2} \quad \text{(Whittaker \& Mark, 1975)}$$

assuming a wood density of 1.0 t m^{-3} at 12% wood humidity, as recorded for *Gymnostoma deplancheanum* and *Arillastrum gummiferum* (CIRAD Forêt, 1992). Total plot biomass was expressed on a tonnes per hectare basis.

6.2.1.2 Litter biomass and nutrient content

Litter biomass (fallen leaves, fruit and wood <1 cm diametre above the mineral soil), litter nutrient content and soil nutrient content were sampled in 6 open maquis and 11 tall maquis formations at Creek Pernod, 8 forest sites on the Goro plateau, and 8 forest sites on eroded oxisol and 8 tall maquis sites on hypermagnesian soil at Kouaoua. Measures of biomass and nutrient content of rainforest litter were made at 6 sites in *Arillastrum* *gummiferum* rainforest on eroded oxisol at Col de Mouirange (Lat 22°12' S; Long 166°40' E; 170 m a.s.l).

Litter sampling at all sites consisted of (i) measuring the depth of the litter layer (L_d, cm) (ii) removing 1 m^2 of litter and (iii) oven drying it at 40°C for 120 hours to obtain dry weight (L_w, g m^{-2}). Litter dry weight was then multiplied by the proportion of litter cover in the vegetation formation (L_c) (chapter 3). Nutrient content was measured for a 5 g sub-sample of litter from each site. Techniques used to analyse nitrogen, phosphorus, potassium, sodium, calcium, magnesium, manganese and nickel concentrations of litter ($L_{E'}$) are given in Appendix 1. Litter biomass (L_b, t ha^{-1}) and litter nutrient content (L_n, kg ha^{-1}) were estimated for each vegetation formation using the following equations.

$$L_b = 0.01 L_w L_c$$

$$L_n = 10 L_b L_E$$

where

L_E = percent of element.

6.2.1.3 Soil nutrient content

Soil nutrient and metal concentration (S_E, ppm) was measured on the fine fraction soil (< 2 mm) of A_o horizon soil 0-7 cm (W, g). Fine soil fractions were obtained from bulk density cores taken below litter samples in successional vegetation types at Kouaoua and Plaines des Lacs (6.2.1.2). Soil samples were then oven dried at 40°C for 24 hrs prior to chemical analysis. Techniques used to analyse the nitrogen, phosphorus, potassium, sodium, calcium, magnesium, nickel and manganese concentrations of soil are given in Appendix 1. The soil element contents (S_n, kg ha^{-1}) were extrapolated from the A_o horizon fine soil fraction, assuming that nutrient levels decline by half for every 10 cm increase in soil depth (Latham *et al*, 1978; Becquer *et al*, 1995; Bourdon *et al*, 1997).

$$Sn = 0.23 W S_E$$

where

S_E = ppm of element.

Values given for the element content of iron crust oxisol and hypermagnesian soil are estimates because A_0 soil occur as pockets separated by rocky ground.

6.2.1.4 Litterfall

Litterfall was measured from December 1993 to January 1995 in tall maquis on iron crust oxisol at Creek Pernod, in tall maquis on hypermagnesian soil and in forest on eroded oxisol at Kouaoua. Sites were selected in typical formations that were undamaged by prospecting or timber cutting and sufficiently far from roads (> 10 m) to minimise edge and dust fall in litter traps. Twelve litter traps were placed at each site at 5 m intervals along two parallel 30 m transects 10 metres apart.

Litterfall was collected in polyethylene sacks (80 cm deep) fixed to a circular metal support (78 cm diametre) that stood 1 metre above the ground. Several holes (1 mm) were made at the base of bags to allow free drainage of water. Litter was removed on a monthly basis, dried at 40°C, sorted by species in terms of leaves, twigs, fruit and seed, and weighed. *Gymnostoma deplancheanum, G. chamaecyparis* and *G. intermedium* cladodes were sub-sampled from each bag between August 1994 and January 1995, to determine the monthly fine litterfall nutrient output of these species. Chemical analysis of *Gymnostoma* cladode litter was carried out using techniques outlined in Appendix 1.

6.2.1.5 Litter breakdown

A litter breakdown experiment was established in *Arillastrum gummiferum* forest and *Gymnostoma deplancheanum* forest at Prony to determine the decay rates of fresh *A. gummiferum* leaves and *G. deplancheanum* cladodes in litter beds of both forests. Litter of *G. deplancheanum* and *A. gummiferum* was selected as the test medium because both species are common on iron crust and were considered to represent the range of foliage types. *Gymnostoma* cladodes and *Arillastrum* leaves differ in size and contain different amounts of lignified tissue which might affect decay rates. Newly fallen undamaged *Arillastrum* leaves and *Gymnostoma* cladodes were obtained from branches in January 1994. These were oven dried at 40°C for 24 hours, weighed into 9-13 g portions and placed in bags made of mosquito wire mesh (1 mm). Forty bags of each were placed on bare ground of each formation in March 1994. Eight bags were removed for each species from each formation after 2 and 7 months.

Gymnostoma samples were scored according to the coverage of fungal hyphae on cladodes (< 1%, 1-25%, 26-50%, 51-75% and > 76 %), then oven dried at 40°C for 24 hours to obtain dry weights. *Arillastrum* leaves were scored according to the area of leaf remaining (< 1%, 1-25%, 26-50%, 51-75%, > 76%), then oven dried at 40°C for 24 hours and weighed. A fire in November 1994 burnt both forest formations and destroyed the remaining samples.

Multiple linear regression (SAS institute software JMP ® version 3) was used to determine whether there were differences in litter breakdown over time between forest types and test species.

6.2.1.6 Annual net primary production of successional communities at Plaines des Lacs

Annual net primary production (NPP, t ha^{-1} yr^{-1}) of successional communities at Plaines des Lacs was calculated from changes in standing biomass over the estimated time elapsed between successional stages (chapter 3) and measures of litter biomass in iron crust communities and rainforest on eroded oxisol. Annual litterfall was not measured in open maquis, forest or rainforest at Plaines des Lacs, but was estimated from litter biomass in these communities assuming an exponential decay based on the measured rates of breakdown of *Gymnostoma deplancheanum* cladodes. This model was constructed assuming that changes in litter biomass from maquis to forest and from forest to rainforest between time periods have arisen at rates corresponding to *G. deplancheanum* litter decay which is slower (2.7 yr^{-1} half life) than rainforest species such as *Arillastrum gummiferum* (2 yr^{-1} half life).

6.2.1.7 Nitrogen balance of ecosystems at Plaines des Lacs

Nitrogen is typically a limiting element in primary succession (Reiners, 1981), so effort focussed on N dynamics. A nitrogen balance was constructed for successional vegetation at Plaines des Lacs from the nitrogen content of *Gymnostoma deplancheanum* and other species biomass (standing and litter) (Jaffré *et al*, 1994 b), litterfall and soil (fine soil volume <2 mm). To explain the changes in nitrogen content of the ecosystem it was assumed that three processes add nitrogen to the ecosystem. (i) Hydrological processes (rainfall and leachates) were assumed to contribute 2 kg ha yr^{-1} to the net nitrogen balance of ecosystems at Plaines des Lacs (cf: Bormann *et al*, 1977; Waterloo *et al*, 1997). (ii) Nitrogen fixation by free living microbes was assumed to be proportional to the total annual litterfall, a determinant of soil metabolic activity, and set to a maximum of 1 kg ha yr^{-1} (Attiwill & Leeper, 1987). (iii) *Gymnostoma deplancheanum* nitrogen fixation, through associated *Frankia* bacteria was assumed to supply all remaining nitrogen, and the rate of fixation was assumed to be proportional to *Gymnostoma* litterfall, an indication of *Gymnostoma* productivity.

The model was fitted by taking estimating the total N content in biomass and litter, and attributing the increase to the three processes, with the constraint that after 400 years (rainforest stage), the model should predict the observed total N content of the ecosystem. A test of the fit of the model is whether it can correctly predict the soil nitrogen content at intermediate stages of the succession.

6.2.2 Results

6.2.2.1 Standing biomass and litter biomass

Estimates of standing biomass for iron crust communities at Plaines des Lacs show increases along the succession sequence from open maquis (14 t ha^{-1}) to tall maquis (150 t ha^{-1}), forest (361 t ha^{-1}), and to rainforest (469 t ha^{-1}) on eroded oxisol (Fig 6.1). *Gymnostoma deplancheanum* contributes about 50% of the standing biomass of maquis and less than 1% of the standing biomass of rainforest. Standing biomass in rainforest is much higher than for iron crust communities because of large *Arillastrum gummiferum* trees which account for 50% of the standing biomass. There is an increase in standing biomass from open maquis (24 t ha^{-1}) to tall maquis (80 t ha^{-1}) on hypermagnesian soils at Kouaoua (fig. 6.1). *Gymnostoma chamaecyparis* accounts for 50% of the standing biomass of open maquis and 65% of tall maquis in which large *G. chamaecyparis* trees are more abundant.

Litter biomass increases along the iron crust succession sequence from open maquis (5 t ha^{-1}) to tall maquis (10 t ha^{-1}) and forest (42 t ha^{-1}), but shows a decline in rainforest (21 t ha^{-1}). Litter biomass in forest (52 t ha^{-1}) on eroded oxisol is slightly higher than in forest on iron crust oxisol. Litter biomass in tall maquis (14 t ha^{-1}) on hypermagnesian soil is slightly higher than in tall maquis on iron crust.

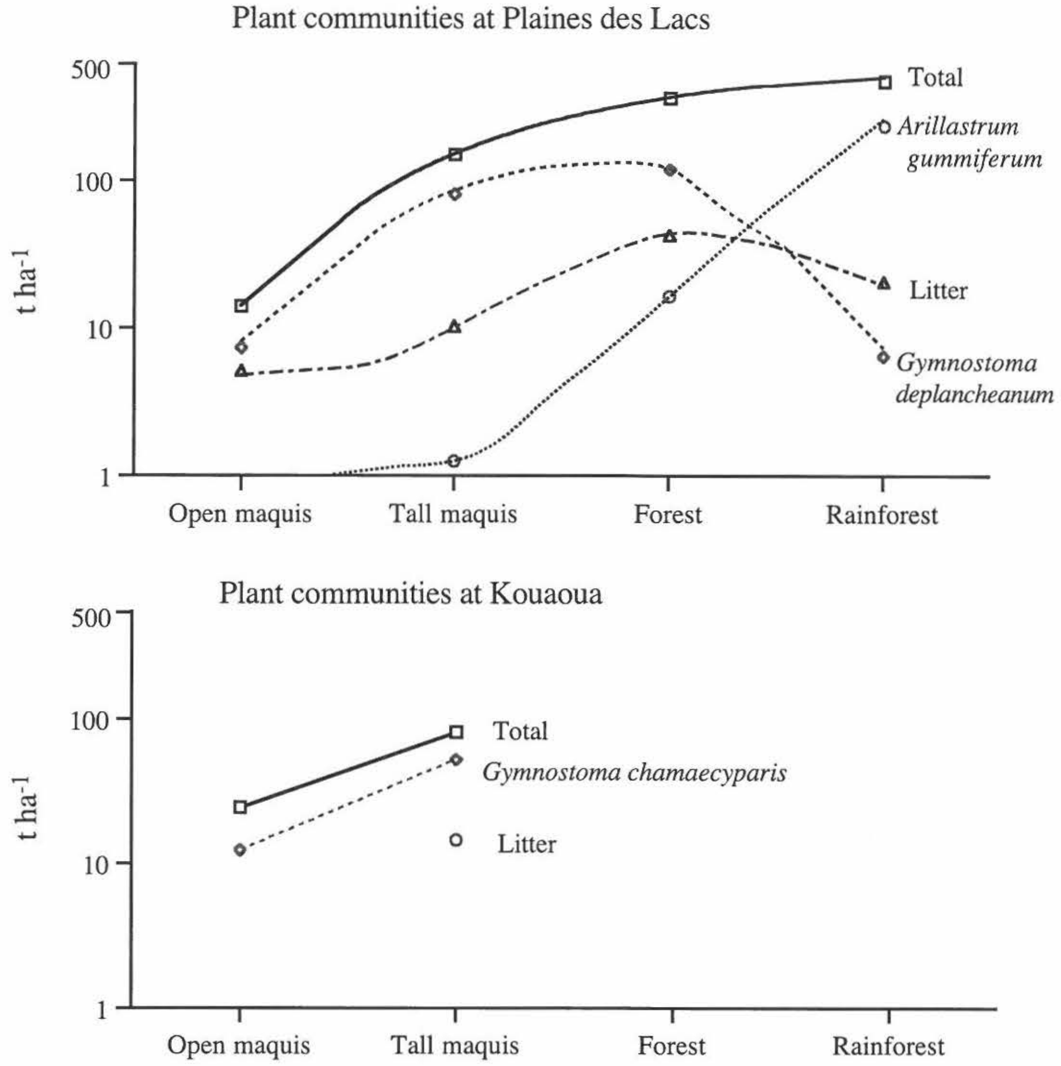


Figure 6.1 Estimated total above ground biomass of stems > 2 cm (d.b.h) and litter biomass of vegetation formations in successional order found on (top) iron crust and eroded oxisol at Plaines des Lacs, and on (bottom) hypermagnesian soil at Kouaoua. The standing biomass of *Gymnostoma deplancheanum*, *Arillastrum gummiferum* (top) and *G. chamaecyparis* (bottom) are shown separately. The litter biomass of rainforest on eroded oxisol at Col de Mouirange.

6.2.2.2 Litter and soil nutrient content

Results of chemical analysis of A_0 horizon soil (fine fraction < 2 mm) and litter are given in Fig. 6.2 a, b. Most soil nutrient contents increase along the iron crust succession sequence and remain high in soil of climax rainforest communities on eroded oxisol. Nitrogen shows the most substantial increase (x 20), followed by sodium (x 10) and calcium (x 6). Potassium levels show a slight increase in soil of forest and rainforest communities. In contrast, phosphorus concentrations appears to increase very slightly (x 2) with time from maquis to forest on iron crust, and only increase in eroded oxisol underneath rainforest. The magnesium, manganese and nickel content of soil underlying iron crust successional communities show no clear trend.

Measures of nutrient and metal contents in litter of successional communities at Plaines des Lacs reveal that nitrogen contents increase from about 6 kg ha^{-1} in open maquis litter to 500 kg ha $^{-1}$ in forest, and decline to 170 kg ha $^{-1}$ in rainforest litter. An increase from maquis to forest and decline in rainforest is also observed for calcium contents, though of a lower magnitude. Phosphorus, potassium, sodium, magnesium, nickel and manganese increases in litter from maquis to forest on iron crust oxisol are marginal compared to nitrogen and calcium. However, these elements become more abundant in litter of rainforest communities on eroded oxisol.

Plant nutrients and metal contents in maquis litter show considerable variation compared to late successional communities and some were below the range of detection of analytical techniques, evident from large standard deviations. Overall, nitrogen ($\leq$ 600 kg ha^{-1}) is more abundant in litter of all communities than calcium ($\leq$ 400 kg ha^{-1}), sodium ($\leq$ 20 kg ha^{-1}), potassium ($\leq$ 8 kg ha^{-1}) and phosphorus ($\leq$ 7 kg ha^{-1}). Litter calcium contents are higher than magnesium ($\leq$ 10 kg ha^{-1}) in all communities, except on hypermagnesian soil where the magnesium content of litter is very high (440 kg ha $^{-1}$) and possibly includes dust contamination from mine roads. Litter nickel contents rarely exceed 14 kg ha^{-1} in iron crust communities except in forest litter on eroded oxisol that contains 251 kg ha^{-1} of nickel. Other heavy metals such as manganese are also relatively high in litter of forest sites (< 60 kg ha^{-1}) compared to maquis (< 20 kg ha^{-1}).

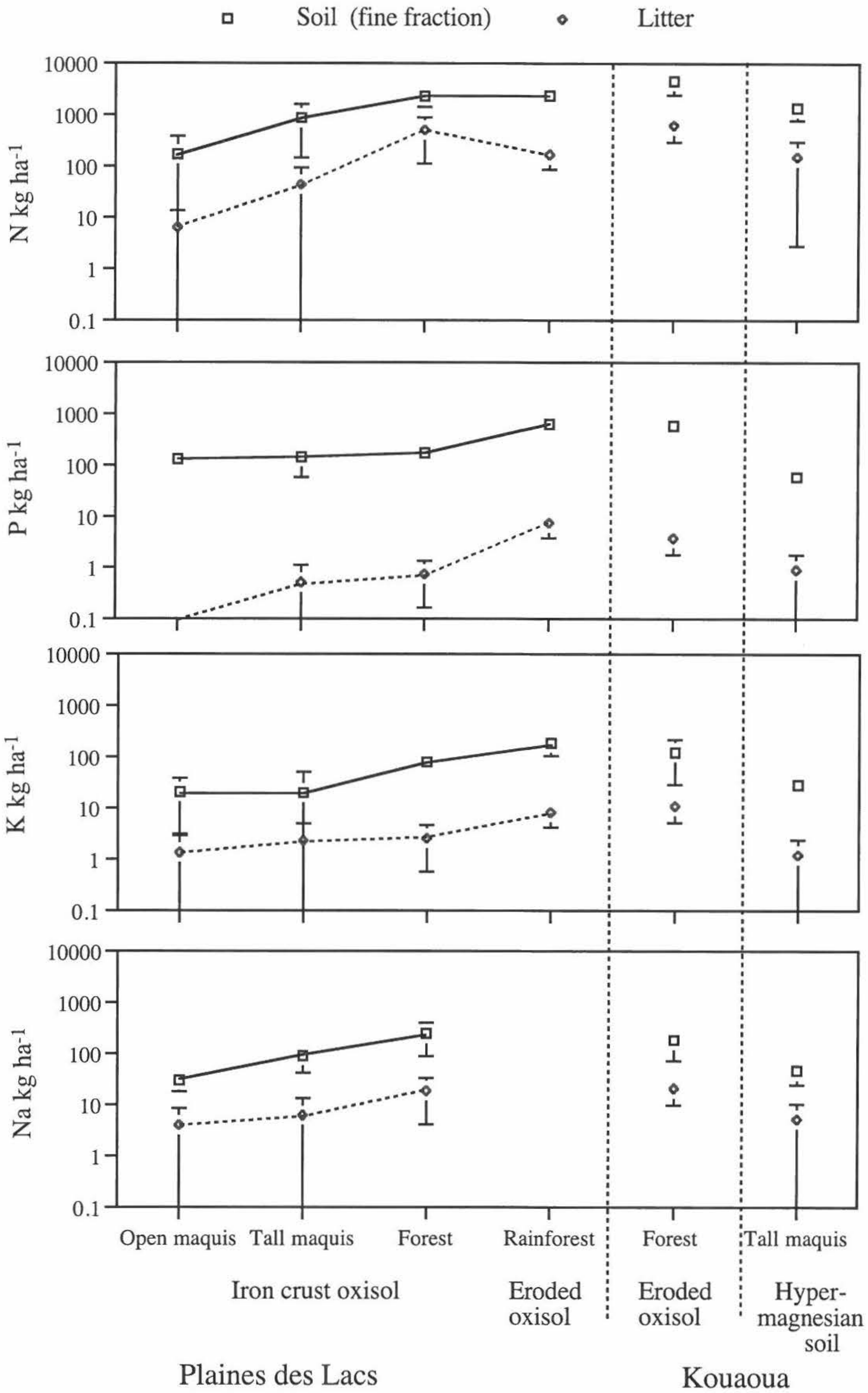


Figure 6.2a Mean (± 1 s.d.) nitrogen, phosphorus, potassium and sodium content of litter and A_0 horizon soil (fine fraction < 2 mm) of maquis and forest on iron crust at Plaines des Lacs, of rainforest on eroded oxisol at Col de Mouirange, of forest on eroded oxisol and tall maquis on hypermagnesian soil at Kouaoua.

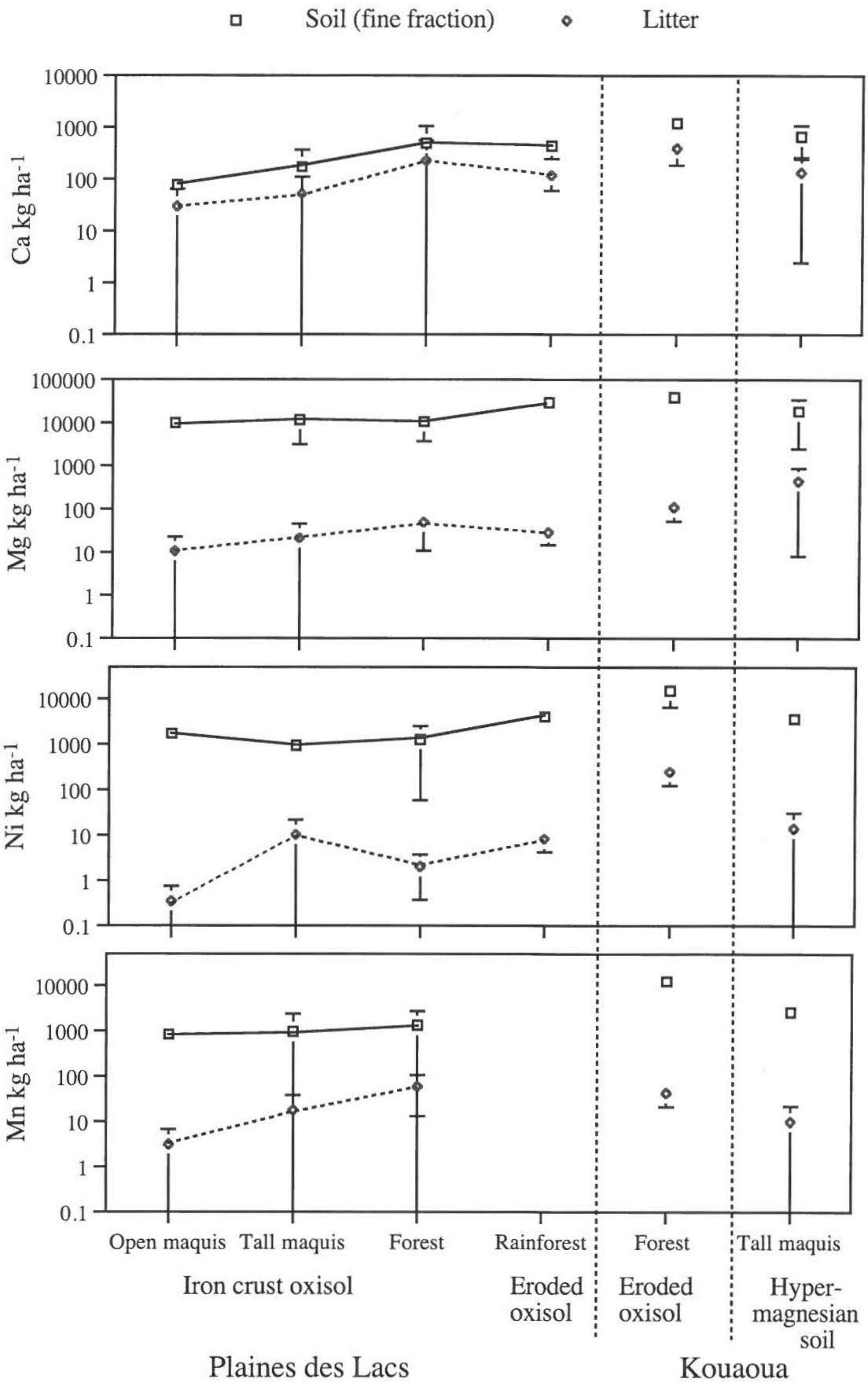


Figure 6.2b Mean (± 1 s.d.) calcium, magnesium, nickel and manganese content of litter and A_0 horizon soil (fine fraction < 2 mm) of maquis and forest on iron crust at Plaines des Lacs, of rainforest on eroded oxisol at Col de Mouirange, of forest on eroded oxisol and tall maquis on hypermagnesian soil at Kouaoua.

6.2.2.3 Litterfall

Monthly litterfall for communities on iron crust oxisol, eroded oxisol and hypermagnesian soil (figs. 6.3, 6.4 and 6.5) indicate several patterns. (i) Litterfall differs between vegetation communities with forest on eroded oxisol producing the most litter (5.02 t ha^{-1} yr^{-1}), followed by tall maquis at Creek Pernod (2.86 t ha^{-1} yr^{-1}) and tall maquis on hypermagnesian soil at Kouaoua (1.58 t ha^{-1} yr^{-1}). (ii) *Gymnostoma* produces most of the litter in all three communities. In tall maquis, 86-90% of the litterfall is produced by *Gymnostoma deplancheanum* and *Gymnostoma chamaecyparis*. *Gymnostoma intermedium* produces 66% of the litterfall in forest on eroded oxisol. (iii) There is a seasonal peak in litterfall in tall maquis on hypermagnesian soil which coincides with the driest period of the year between July and December.

Monthly seed and fruit fall was highly variable between litter traps and many contained no seed. Monthly fruit and seed fall averaged over all traps is given in fig. 6.6 for tall maquis at Creek Pernod, in fig. 6.7 for forest at Kouaoua and fig. 6.8 for tall maquis at Kouaoua. Fruit and seed dispersal occurs year round, though more species disperse during the wet season from December to March. In contrast, *Styphelia veillonii, S. cymbulae* and *Tristaniopsis callobuxus* produced fruit during the dry season. *Gymnostoma deplancheanum* and *G. chamaecyparis* produce approximately the same amount of seed. In contrast, *Gymnostoma intermedium* seed fall was barely registered in forest litter traps despite the overlying canopy being dominated by this species.

Cladode nutrient and metal concentrations of *Gymnostoma deplancheanum, G. chamaecyparis* and *G. intermedium* litterfall were highly variable so values were averaged for the six month period. The foliar nutrient and metal content for *Gymnostoma deplancheanum, G. chamaecyparis* and *G. intermedium* cladode litterfall are presented in fig. 6.9. Calcium and nitrogen occur at much higher levels than other elements in *Gymnostoma* litterfall. *Gymnostoma* species examined release moderate amounts of sodium, potassium and magnesium (< 1 kg ha^{-1}) in monthly litterfall but liberate very little phosphorus (< 30 g ha^{-1}). The nickel content of litterfall is relatively low for *G. deplancheanum* and *G. chamaecyparis* (< 30 g ha^{-1}), and slightly higher for *G. intermedium* (< 90 g ha^{-1}). Manganese is also relatively low in litterfall of *Gymnostoma* except for *G. intermedium* which may contribute up to 2.8 kg ha^{-1}.

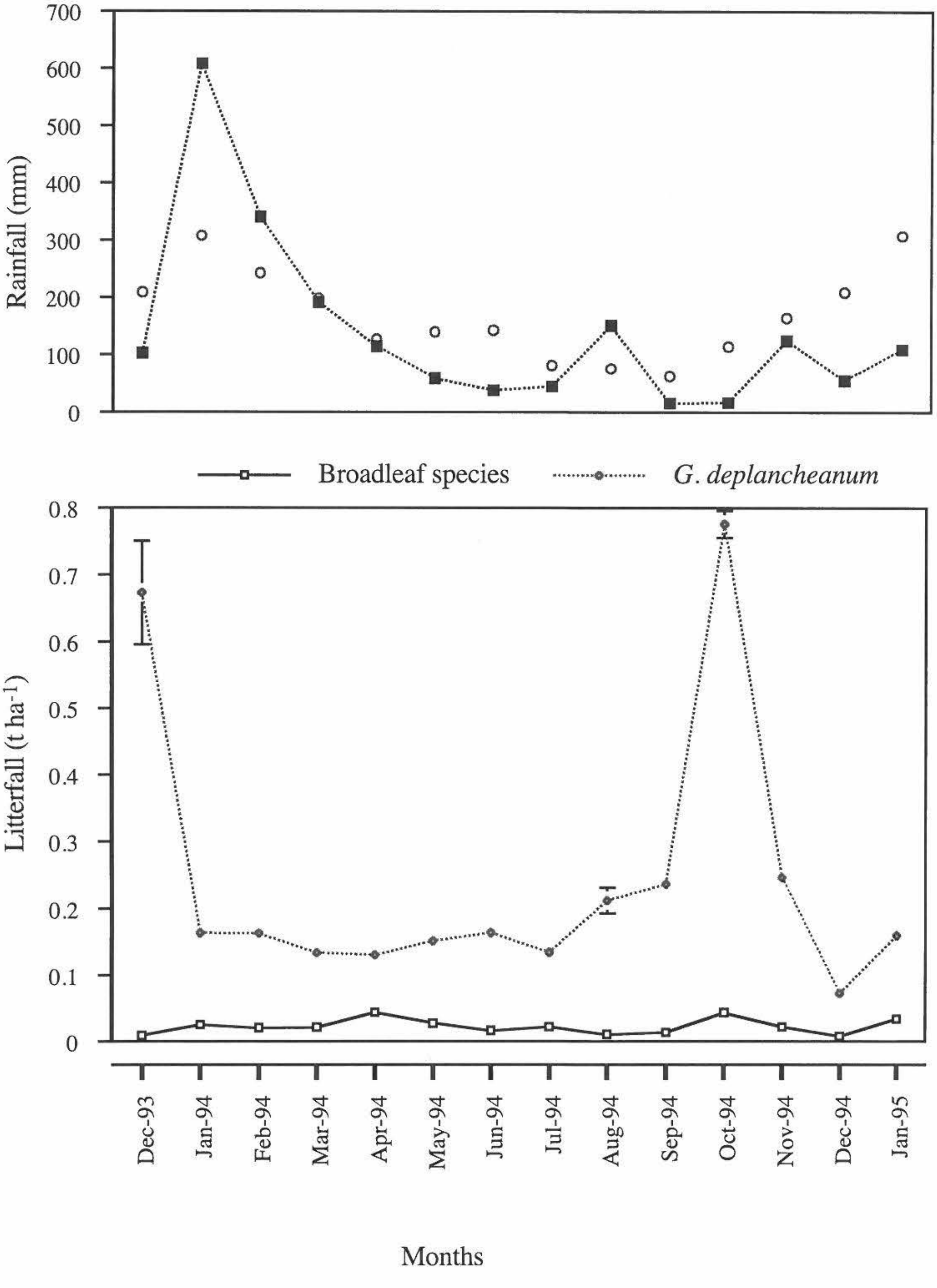


Figure 6.3 Mean monthly rainfall (1983 to 1992; circle), monthly rainfall (top) and total monthly litterfall of *Gymnostoma deplancheanum* ± 1 s.d and other species in tall maquis ± 1 s.d (bottom) at Plaines des Lacs (Creek Pernod) from December 1993 to January 1995. Rainfall values are from Ouenarou (170 m a.s.l), 10 km to the west of the litter trap site. The standard deviation was calculated from the 12 litter traps at Creek Pernod.

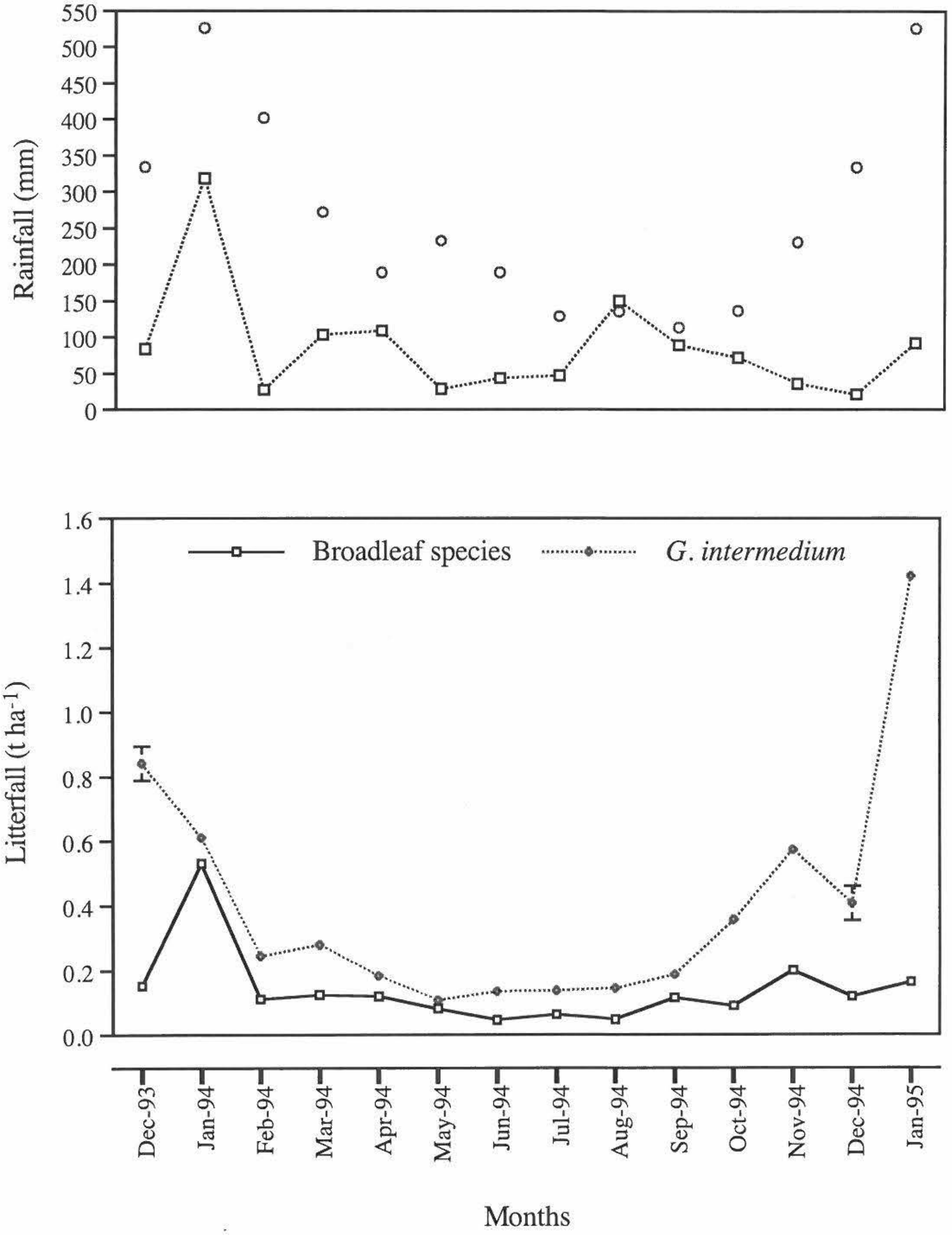


Figure 6.4 Mean monthly rainfall (1986 to 1994; circle), monthly rainfall (top) and total monthly litterfall of *Gymnostoma intermedium* ± 1 s.d and other species in forest ± 1 s.d (bottom) at Kouaoua from December 1993 to January 1995. Rainfall values are from Mt Reve (765 m a.s.l), 2 km to the south west of the littertrap site.The standard deviation was calculated from the 12 litter traps at Kouaoua.

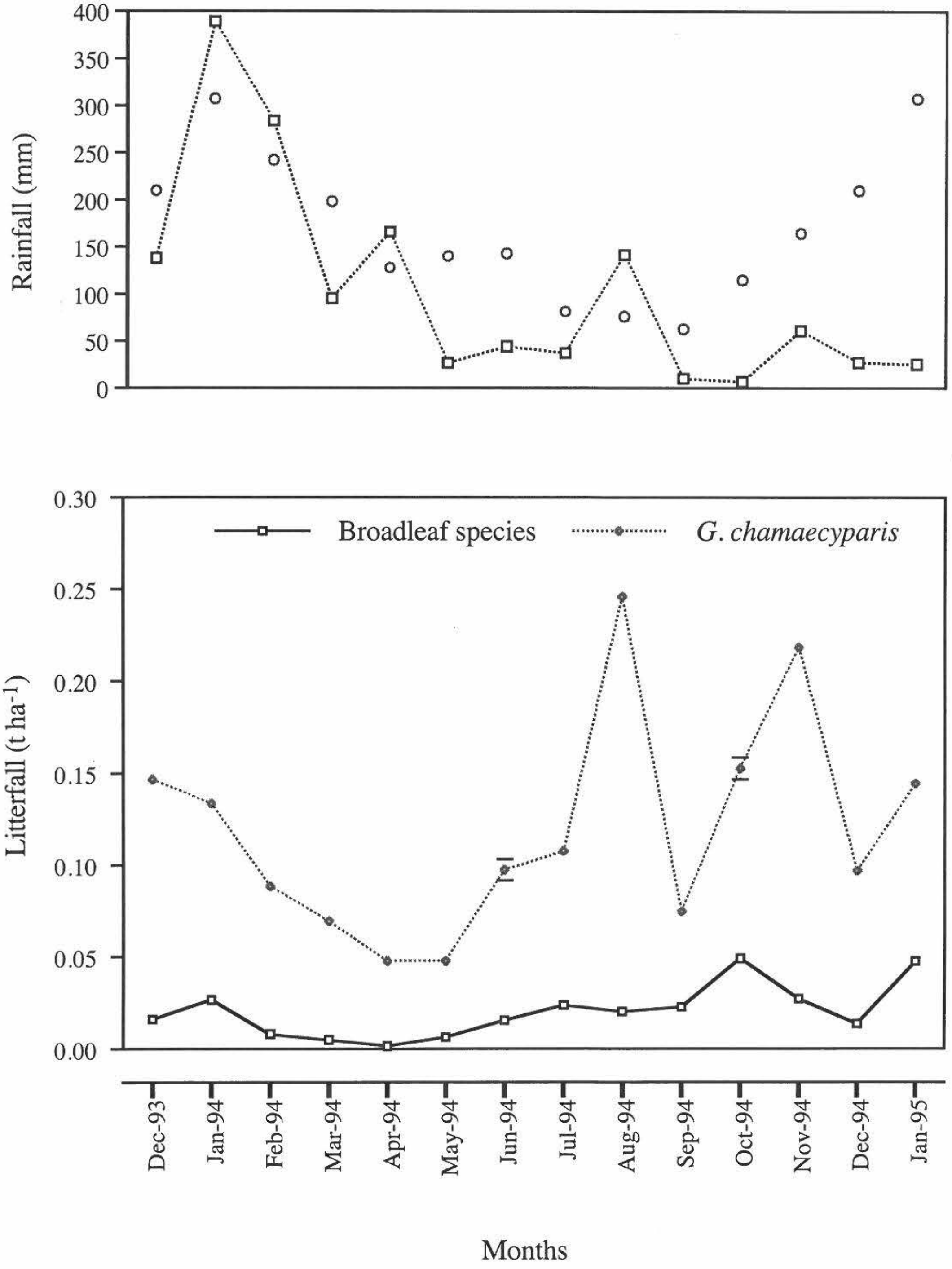


Figure 6.5 Mean monthly rainfall (Kouaoua village, 1983-1992; 2 m a.s.l; circle), monthly rainfall (top) and total monthly litterfall of *Gymnostoma chamaecyparis* ± 1 s.d and other species in tall maquis ± 1 s.d (bottom) at Kouaoua, from December 1993 to January 1995. Monthly rainfall values are from an ORSTOM rainfall station (Kou 1, 200 m a.s.l), 1km to the north of the littertrap site. The standard deviation was calculated from the 12 litter traps on serpentinite at Kouaoua.

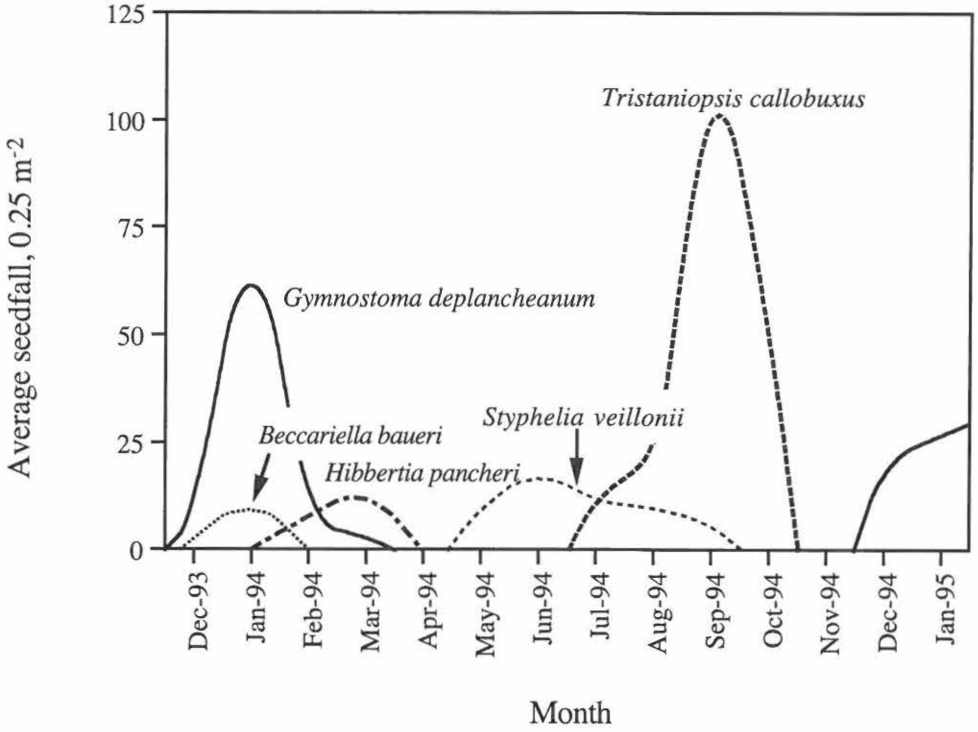


Figure 6.6 Trends in average monthly seedfall for species recovered from litter traps in tall maquis at Plaines des Lacs (Creek Pernod).

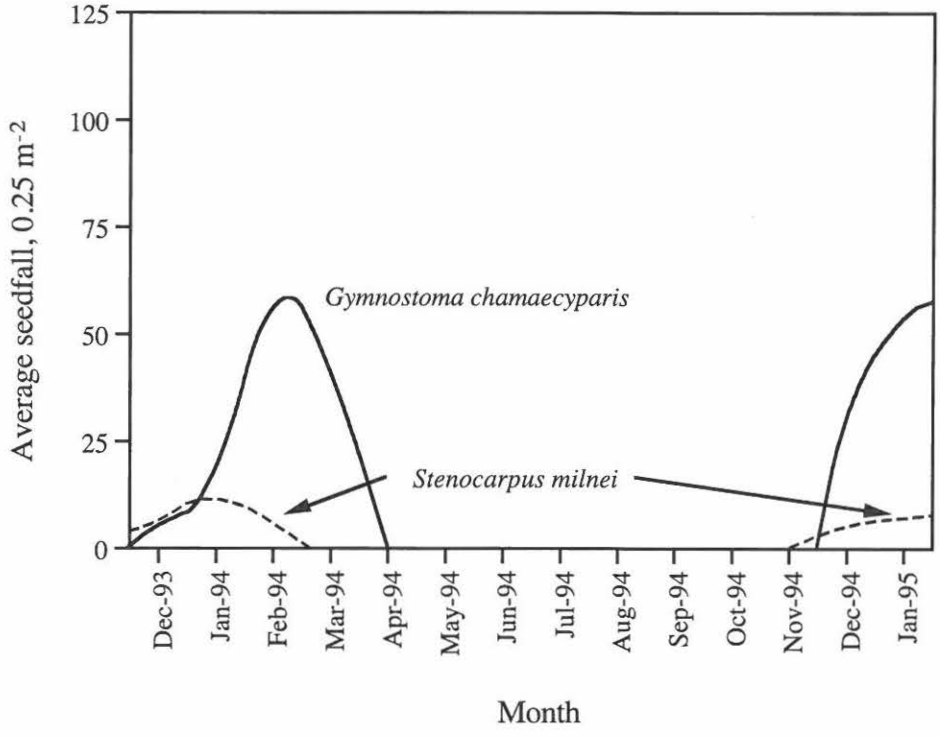


Figure 6.7 Trends in monthly average monthly seedfall for species recovered from litter traps in tall maquis on hypermagnesian soil at Kouaoua.

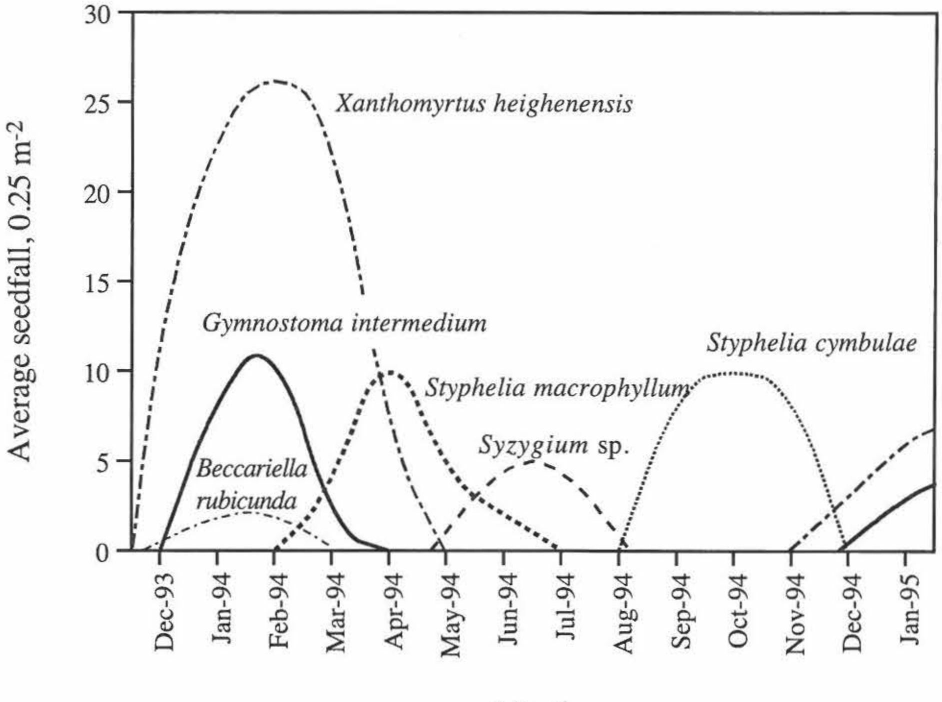


Figure 6.8 Trends in average monthly seedfall for species recovered from litter traps in forest on eroded oxisol at Kouaoua.

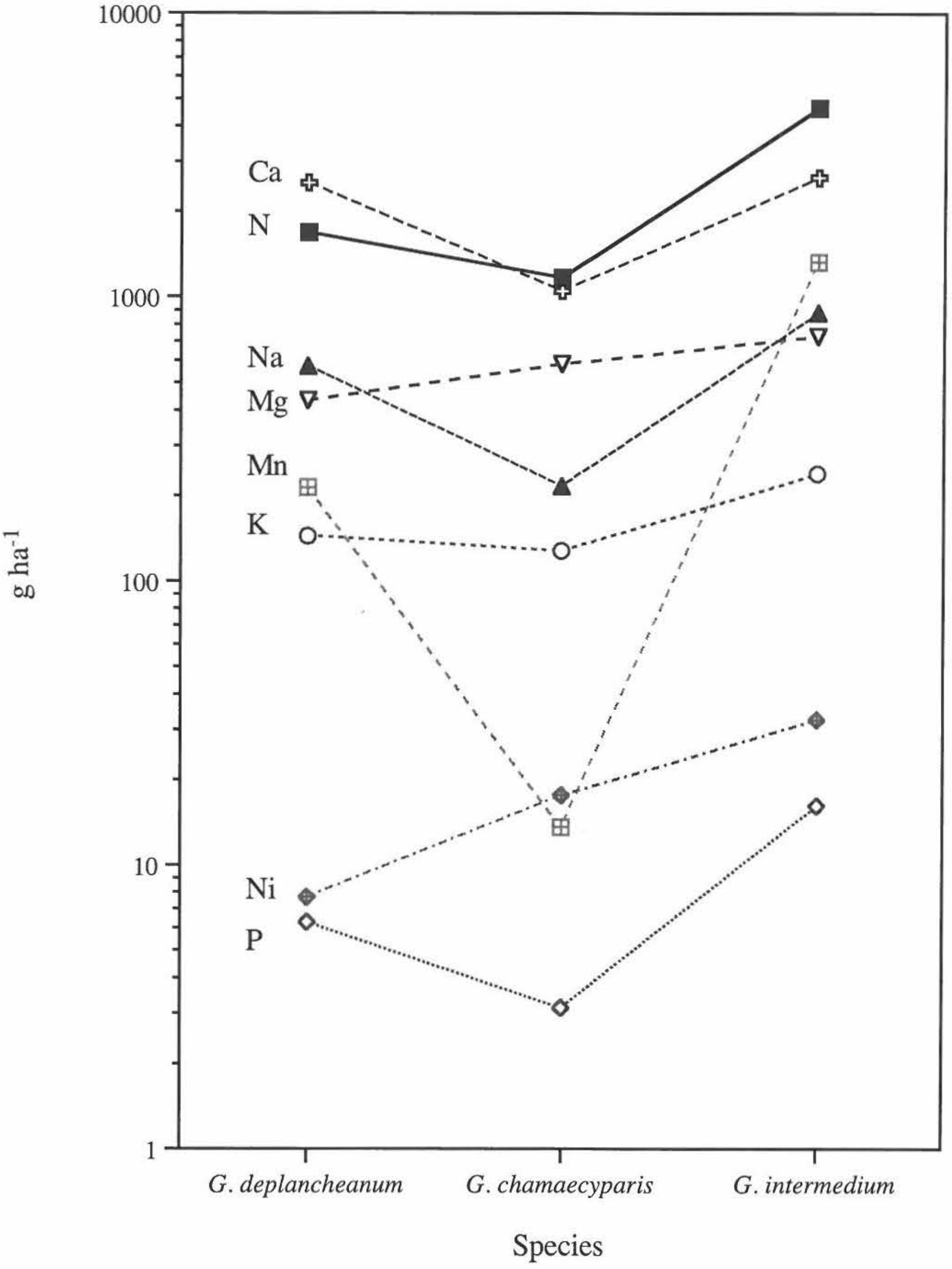


Figure 6.9 Average monthly foliar nutrient and metal content of *Gymnostoma deplancheanum*, *G chamaecyparis* and *G. intermedium* cladode litterfall.

6.2.2.4 Litter breakdown

Results of *Gymnostoma deplancheanum* cladode and *Arillastrum gummiferum* leaf weight loss from bags measured over the 7 month period are given in fig. 6.10. Regression indicated that the weight of foliar material showed a significant decline over the 7 month period ($F = 65.05$; $p < 0.0001$), but showed no significant difference between cladode and leaf breakdown or forest. However, *Arillastrum* appears to breakdown slightly faster than *Gymnostoma*. Qualitative measures of fungal hyphae cover on *Gymnostoma* cladodes (fig. 6.11) show that about 75% of cladodes in bags were covered by hyphae after 7 months. Qualitative measures of *Arillastrum* leaf area decay indicate that few bags contained intact leaves after 7 months.

Assuming that there is a constant exponential decay of litter, *Arillastrum* leaves are 50% decayed after 2 years and *Gymnostoma* cladodes after 2.7 years.

6.2.2.5 Annual net biomass production (NPP) of ecosystems at Plaines des Lacs

Several patterns emerge from estimates of NPP of communities at Plaines des Lacs (fig. 6.12). Annual NPP is very low ($\approx$ 0.5 t ha yr^{-1}) in open maquis but rises in tall maquis stands ($\approx$ 3.4 t ha yr^{-1}) with the establishment of an abundant canopy of *Gymnostoma deplancheanum* trees that generates not only a major increase in standing biomass production but also litterfall (2.86 t ha yr^{-1}). Forest communities show lower levels of standing biomass production ($\approx$ 1.6 t ha yr^{-1}), but remain very productive in terms of litterfall ($\approx$ 8.6 t ha yr^{-1}). Annual standing biomass rainforest ($\approx$ 1.2 t ha yr^{-1}) on eroded oxisol is similar to forest on iron crust, but produces much less annual litterfall ($\approx$ 5.3 t ha yr^{-1}) due to the near absence of *Gymnostoma* which is replaced by rainforest tree species.

6.2.2.6 Nitrogen balance of plant communities at Plaines des Lacs

Figure 6.13 illustrates the nitrogen balance model for ecosystems at Plaines des Lacs. The model gives a good fit to the soil nitrogen content in the open and tall maquis stages but a low estimate for the forest stage. This may be because (i) the estimates of soil nitrogen content are very variable, (ii) the forest stages takes more than 120 years to develop. Also, (iii) the

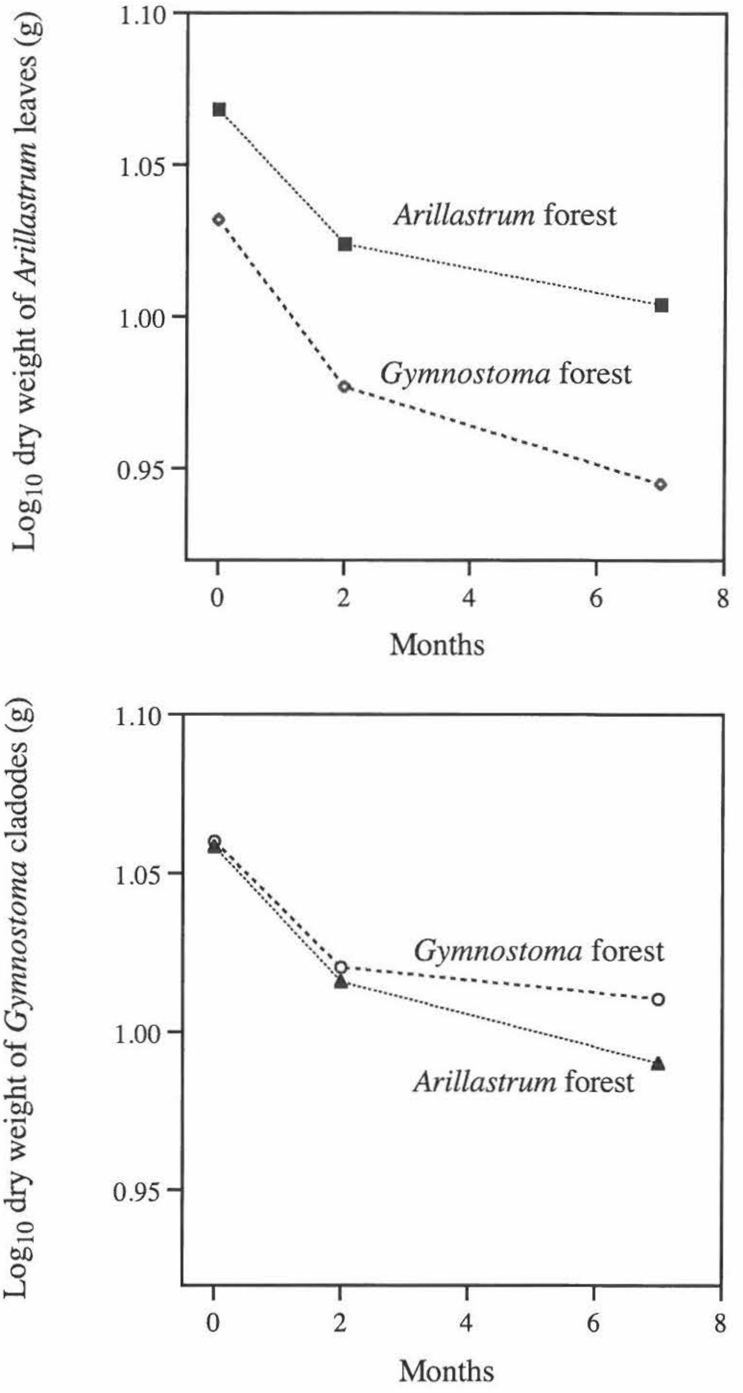


Figure 6.10 Mean log$_{10}$ dry weights of 48 samples of bagged *Arillastrum gummiferum* leaves (top) and 48 samples of bagged *Gymnostoma deplancheanum* cladodes (bottom) removed from forest at Prony dominated either by *Arillastrum* or *Gymnostoma* after 2 and 7 months.

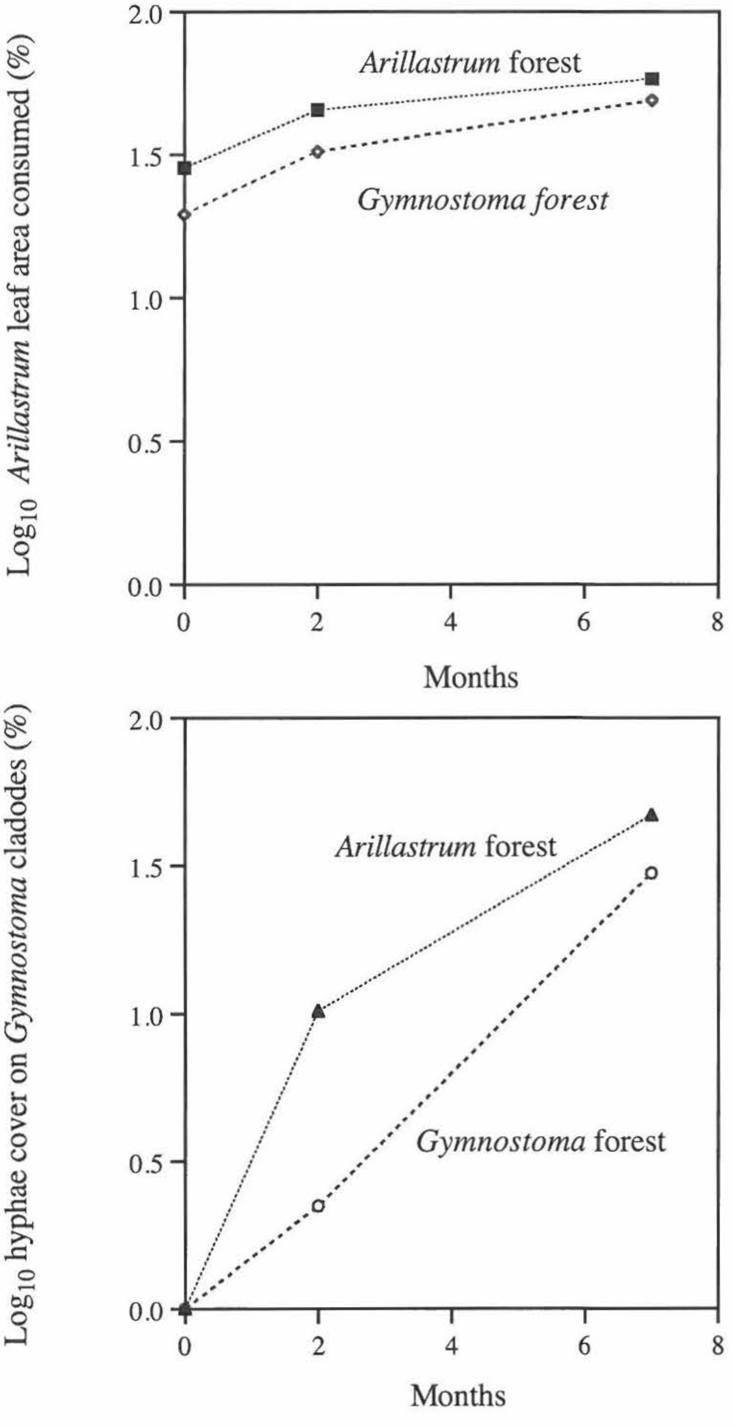


Figure 6.11 (top) Log$_{10}$ percentage of *Arillastrum gummiferum* leaf area consumed and (bottom) log$_{10}$ percentage of fungal hyphae covering on *Gymnostoma deplancheanum* cladodes in forest at Prony after 2 and 7 months.

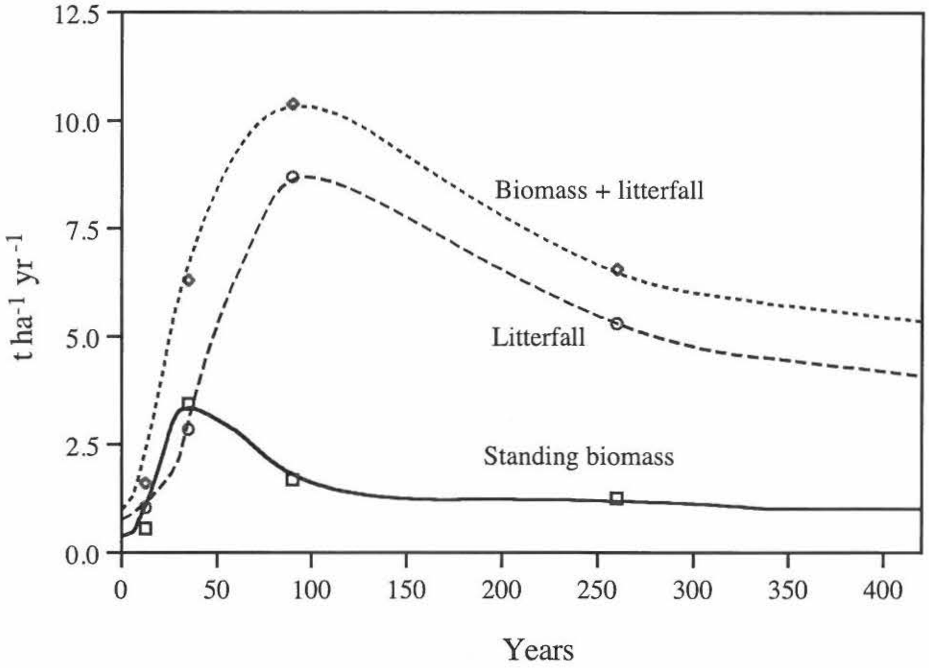


Figure 6.12 Estimated annual net primary productivity of successional communities at Plaines des Lacs. Fitted lines give trends.

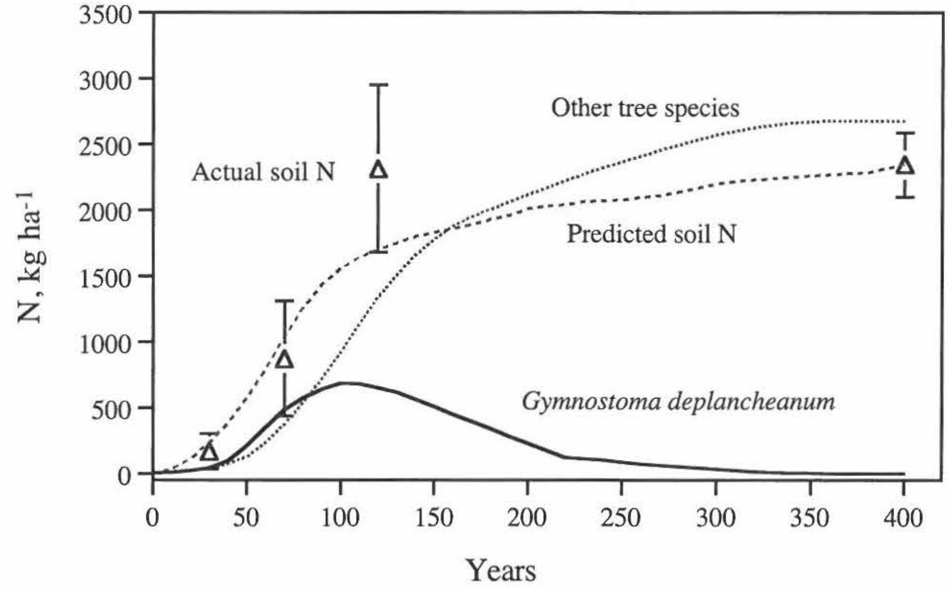


Figure 6.13 The predicted nitrogen content of soil, all tree species and *Gymnostoma deplancheanum* alone, in successional communities at Plaines des Lacs based on the nitrogen balance model estimated from net nitrogen inputs from *G. deplancheanum* and free living N fixation + hydrological sources. Actual median N concentrations (± 2 s.e.d) are given for soil underneath maquis, forest and rainforest communities. Note that the values for trees were fitted to the observed data and thus show observed trends.

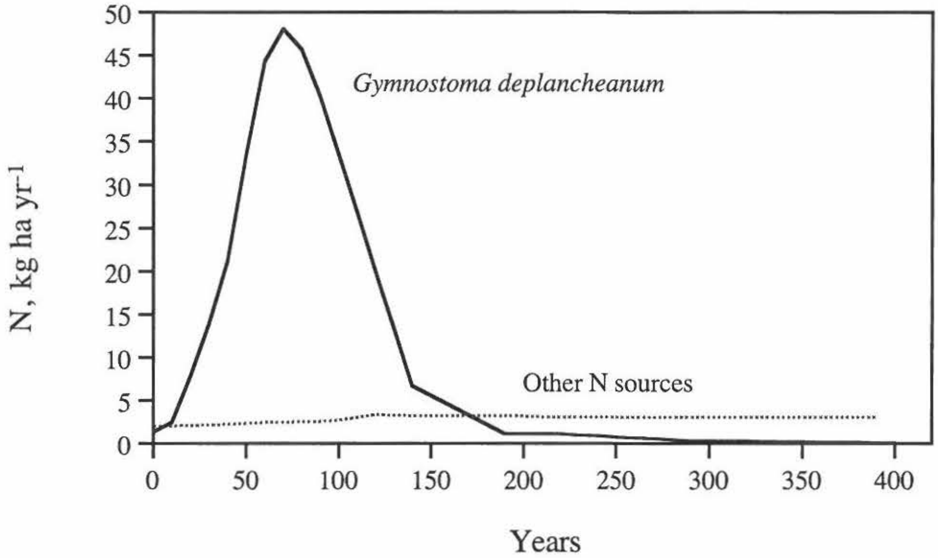


Figure 6.14 Estimated annual net nitrogen fixation of the *Gymnostoma deplancheanum / Frankia* association and other sources of nitrogen (non -associative fixation, rainfall). Estimated net annual nitrogen fixation yield of *G. deplancheanum* assumes that rates of N fixation are proportional to *Gymnostoma* annual litterfall.

model does not include denitrification which probably causes losses of nitrogen from the ecosystem.

The estimated net N inputs from *Gymnostoma/Frankia,* rain and free living bacteria (fig. 6.14) suggests that the *Gymnostoma/Frankia* association is responsible for 76% of the nitrogen entering the ecosystem over the first 400 years. This initial pulse of N over the first 200 years may supply much of the nitrogen in the ecosystem for the following centuries.

6.3 Patterns of seedfall and regeneration in maquis and forest

Tall maquis on iron crust at Plaines des Lacs and on hypermagnesian soil at Kouaoua is often dominated by *Gymnostoma* trees and often contains very few understorey species (Jaffré *et al,* 1994 b). The objective of field surveys was to compare seedling recruitment with adult populations and annual seedfall collected from litter traps in tall maquis and forest at Kouaoua and Plaines des Lacs. Differences between seedfall and the abundance of seedling of species can give an indication of the suitability of understorey environments for seedling recruitment.

6.3.1 Methods

Surveys of understorey seedling and adult abundance were conducted in tall maquis on iron crust at Plaines des Lacs, in tall maquis on hypermagnesian soil and in forest on eroded oxisol at Kouaoua. Ten 4 m^2 quadrats were established at 5 m intervals along two transects containing litter traps so that comparisons could be made between understorey composition and seedfall. Records were made of height and number of individuals of species found in each quadrat. The amount of seedfall over the 40 m^2 area at each site was estimated from litter traps (6.2.1.4).

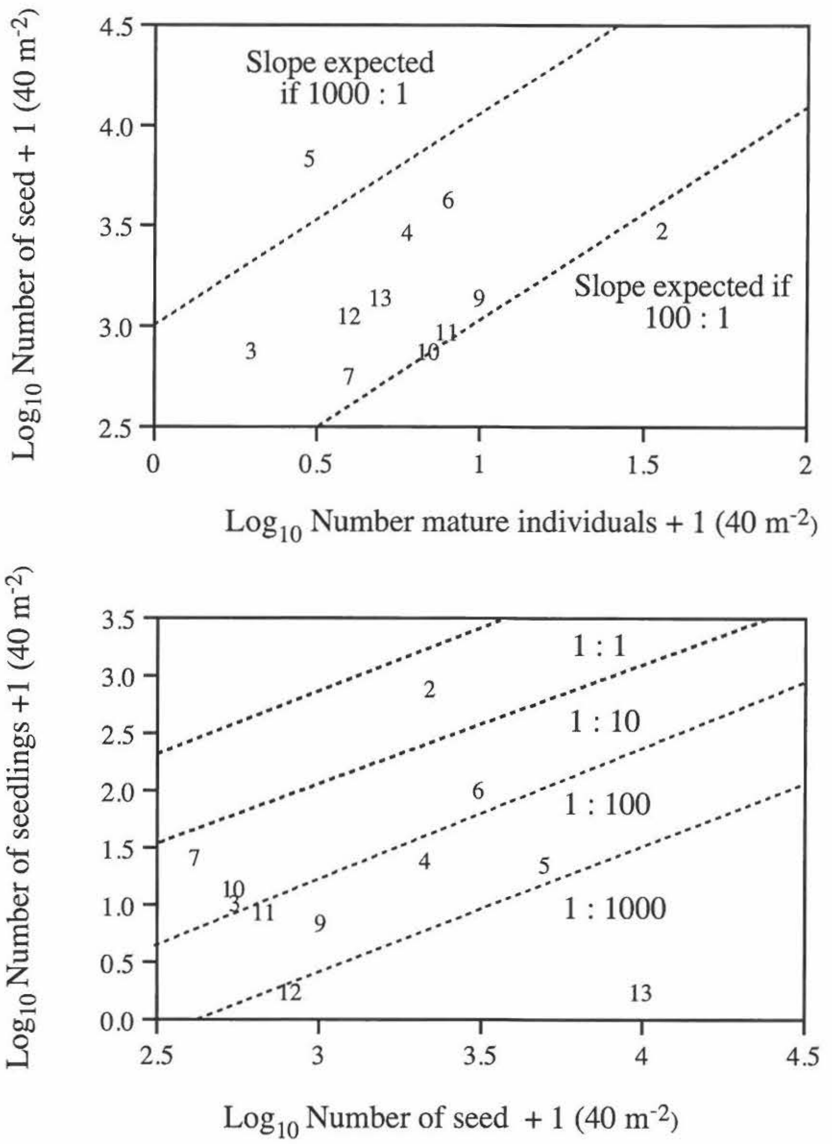
Multiple linear regression (SAS institute software JMP ® version 3) was used to test whether $\log_{10}$ seed fall + 1 varied with (i) the $\log_{10}$ number of adults + 1 and (ii) to test whether $\log_{10}$ number of seedlings + 1 for species recorded from underneath litter traps varied with $\log_{10}$ seed fall + 1.

6.3.2 Results

Several patterns emerge between measures of seedling abundance, adults populations and seedfall for species recorded from litter traps (fig. 6.15). There was a weak positive correlation between seed fall and the number of mature plants of each species ($r^2 = 0.29$; F-ratio = 4.64; $p < 0.05$) as might be expected, which suggests that seedfall varies with the size of the mature plant population. *Gymnostoma deplancheanum* is the most abundant tree species recorded from all three surveys and may release up to 2200 seeds per year over a 40 m^2 area. In contrast, animal dispersed species such as *Beccariella baueri*, *B. rubicunda* and *Hibbertia pancheri* are represented by only isolated mature trees that produce fewer seed. Multiple linear regression revealed no significant trend between seed fall and seedling abundance ($r^2 = 0.02$; F-ratio = 0.22; $p = 0.64$) at all three sites. Seed : seedling ratios suggest that the major factor is very great variation in establishment rates between species. Tree species that are abundant in the canopy of tall maquis such as *Gymnostoma deplancheanum* and *G. chamaecyparis* show high levels of regeneration in the understorey which suggests that both species have been favoured by a regeneration history that is very productive in terms of annual seedfall. Most of the other plant species, with the exception of *Beccariella rubicunda*, show poor seedling regeneration that may have arisen because they produce few seed which are poorly dispersed, are absent in seed banks or are excluded by environmental conditions that are unsuitable for establishment. Poor regeneration by many species may also have arisen because seedfall was heavily predated. Moreover, seed or seedlings might be excluded either by allelochemicals produced through slow litter decay of *Gymnostoma* cladodes or the physical depth of litter.

6.4 Effects of Gymnostoma leachates on plant growth

The aim of this study was to test whether cladode litter leachates of *Gymnostoma deplancheanum*, *G. chamaecyparis* and *G. intermedium* have an allelopathic effect on ultramafic maquis species under controlled conditions.



Tall maquis on iron crust

1. *Beccariella baueri*
2. *Gymnostoma deplancheanum*
3. *Hibbertia pancheri*
4. *Styphelia veillonii*
5. *Tristaniopsis callobuxus*

Tall maquis on hypermagnesian soil

6. *Gymnostoma chamaecyparis*
7. *Stenocarpus milnei*

Forest on eroded oxisol

8. *Beccariella rubicunda*
9. *Gymnostoma intermedium*
10. *Cunonia veillardii*
11. *Styphelia macrophyllum*
12. *Styphelia cymbulae*
13. *Xanthomyrtus heighenensis*

Figure 6.15 Log$_{10}$ number of seed plotted +1 against log$_{10}$ number of mature individuals +1 (top), and the log$_{10}$ number of seedlings +1 plotted against the log$_{10}$ number of seed +1 (bottom) for species recorded from litterfall traps and the understorey survey at Plaines des Lacs and Kouaoua. Fitted splines show trends.

6.4.1 Methods

Gymnostoma deplancheanum, G. chamaecyparis and *G. intermedium* cladodes were collected from branches that had been cut and allowed to dry for one month. The cladodes were then hand sorted to remove other material. The technique used to extract leachates consisted of placing 25 g of cladodes for weekly periods in a 1.25 liter polyethylene plastic funnel with mesh to prevent litter falling through. The base of the funnel was placed flush with the soil at the middle of each pot (fig. 6.16). Bottles containing either litter or no litter (control) were watered with 50-70 ml of tap water twice daily for 30 seconds by mist jets connected to an automatic watering system.

The soil medium used in this experiment consisted of mixture of 3.5 kg of non-ultramafic alluvial soil (Eutric fluvisol: Latham *et al,* 1978) and 1.5 kg of coarse river sand that had been sieved (5 mm), thoroughly homogenised and placed into 5 liter pots. Non-ultramafic soil was used to provide better nutrient conditions for growth. The outside of pots were painted white to reduce soil heating caused by high solar radiation (Bonzon, pers. comm) Air temperature in the glasshouse at ORSTOM Nouméa from August to November 1993 varied between 24 to 42°C. Relative humidity in the glasshouse varied from 90 to 50% (day/night) and the photoperiod from 12 to 13 hours.

The design of the experiment consisted of four treatments (3 *Gymnostoma* species leachates and a control) that were applied to six species: *Gymnostoma deplancheanum, G. chamaecyparis, G. intermedium, Carpolepis laurifolia* (Myrtaceae), *Grevillea exul* var. *rubiginosa* (Proteaceae) and *Austrobuxus carunculatus* (Euphorbiaceae) replicated three times (refer to 7.1). Blocks containing one replicate of each species/treatment were randomly allocated to different parts of the glasshouse. Each pot contained 4 one year old seedlings that had been evenly spaced around the funnel containing the treatment. All seedlings were grown prior to experiment in a soil mixture containing 2/3 eroded oxisol 1/3 coarse river sand.

Measures of stem height, the number of leaves, maximum root length, the number of primary roots and the number of proteoid roots (for *Grevillea*) were carried out prior to placing seedlings in pots and at the end of the experiment after 4 months. Roots, stems and leaves of harvested plants were oven dried at 105°C for 24 hours and weighed.

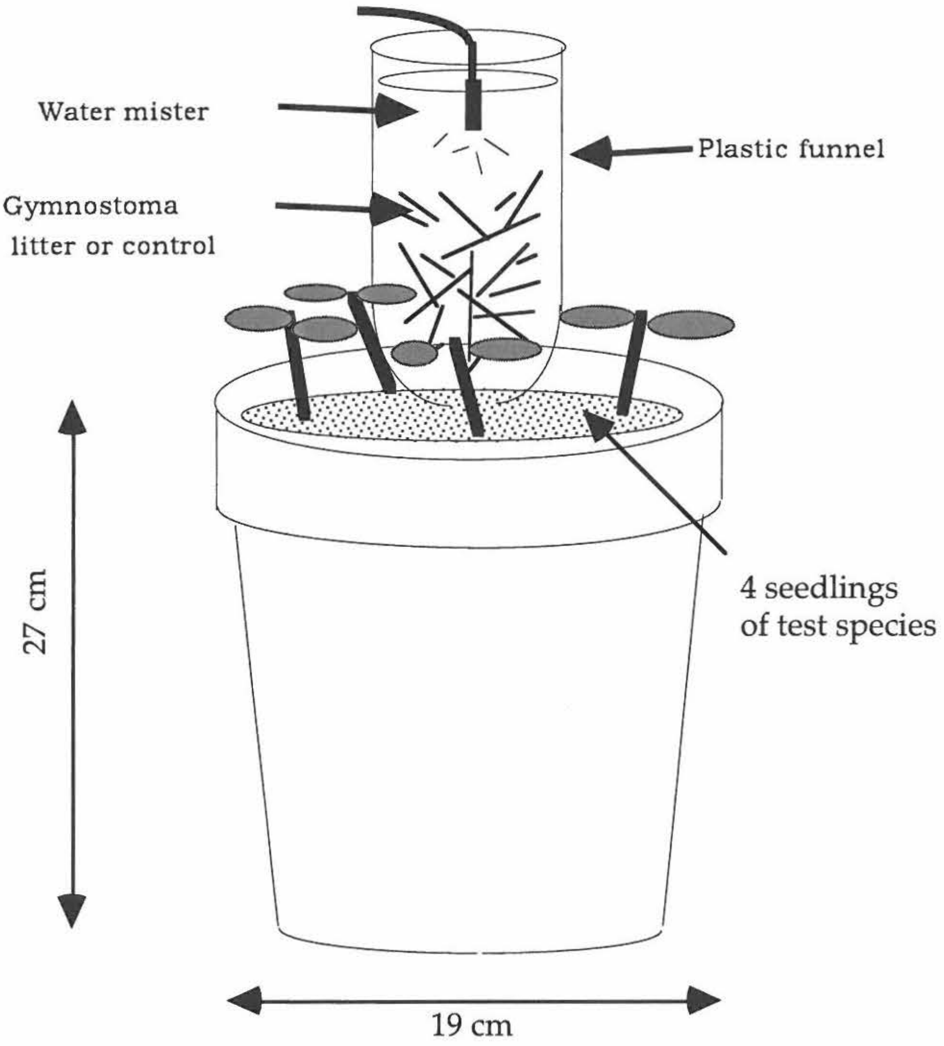


Figure 6.16 Diagram of litter leachate experiment showing litter inside receptacle with the mist system on top and the placement of plants around the litter treatment.

6.4.1.1 Statistical analysis

Measures of the four plants in each pot were averaged at the beginning and end of the experiment. Common log transformation ($\log_{10}$) was carried out prior to ANOVA analysis on stem and root growth, final height and total plant dry weight so as to achieve normality of the residual error and to homogenise variance. Relative stem growth (cm) and relative root growth (cm) were calculated by subtracting $\log_{10}$ (initial measure) from $\log_{10}$ (final measure) over the time period. ANOVA (SAS institute software JMP ® version 3) was used to test whether there were significant species effects and treatment effects at the pot level in terms of $\log_{10}$ relative stem and root growth, $\log_{10}$ final height, $\log_{10}$ total plant dry weight, final number of leaves, number of proteoid root clusters.

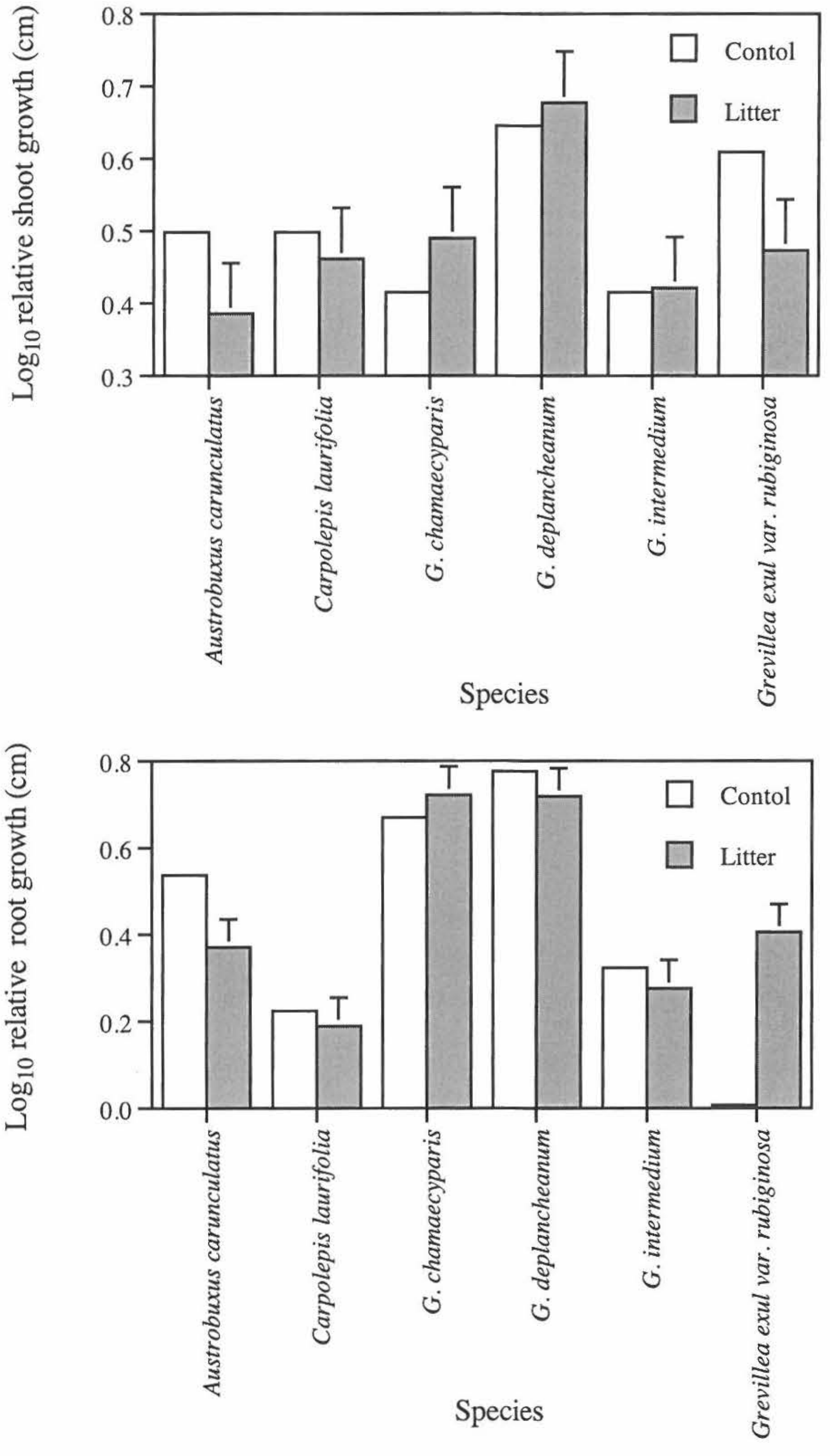


Figure 6.17 Log$_{10}$ relative shoot growth (top) and log$_{10}$ relative root growth (bottom) for test species ± 1 s.e.d, subject to either a litter leachate treatment or a control treatment (water).

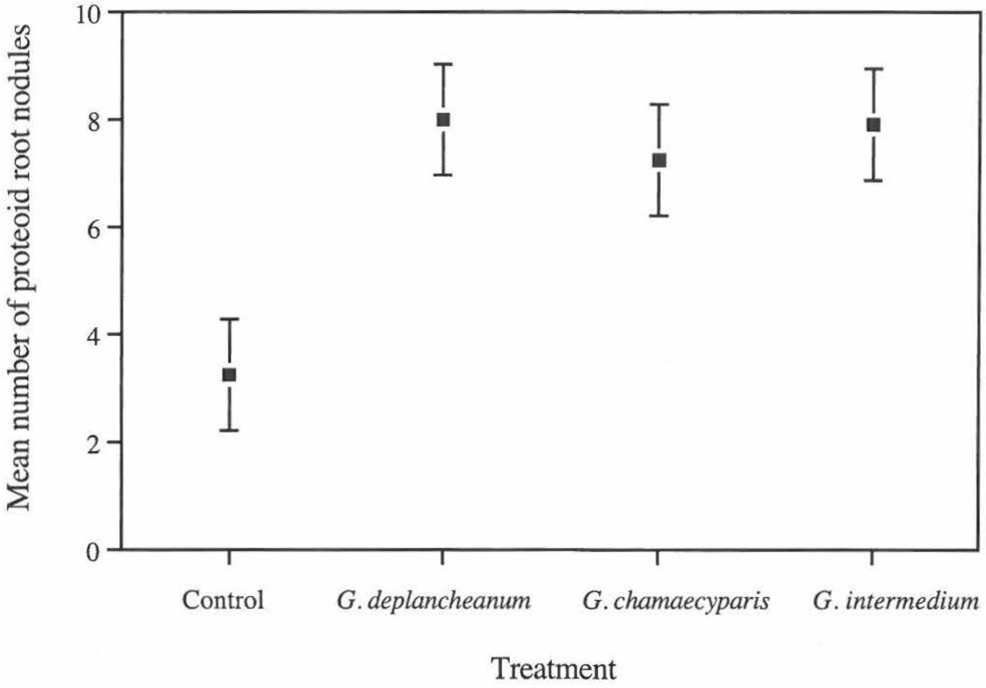


Figure 6.18 Mean number of proteoid root clusters (± 2 s.e.d) on *Grevillea exul* var. *rubiginosa* seedlings harvested after 4 months from the control and three *Gymnostoma* species litter treatments.

6.4.2 Results

Analysis of variance indicated a significant difference in growth between species in terms of $\log_{10}$ relative stem and root growth, $\log_{10}$ final height, $\log_{10}$ total plant dry weight and final number of leaves. However, the ANOVA was unable to show any differences between treatments in terms of plant growth measures which suggests that *Gymnostoma* litter leachates are unlikely to cause an allelopathic reduction in growth. Log_{10} relative shoot and primary root growth for each species are presented in fig 6.18. One unexpected pattern to emerge is that *Grevillea* seedlings grown in pots containing a litter treatment showed a significant increase ($r^2 = 0.24$; F-ratio = 4.75; $p < 0.0059$) in proteoid root cluster numbers compared to control pots (fig. 6.18). This suggests that litter may provide an important source of either proteoid root forming bacteria or nutrients for proteoid roots.

6.5 Physical effects of litter on seed and seedling establishment[†]

Gymnostoma produces most of the litter in tall maquis and forest formations. This litter may attain depths of 15-20 cm, but averages 3-7 cm. Establishment of seed may be hindered in deep litter beds because *Gymnostoma* cladodes form a barrier to seed penetration and create aerated dry conditions for seed germinating on the surface. The objectives of this glasshouse experiment were to address several questions. (i) Does *Gymnostoma* litter impede seed or germinants from gaining contact with mineral soil? (ii) Are seedlings able to penetrate upwards through litter? (iii) Does litter increase survival rates of seedlings under water stressed conditions?

6.5.1 Methods

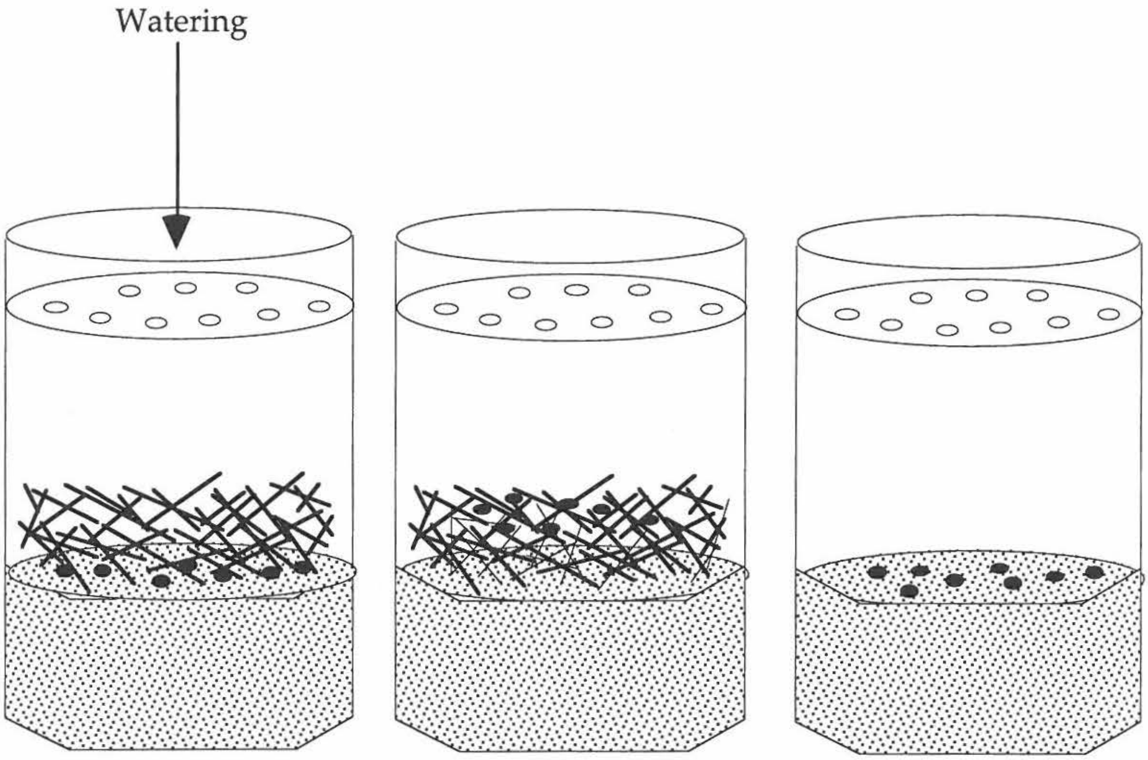
The experiment consisted of three litter treatments crossed by two watering regimes applied to seed of six maquis species, with three replicates of each in a different block in the glasshouse. Test species were selected to represent a range of seed sizes. Seed size was calculating from measures of seed length and width. *Dodonaea viscosa* (Sapindaceae) posses the smallest seed which weigh on average 1.5 mg for an area of 4 mm^2. *Acacia spirorbis*

[†] Physical effects of litter published as McCoy *et al* (1995).

(Mimosaceae) seed is much larger (16 mm^2) and weighed 30 mg. The average weight and size of *Gymnostoma deplancheanum* (Casuarinaceae), *Alphitonia neocaledonica* (Rhamnaceae), *Grevillea exul* var. *rubiginosa* (Proteaceae) and *Beccariella baueri* (Sapotaceae) seed are given in table 4.6. Fresh seed was collected in November 1994. Techniques used to separate seed from fruit are given in chapter 4 for the germination experiment at Prony. Seed of *Acacia* and *Alphitonia* was placed in boiling water and allowed to cool to break the seed dormancy.

The three treatments consisted of 20 seed of a species placed either (i) on the surface of *Gymnostoma* litter, or (ii) at the base of litter or (iii) on bare soil (fig. 6.19). *Gymnostoma deplancheanum* litter used in treatments was collected at Creek Pernod and allowed to air dry under shelter for one month prior to the glasshouse experiment which ran from November 1994 to February 1995 at ORSTOM Noumea. A 5 cm depth (50 g) was selected for the litter treatment as being typical of natural conditions (chapter 3). Branches and seed pods were removed and the litter was shaken over a 5 mm sieve to remove any seed. Iron crust oxisol gravel was used as the soil media in order to obtain moisture and nutrient regimes similar to those experienced by test species under natural conditions. Chemical and physical properties of this substrate are given in table 2.2. Oxisol gravel oven dried at 105°C to standardise the moisture content across the experiment and was sieved through a 5 mm mesh sieve to remove large aggregates, and 550 g was placed into a 1 liter clear plastic pot.

All treatments were subject to either daily watering or water stressed conditions. The daily watering regime was by a mister in each pot connected to an automatic system that watered twice daily for 20 seconds (50-60 ml). A pilot experiment was carried out for the water stressed treatment to determine the time taken for treatments to reach 1/3 moisture capacity. The pilot experiment consisted of watering 25 five pots containing soil and litter and 25 pots containing soil until water poured through the base of the pot (reached with 100 ml of water). The saturated pots were then weighed at intervals to determine moisture weight loss over a period of 144 hours (fig. 6.20). Pots containing just soil reached a 1/3 soil moisture level after 72 hours. Weight loss was much slower for pots containing soil and litter because litter reduced surface evaporation and absorbed water. Pots containing litter were watered with less water (50 ml/72 hours) than the bare soil treatment (100 ml/72 hours). Clear plastic discs with holes < 2 mm were placed on top of water stressed pots during manual watering to simulate rainfall conditions.



Seed below litter Seed on litter Seed on bare soil

Figure 6.19 Schematic drawing of seed placement in relation to litter and soil.

Records were made each week of the number of visible shoots and the height of established seedlings in each pot over a 4 month period. For treatments containing seed below the litter, records of germinations were made if seedlings were visible through the litter from either the side or the top of the clear plastic pot. Records were made at the end of the experiment of the total number of seed that had germinated, the total number of seedlings that had died, and the stem height and root length of each seedling.

6.5.1.1 Statistical analysis

Angular transformation (arc sine root) was carried out on the proportion of germinations at the end of the experiment to normalise residual errors. ANOVA was carried out using Genstat 5 to identify the differences in proportion of germinations within and between species for the different treatments and water regimes. Measures of final seedling

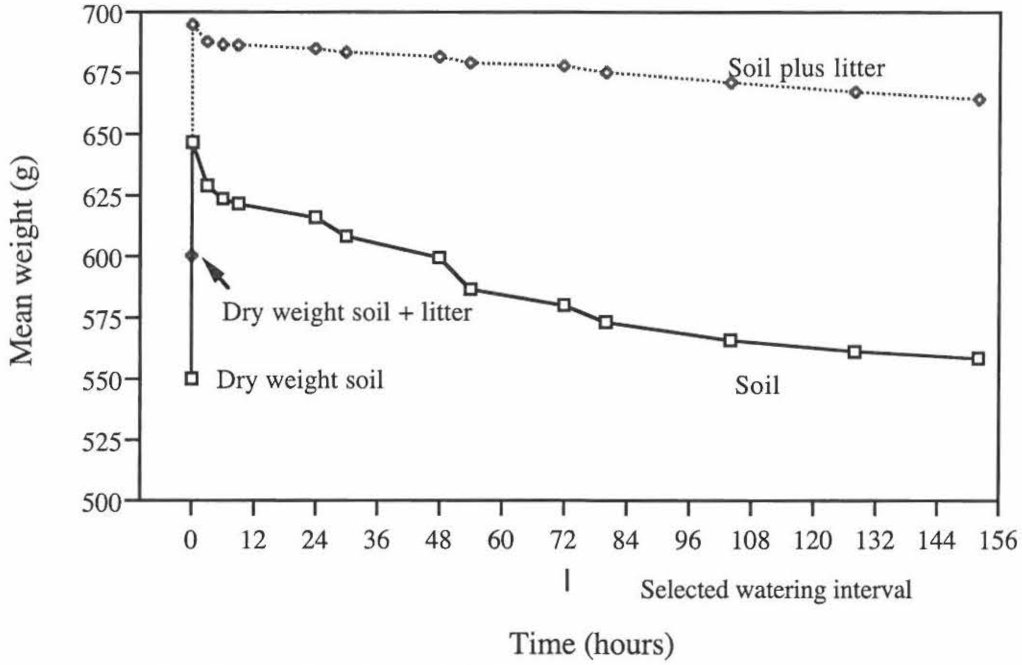


Figure 6.20 Loss of weight with time of the saturated iron crust oxisol gravel treatment and the iron crust oxisol gravel with litter treatment under glasshouse conditions (n = 25).

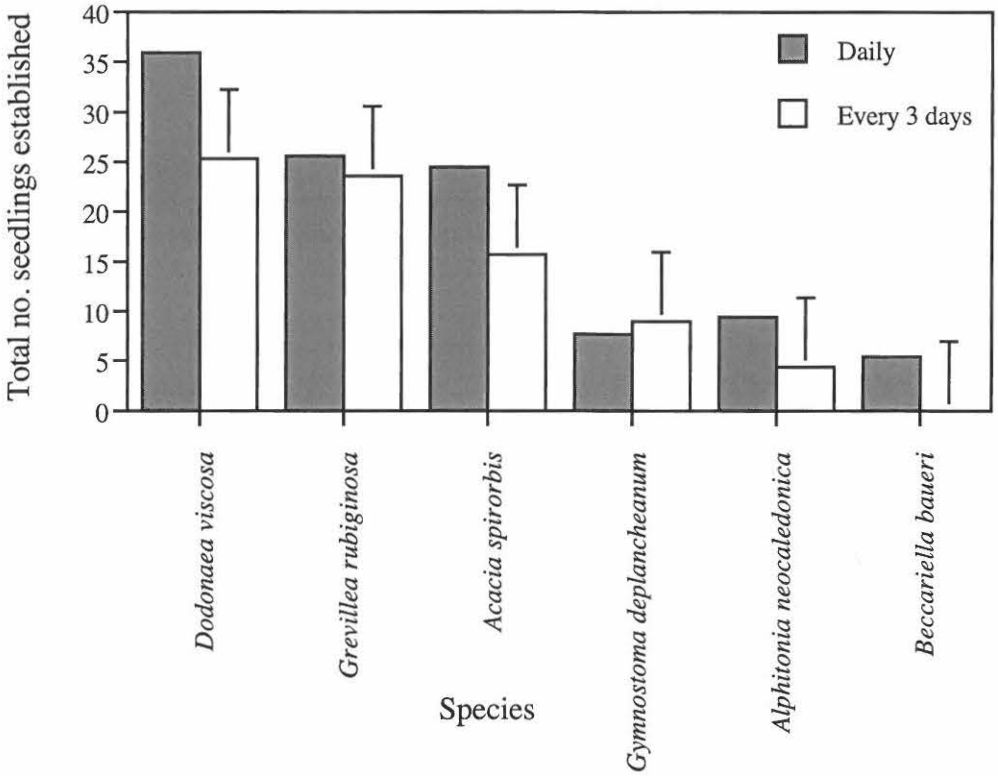


Figure 6.21 Total number of germinants (± 1 s.e.d) at the end of the experiment for each test species subject to either daily or 3 daily watering.

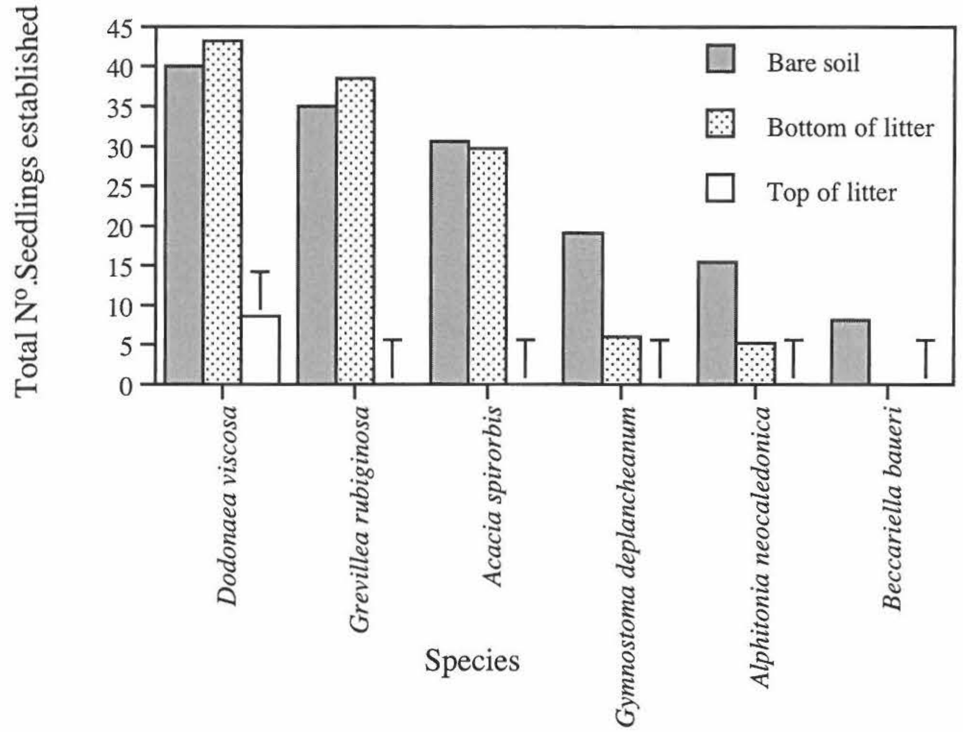


Figure 6.22 Total number of seeds (± 1 s.e.d) of each species which germinated on bare soil, below litter and on top of litter during the experiment. Treatment values which are greater than twice the s.e.d are significant at the 95 % confidence level.

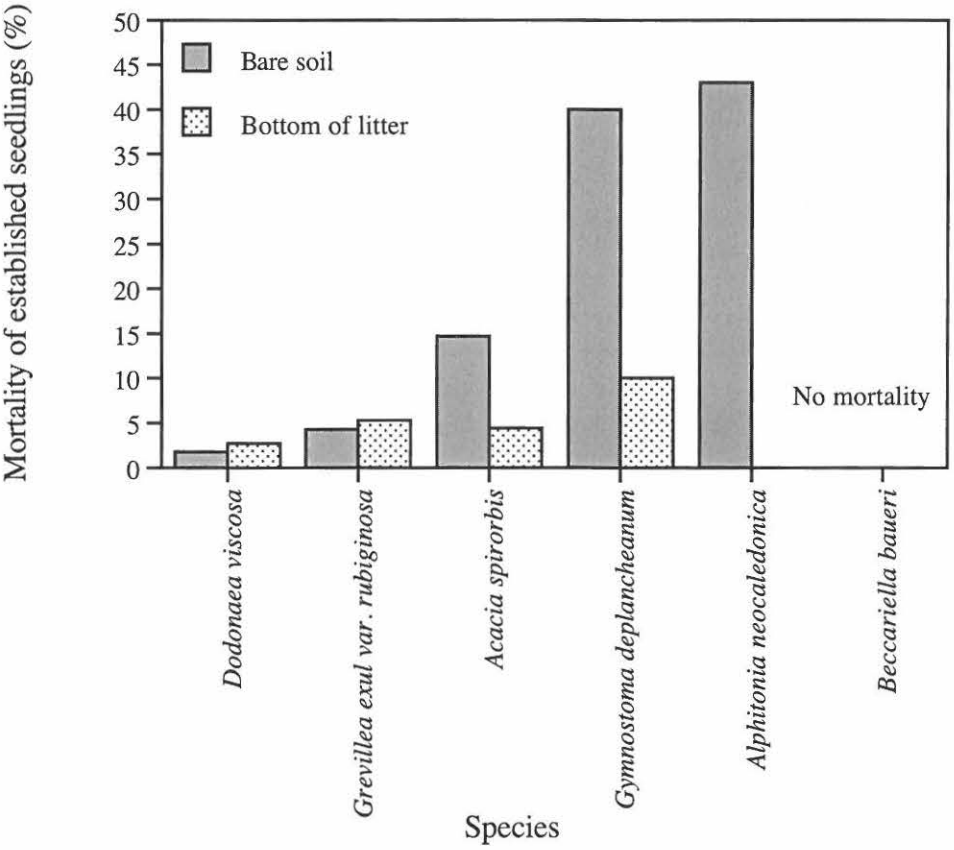


Figure 6.23 Percentage of seedling mortality for each species during the experiment for bare soil and seed at the bottom of litter treatments.

height across the three treatments were examined by REML (Restricted maximum likelihood estimation) variance components analysis to reveal if there were any different in growth (measured as height) between species for water regimes and treatments.

6.5.2 Results

6.5.2.1 Effects of treatments and water regimes on germination

ANOVA showed that seedling establishment was significantly different between species (F-ratio = 37.63; $p < 0.001$) and between treatments (F-ratio = 49.90; $p < 0.001$). The angular transformed proportion of germinations at the end of the experiment for each species for the three treatments is given in fig. 6.21. *Dodonaea* was the only species to establish from treatments where seed was placed on top of the litter. This arose because small *Dodonea* seed fell through the litter to the bare soil. In contrast, the large seed size of the other species limited their passage through the litter to the soil surface. The top of the litter dried under both water regimes and this probably affected seed or emerging seedlings on the litter surface.

ANOVA did not reveal a significant difference in the proportion of germinations between watering regimes. However, there is a slight trend which suggests that there were more germinations on treatments that were watered daily (fig. 6.22).

REML variance components analysis revealed a strong difference in the height of seedlings between species at the end of the experiment ($\chi^2 = 38.68$; $p < 0.01$) but did not show strong differences at the treatment or water regime level. Table 6.1 gives the mean height of seedlings for each species after 4 months.

Table 6.1. Mean seedling stem height after four months

Species	**Height (cm)**
Gymnostoma deplancheanum	2.6
Beccariella baueri	1.9
Alphitonia neocaledonica	3.1
Dodonaea viscosa	4.0
Grevillea exul var. *rubiginosa*	7.0
Acacia spirorbis	4.3

6.5.2.2 Established seedling mortality

Figure 6.23 gives the seedling mortality of each species at the end of the experiment. These estimates are based on very small totals so they must be treated with caution. In general, the highest mortality was recorded for seedlings on bare soil treatments which suggests that litter may be beneficial to seedling survival by acting as a mulch. It also suggests that allelopathy may not play a role in seedling mortality. The species showing the highest mortality on bare soil are the pioneer species *Gymnostoma* and *Alphitonia* which naturally occur on disturbed substrates. Both of these species produce large amounts of seed.

6.6 Discussion

Surveys indicate that the standing biomass in successional communities on iron crust oxisol and hypermagnesian soil increase with time (fig. 6.1). Ages of maquis biomass development at Plaines des Lacs are reliable and correspond with fire events less than 100 years ago. Furthermore, the ages of fire events are consistent with counts of annual tree rings of mature *Dacrydium araucarioides* trees in these formations (fig 3.8). The age of forest and rainforest is less reliable because of the lack of physical evidence of fire in these formations. Estimates of standing biomass for forest and rainforest at Plaines des Lacs are high compared to many taller rainforests (Kellman, 1970; Uhl, 1978; Brown & Lugo, 1990), and are possibly overestimated by 20%. A 20% bias is also likely to be applicable to standing biomass estimates of maquis and calculations of annual net primary production (fig. 6.12) and N fixation rates by *Gymnostoma deplancheanum* (figs. 6.13 & 6.14). This overestimation of standing biomass possibly arose because this non-destructive method (Whittaker & Mark, 1975) assumed that all species had (i) a high wood density similar to *Gymnostoma* and *Arillastrum* and (ii) a linear relationship between height and diametre of stems.

6.6.1 Nutrient development in ultramafic communities

Biogeochemical cycles of elements may be classified into two major groups (i) those in which there is a gaseous phase (eg: N_2 and CO_2) and (ii) those in which the atmospheric component is limited to dust, and the soil component dominates. Elements are accumulated by plants from the atmosphere and soil and are stored or cycled depending on their availability

(Vitousek, 1984; Vitousek & Sanford, 1986; Bruijnzeel, 1989; Grubb, 1989; Brown & Lugo, 1990).

In the global context of tropical forests, ultramafic successional communities at Plaines des Lacs and Kouaoua fit in at the lower end of the range in terms nutrient availability because soils have low amounts of essential plant nutrients such as nitrogen, phosphorus and potassium (table 2.2). Furthermore they contain only trace amounts of calcium derived from pyroxene minerals in peridotite (Latham, 1986). Nutrient accumulation as biomass may be therefore largely dependent on atmospheric inputs.

Nitrogen is an important element in plant successional development because of its functional role in photosynthesis and plant growth (Reiner, 1981; Attiwill & Leeper, 1987). An important source of N is through atmospheric fixation by free living bacteria in soil or plant associations with nitrogen fixing prokaryote bacteria (eg: *Frankia, Rhizobium*) (Attiwill & Leeper, 1987; Danso *et al*, 1992). Fixation by these organisms results in the mineralisation of N_2 into NH_4 and NO_3 which are available for uptake in plants and contribute a major component of the standing biomass of communities along with carbon (Reiners, 1981; Attiwill & Leeper, 1987).

In the case of plant communities on iron crust and hypermagnesian soil, the rate of biomass accumulation is slow at early successional stages, and it takes 20-30 years for maquis communities to attain the same of level as 3-10 year old secondary tropical forests found on more fertile laterites or volcanic soils (fig. 6.24). However at later successional stages, rates of biomass accumulation are equivalent to many secondary forests and coincide with the development of a *Gymnostoma* tree canopy after 50-70 years. This pattern suggests that (i) low nitrogen availability may be limiting biomass development in early successional stages and (ii) that *Gymnostoma* performs a functional role in the development of successional communities by providing a major source of nitrogen through its biological fixation association with *Frankia* (Jaffré *et al*, 1994 b)

According to the nitrogen balance model (fig. 6.13), *Gymnostoma deplancheanum* contributes up to 76% of the nitrogen in successional communities at Plaines des Lacs. Rainfall may contribute up to 16% of net nitrogen in biomass and free living sources may contribute up to 8%. The model indicates that net nitrogen fixation by *Gymnostoma* peaks at approximately 43 kg ha yr^{-1} in 70 year old stands and then shows a decline

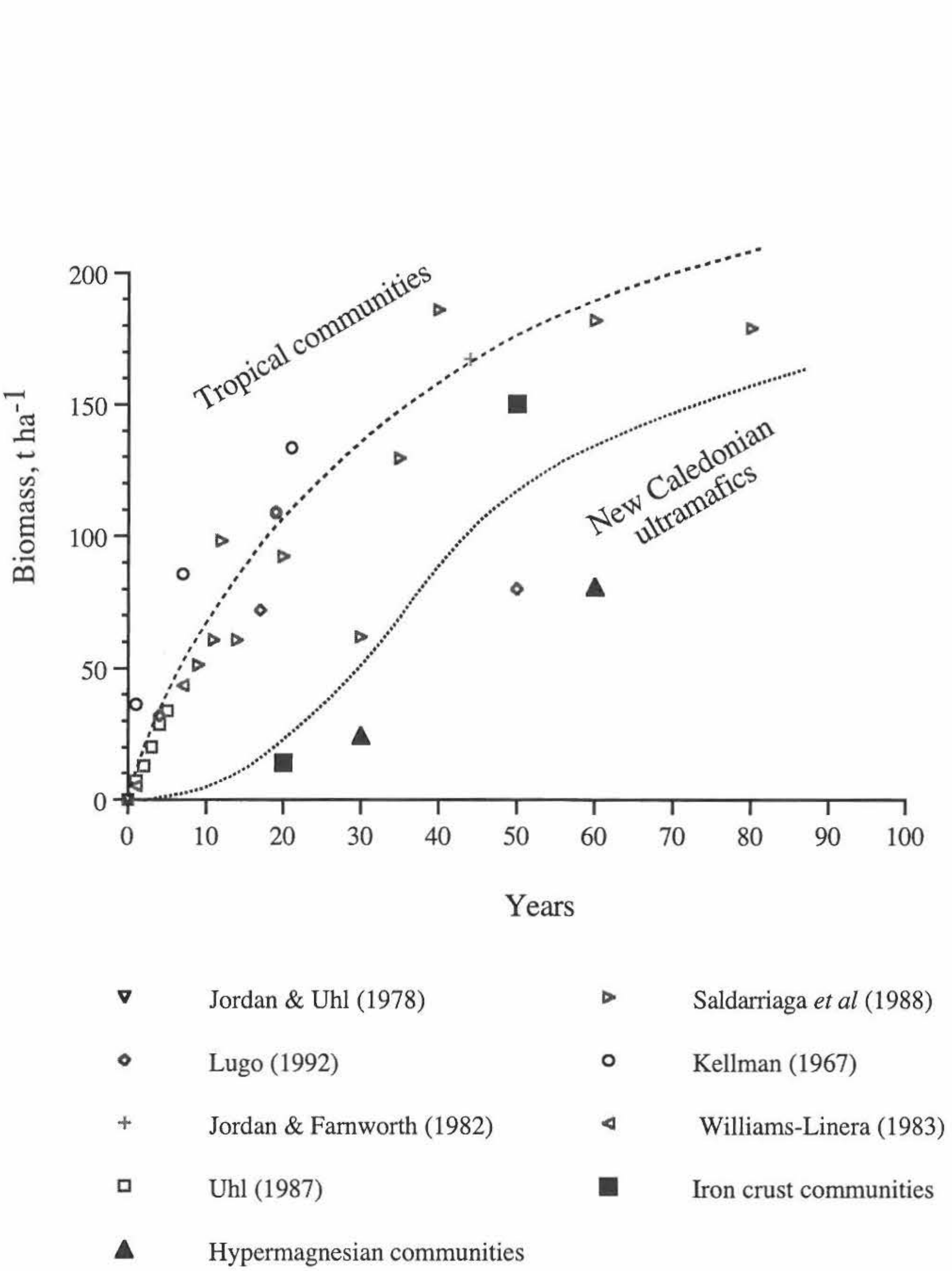


Figure 6.24 Comparison of the total above ground biomass of different successional stages of tropical forests including the iron crust and hypermagnesian maquis communities with time. The dashed line indicates the trends through the New Caledonian maquis and tropical forests in other countries.

Table 6.2: The chemistry of bulk precipitation in various Pacific islands. Bulk rainfall chemistry at Plaines des Lacs was estimated from the average rainfall at Chutes de la Madelaine (1962-1995; 2834 mm yr^{-1}) and the chemistry of bulk precipitation from Viti Levu, Fiji (Waterloo *et al*, 1997). The average rainfall chemistry of a coastal catchment at Dumbea in New Caledonia (Trescasses, 1969 b) was not used becuase of less data but is given for comparison.

	Viti Levu Fiji		Dumbea New Caledonia	Plaines des Lacs New Caledonia	
	Min	Max	Average	Est. min	Est. max
kg ha^{-1} yr^{-1}					
Na	11.2	15.3	51.0	15.0	20.5
K	2.1	4.9	7.7	2.8	6.6
Mg	1.1	1.3	2.8	1.5	1.7
Ca	1.4	1.9	14.2	1.9	2.5
NH_4	4.1	5.9	-	5.5	7.9
NO_3	1.9	3.8	-	2.5	5.1
N-total	2.4	8.8	-	3.2	11.8
Cl	22.2	28.2	121.9	29.8	37.8
HCO	16.0	20.1	345.7	21.5	27.0
SO_4	11.8	16.0	-	15.8	21.5
PO_4	0.4	1.1	-	0.5	1.5
P-total	0.3	0.5	-	0.4	0.7
Si	0.8	1.7	17.0	1.1	2.3
Al	0.5	1.1	-	0.7	1.5
Fe	0.3	0.8	-	0.4	1.1
Mn	0.3	0.6	-	0.4	0.8

coinciding with a decrease in *Gymnostoma* abundance in later successional communities (fig. 6.14). This estimated peak is lower than younger *Casuarina equisetifolia* plantations that fix up to 86 kg ha yr^{-1} (Verma *et al*, 1987; Dommergues, 1995). At late successional rainforest stages plants are likely to rely more on recycling N from biomass accumulated in large trees.

Phosphorus and potassium play central roles in plant metabolic and physiological processes (Epstein, 1977). Inputs of these elements in nutrient deficient tropical systems such as oxisols are from the gradual accumulation from soil sources and from rainfall (Bruijnzeel, 1987, 1989). Estimates in table 6.2 suggest that rainfall at Plaines des Lacs may contribute up to 0.7 kg ha^{-1} yr^{-1} of P and 6.6 kg ha^{-1} yr^{-1} of K to vegetation communities. Phosphorus inputs may be tied up in iron oxides and therefore unavailable to plants as is the case in many tropical forests on acidic laterite soils (Sanchez, 1976).

Results of nutrient surveys indicate that the P and K content of litter and soil are low in maquis (fig. 6.2 a). This suggests that much of the atmospheric P and K is either leached or immobilised in early successional communities because vegetation and litter cover are insufficient to intercept large amounts of rainfall and therefore accumulate these elements. At later successional forest and rainforest stages, soil and litter contain slightly higher P and K contents suggesting that these elements are intercepted by extensive vegetation cover and accumulated in biomass. Phosphorus and potassium contents in rainforest litter and soil are higher than on iron crust possibly due to the accumulation and cycling of P and K in large trees.

Most ultramafic species contain low concentrations of P and K in their leaves (Jaffré, 1976; Jaffré, 1980; Jaffré *et al*, 1994 b) in response to their deficiencies in underlying soil and the low input from dust in rainfall. Low supply of P and K at the physiological level usually results in slow growth at the plant and community levels (Beadle, 1963; Beadle, 1966). This may partially explain the slow biomass development of early successional stages. Furthermore, low phosphorus availability has also been closely linked to reductions in nitrogen fixation by *Frankia* and *Rhizobium* (Cole & Heil, 1981; Yang *et al*, 1995; Reddell *et al*, 1997 a, b; Yang *et al*, 1997). Phosphorus availability may be critical to the growth and the development of key successional species such as *Gymnostoma*.

Nutrient deficiencies are partially overcome in *Casuarina* spp., *Gymnostoma papuanum* and most Proteaceae by cluster (proteoid) root associations that enhance the release and sorption of plant nutrients such as phosphorus and potassium from organic material and soil (Racette *et al*, 1990; Lamont, 1993; Diem & Arahou, 1996). Field examinations at Kouaoua and Plaines des Lacs indicate that *Gymnostoma deplancheanum, G. chamaecyparis* and *G. intermedium* also posses cluster root associations. In addition, the roots of *Gymnostoma chamaecyparis* and many other maquis species (*Grevillea, Alphitonia, Costularia, Styphelia, Longetia, Carpolepis*) are often heavily infected (≈30-80%) by endomycorrhizae which may facilitate nutrient absorption (Amir *et al*, 1997; Amir & Pineau, 1998). However the efficiency of these mechanisms will depend on the availability of other plant nutrients, the tolerance of bacteria to toxic metals (Hartley *et al*, 1997) and properties of the ultramafic soil such as soil aeration, moisture and organic content (Lamont, 1993).

Calcium is important for physiological processes in plants, especially the regulation of metal sorption (Epstein, 1977). On ultramafics, calcium absorption by plants from rainfall (≈ 2.5 kg ha^{-1} yr^{-1}; table 6.2), sources in soil, and decayed litter is likely to be particularly important in reducing the excess assimilation of metals by plant roots (Jaffré, 1980). Calcium contents in litter and soil show slight increases from maquis to forest on iron crust, and occur at high levels in soil and litter of hypermagnesian and eroded oxisol communities at Kouaoua (fig. 6.2 b). In maquis communities on hypermagnesian soil at Kouaoua, the high Ca content of litter may serve plants as a mechanism to counteract the strong Ca : Mg ratio imbalance found in the A_0 horizon of hypermagnesian soil (Jaffré, 1980). Levels of calcium are particularly high in forest found on eroded oxisol possibly because of the closer proximity of Ca sources in peridotite which often occur 2 m below the soil surface. Calcium contents are only slightly higher in soil than in litter of successional communities on iron crust which suggests that calcium mobilisation is slow.

6.6.2 Litterfall

A considerable amount of research has been conducted on litterfall in tropical forest ecosystems (Proctor *et al*, 1983; Vitousek, 1984; Vitousek & Sanford, 1986; Brown & Lugo, 1990). Litterfall is only one facet of nutrient cycling, but it does provide important information concerning the efficiency within communities in terms of the transfer of nutrients from above ground biomass to soils (Vitousek, 1984; Vitousek & Sanford, 1986; Proctor,

Table 6.3 Annual litterfall nutrient, and metal inputs for tropical and temperate forests in the Asia-Pacific region. Also given are litterfall and nutrient input values for *Casuarina* and other tropical plantation species. Annual nutrient input values for *Gymnostoma deplancheanum* , *G. chamaecyparis* and *G. intermedium* were estimated from average values for elements measured over the 6 month period.

						Nutrient inputs from litterfall					
Location	Altitude	Soil type	Vegetation type	Age yr	Litterfall t ha^{-1} yr^{-1}	N	P	K	Ca	Mg	Ni
						kg ha^{-1} yr^{-1}					
Sabah		Ultramafic									
Proctor *et al* (1989)	280	Inceptisol	Rainforest		6.51	85	1.5	9	56	25	2.1
	330	"	Rainforest		7.37	76	1.6	6.5	46	23	2.2
	480	"	Rainforest		5.22	60	1.8	7.6	47	8	0.9
	610	"	Rainforest		5.6	60	1.2	13	59	24	1.1
	790	"	Montane rainforest		5.53	60	1.1	5.1	38	16	0.2
	870	"	Montane rainforest		4.8	42	1.1	4.9	27	13	0.1
		Non-ultramafic									
Burgouts *et al* (1992)	150	Ultisol	Dipterocarp rainforest		11.2						
Sarawak											
Proctor *et al* (1983)	50	Podsols	Alluvial rainforest		11.5	110	4.1	4.4	290	4.7	
	225	"	Dipterocarp rainforest		8.8	81	1.2	33	13	8.9	
	170	"	Heath forest		9.2	55	1.6	4.8	83	4.5	
	300	Limestone	Rainforest		12	140	4.5	16	370	330	
Papua New Guinea											
Bino & Kanua (1996)	2000	Volcanic	*Casuarina oligodon*	2.75	4.8	39	3	10	39	7	
Harding (1994)	1500	"	*Casuarina oligodon*	15	8						
Edwards (1982)	2500	"	Montane rainforest		7.6	90	5	28	27	19	
Enright (1979)	950	"	Rainforest		8.8	168	7	2.2	18	1.2	
Australia											
Spain (1984)	60	Krasnozem	Rainforest		9.6						
	680	"	"		8.6						
	700	"	"		8.1						
Brasell *et al* (1980)	760	Krasnozem	Rainforest		9.1	130	12	66	230	28	
	700	"	"		9.9	120	10.2	51	160	34	
	760	"	*Araucaria cunninghamii*	45	8.2	82	10	50	177	22	
	700	"	"	44	9.9	108	10.9	46	200	40	
Hueneke (1973)	600	Sandy	*Casuarina stricta* woodland	5	1.1						
		"	"	12	3.6						
		"	"	23	5.5						
		"	"	50	4.3						
Clarke & Allaway (1996)	2	Estuarine	*Casuarina glauca* forest		8.5						
Attiwill *et al* (1978)	400	-	*Eucalyptus obliqua* forest	50	3.56		1.03	5.5	21	8.3	
	200	-	"	50	5.5			8.9	30	9.4	
Ashton (1975)	700	-	*Eucalyptus regnans* forest	220	8.08	58	1.9	7.5	49		
Hawaii											
Vitousek *et al* (1995)	1190	Volcanic	Montane rainforest	200	5.2	25	1.8	8	68	10	
	1220	"	"	2000	7	67	4.6	24	90	16	
	1400	"	"	3400	5.2	28	1.1	5	136	9	
	1200	"	"	6000	5.2	36	1.3	12	84	10	
New Zealand											
Daniel & Adams (1984)	670	Brown earth	Podocarp hardwood forest		4.6	44	2.8	20	51	12	
Miller (1968)		-	*Nothofagus truncata* forest		6	34	2.3	10	62	9.6	
New Caledonia		Ultramafic									
This study	200	Iron crust oxisol	*G. deplancheanum* tall maquis	50	2.9	52	0.2	4.5	78	13	0.2
	700	Eroded oxisol	*G. intermedium* forest		5	88	0.7	9.7	107	29	1.3
	150	Hypermagnesian	*G. chamaecyparis* tall maquis	70 ?	1.6	19	0.05	2.1	17	9.6	0.3

1987). A summary of annual litterfall in temperate and tropical forests in the Asia Pacific is given in table 6.3. Generally, rainforest communities found on moderately fertile soils in Sarawak (Proctor *et al*, 1983), New Guinea (Edwards, 1982) and northern Queensland (Brasell *et al*, 1980; Spain, 1984) produce large amounts of litter. Successional communities at Plaines des Lacs and Kouaoua fall within the range of low litter output forest communities growing on nutrient poor substrates in Australia (Hueneke, 1973; Attiwill *et al*, 1978). According to Vitousek (1984) plant communities on nutrient poor soils recycle elements efficiently, in particular P.

Another factor which appears to also have reduce litterfall outputs in tropical communities is climate, in particular low rainfall (Vitousek, 1984). Rainfall in relatively low at the base of Kouaoua compared to summits and the Plaines des Lacs and might explain the low litterfall of tall maquis on hypermagnesian soil. However, since rainfall records cover a limited period it is difficult to clearly distinguish rainfall effects from substrate effects on litterfall (fig. 6.5).

Litterfall of *Gymnostoma* dominated tall maquis and forest in New Caledonia is slightly lower than rainforest on ultramafics in Sabah (Proctor *et al*, 1989). This lower litterfall output is, in part, probably related to the younger age of these vegetation formations which are less than 100 years old.

6.6.3 The role of *Gymnostoma* in nutrient dynamics

Gymnostoma is the largest contributor to litterfall in successional communities at Plaines des Lacs and Kouaoua (fig. 6.3, fig. 6.4, fig. 6.5) and is therefore likely to contribute a large part of the nutrients to the efficient nutrient recycling of these communities. Annual inputs of P from *Gymnostoma deplancheanum*, *G. intermedium* and *G. chamaecyparis* litterfall are low compared to ultramafic and non-ultramafic forest communities (table 6.3), suggesting that these species either have a much lower P content or are highly efficient at conserving this element. In contrast, the Ca content of *Gymnostoma* litter is high compared to ultramafic rainforest on Sabah (Proctor *et al*, 1989), and comparable to non-ultramafic rainforests in Australia (Brasell *et al*, 1980), Sarawak (Proctor *et al*, 1983) and Hawaii (Vitousek *et al*, 1995). Moreover, the Ca content of cladode litter is much higher than the Mg content. Nickel in cladode litterfall is lower than for rainforest on ultramafics in Sabah (Proctor *et al*, 1989) which suggests that this element may be either excluded by *Gymnostoma* at the

Table 6.4: The mean nutrient and metal content (%) of *Gymnostoma deplancheanum* , *G. chamaecyparis* and *G. intermedium* cladodes, whole plant and monthly cladode litterfall compared to other dicotyledon species. Values for cladodes, whole plants and other dicotyledons are from Jaffre *et al* (1994 b).

		N %	P %	K %	Na %	Ca %	Mg %	Ni %	Mn %
Plant communities on iron crust oxisol									
Average of 100 dicotyledon species									
Leaves *		0.910	0.032	0.590	0.210	1.100	0.240	0.003	0.095
Gymnostoma deplancheanum									
Cladodes *	Mean	0.810	0.016	0.520	0.480	1.170	0.210	0.002	0.054
	st.dev	*0.060*	*0.001*	*0.110*	*0.500*	*0.080*	*0.040*	0.001	*0.043*
Whole plant *	Mean	0.550	0.010	0.250	0.270	1.120	0.120	-	-
	st.dev	*0.040*	*0.002*	*0.040*	*0.030*	*0.400*	*0.020*	-	-
Litterfall	Mean	0.595	0.002	0.051	0.202	0.889	0.153	0.002	0.075
	st.dev	*0.188*	*0.004*	*0.041*	*0.115*	*0.084*	*0.032*	*0.000*	*0.005*
Plant communities on hypermagnesian soil									
Average of 100 dicotyledon species									
Leaves *		1.030	0.034	0.590	0.210	1.040	0.510	0.011	0.027
Gymnostoma chamaecyparis									
Cladodes *	Mean	0.810	0.015	0.290	0.023	0.620	0.370	0.006	0.007
	st.dev	*0.060*	*0.002*	*0.070*	*0.030*	*0.140*	*0.030*	*0.002*	*0.003*
Whole plant *	Mean	0.410	0.009	0.170	0.120	0.660	0.220	-	-
	st.dev	*0.030*	*0.002*	*0.050*	*0.020*	*0.140*	*0.030*	-	-
Litterfall	Mean	0.752	0.002	0.082	0.140	0.675	0.374	0.011	0.0088
	st.dev	*0.424*	*0.004*	*0.047*	*0.065*	*0.072*	*0.039*	*0.001*	*0.001*
Forest communities on eroded oxisol									
Average of 118 dicotyledon species									
Leaves *		1.340	0.044	0.860	0.250	1.550	0.490	0.011	0.025
Gymnostoma intermedium									
Cladodes *	Mean	0.810	0.014	0.420	0.360	0.920	0.180	0.001	0.2913
	st.dev	*0.070*	*0.001*	*0.070*	*0.050*	*0.160*	*0.050*	*0.000*	*0.118*
Whole plant *	Mean	0.410	0.008	0.180	0.130	0.860	0.080	-	-
	st.dev	*0.030*	*0.001*	*0.030*	*0.020*	*0.080*	*0.010*	-	-
Litterfall	Mean	0.903	0.003	0.047	0.171	0.513	0.142	0.006	0.2584
	st.dev	*0.356*	*0.003*	*0.031*	*0.086*	*0.114*	*0.035*	*0.002*	*0.050*

root level or translocated from cladodes prior to senescence. In contrast, manganese levels in fresh cladodes and cladode litterfall of *Gymnostoma intermedium* are higher than the average foliar content of common forest species found on eroded oxisols (table 6.4).

One distinguishing feature of *Gymnostoma* and other the *Casuarina* species that is likely to influence litterfall nutrient inputs in communities dominated by these trees is their cladode anatomy. Cladodes differ from the foliage of most angiosperms in that they contain larger amounts of support tissue (Barlow, 1981). *Gymnostoma* cladodes therefore contain much less nutrients per unit weight compared to most maquis species (Table 6.4). *Gymnostoma* appears to translocate most of the phosphorus and potassium from cladodes prior to their senescence. However, nutrient translocation in cladodes shows some variation between *Gymnostoma* species. In *Gymnostoma deplancheanum*, 27% of N, 87.5% of P, 90% of K and 24% of Ca are translocated from cladodes prior to senescence. In *G. chamaecyparis*, 8% of N, 86.6% of P, 71% of K and < 1% of Ca are translocated from cladodes prior to senescence. In *G. intermedium*, < 1% of N, 78% of P, 89% of K and 45% of Ca is translocated from cladodes prior to senescence. Cladode litterfall values for phosphorus and potassium are particularly high and may also represent losses from leaching by rainfall.

Another process that is also likely to be influencing nutrient cycling in ultramafic communities is *Gymnostoma* litter decay. Litter breakdown is mediated through the decomposer cycle or by fire, and involves a loss of structure and the conversion of the organic matter by (i) fragmentation, (ii) leaching and (iii) catabolism to simpler compounds with a loss of energy (Attwill, 1967; Swift *et al*, 1979; Burghouts *et al*, 1992). The rate at which organic material is converted by decomposers is dependent on the amount and suitability of litter and microclimatic conditions for decomposer populations (Swift *et al*, 1979; Vitousek, 1984; Bruijnzeel, 1991). In the case of *Gymnostoma deplancheanum*, measures of litter breakdown in forest on iron crust oxisol indicate that cladode breakdown is slower than large leafed rainforest species such as *Arillastrum gummiferum* (fig. 6.10), and it may take 2.7 years for 50% of cladode biomass to decay. Studies of *Casuarina* litter elsewhere have suggested that cladode breakdown is slow (NRC, 1984) because bacteria and fungal decomposers are unable to rapidly transform much of the cladode material due to its high lignin and silica content and low nitrogen and phosphorus content (Constantinides & Fownes, 1994). Qualitative measures of fungal hyphae on *G. deplancheanum* cladodes support this argument and shows that cladode weight loss from litter bags after 7 months was marginal despite 75% of cladodes having a covering of fungal hyphae (fig. 6.11). Like Casuarinaceae communities elsewhere, *Gymnostoma* litter forms a deep loose interlocking litter that allows some light penetration and aeration at depth (NRC, 1984). This type of microclimate may be unsuitable for the proliferation of decomposer populations such as termites which are capable of rapidly transforming course leaf material (Spain & Hutson, 1983). Termite mounds were found in forest patches on iron crust but were rare and small in size, and therefore unlikely to have major effects on litter decomposition.

Slow cladode decay appears to have generated several patterns at the community level. Maquis and forest communities posses deep litter beds compared to rainforest which may affect not only decomposer populations but also raise the flammability of maquis and forest communities. This increase in litter biomass in maquis and forest communities is caused by an increase in the abundance of *Gymnostoma deplancheanum* on iron crust oxisol (fig. 6.13). *Gymnostoma* contributes very little to biomass of rainforest on eroded oxisol and is replaced by large emergent rainforest *Arillastrum gummiferum* trees. A decrease in litter biomass and an increase in nutrient availability also mark this transition from forest to rainforest. Rainforest species such as *Arillastrum* generate a leaf litter that decays more rapidly than *Gymnostoma*, possibly because nitrogen, phosphorus content in rainforest litter are higher than in maquis and forest (fig. 6.2 a).

6.6.4 Effects of Gymnostoma litter on community dynamics

Research on *Casuarina* has shown that (i) mature *Casuarina* plantations in the USA, India and Africa are often devoid of other native plant species (Midgeley *et al*, 1981; NRC, 1984; Suresh & Rai, 1987, 1988; Mailly & Margolis, 1992; Parotta, 1995) and (ii) certain crop species often produce lower yields when intercropped with *Casuarina* (Chaturvedi *et al*, 1992; Sanker & Rai, 1993; Constantinides & Fownes, 1994). Such patterns of low plant diversity and productivity have also been recorded in natural pure canopy stands of *Casuarina* and exotic *Pinus* spp. plantations in Australia (Storey, 1967; Clark & Hannon, 1967; Harris & Kimber, 1983).

Measures of understorey abundance in pure canopy stands of *Gymnostoma* tall maquis and forest at Kouaoua and Plaines des Lacs show that seedling recruitment in many species is variable compared to their seedfall input (fig. 6.15). This suggests that understorey conditions have species specific effects on the survival of germinant seedlings. The absence of *Gymnostoma intermedium, Styphelia cymbulae, S. macrophyllum* and *Xanthomyrtus heighenensis* seedlings in the forest understorey despite being abundant on adjacent road cuttings argues that light levels may be too low for these species to maintain juvenile populations. In contrast, *Gymnostoma deplancheanum* shows as much regeneration in tall maquis as it does in open conditions on road cuttings (4.2.3) which argues that light might not be limiting seedling survival in tall maquis.

Tall maquis on iron crust and hypermagnesian soil contain a large number of mature trees and shrubs that compete for a limited source of nutrients in soils that frequently experience moisture deficits. Another possible explanation for low seedling numbers in tall maquis is that nutrient and moisture availability are more likely to stress seedling root systems than adult shrubs that posses deep roots and therefore cause seedlings to be out competed by larger plants. A similar argument is often attributed to "halo effects" surrounding *Casuarina* trees in Australia (Story, 1967; Harris & Kimber, 1983).

Shannon & Clarke (1971) observed that deep litter in *Casuarina glauca* woodland contained fewer seedlings and suggested that the lack of seedling recruitment arose because germinating seedlings were impeded by deep litter. Litter depths of successional communities surveyed range from 5 cm in tall maquis to 20 cm in forest. Deep litter beds might have a physical effect on seedlings by reducing the likelihood of seeds germinating or seedling radicles penetrating litter to obtain soil moisture (Alhgren & Ahlgren, 1981; Augsperger & Molofsky, 1992; Parotta, 1995). Alternatively, slow litter decay may also cause allelochemicals in organic compounds to accumulate and affect the growth performance of colonising seedlings (Harris & Kimber, 1983; Rice, 1984).

A considerable amount of research has been conducted on the phytotoxicity of substances found in plant litterfall (Rice, 1984; Chaturvedi *et al*, 1992; Sanker & Rai, 1993). Most of this work has used bioassays focussing on either leachates of litter or concentrates of compounds extracted from litter such as polyphenol, terpenes and other volatiles to test for allelopathic effects on the growth and yield commercial plant species. Concentrated solutions of *Casuarina* cladodes have been shown to reduce growth in duck weed (Sutton & Portier, 1989). In contrast, bioassay trials on maquis species treated with water or leachates of *Gymnostoma deplancheanum, G. chamaecyparis* and *G. intermedium* cladode litter reveal that *Gymnostoma* litter leachates had no suppressive affect on growth (fig. 6.17). These results are consistent with bioassay trials by Clark & Hannon (1971) and Sanker & Rai (1993) who also concluded that aqueous leachate extracts of *Casuarina* cladodes had no negative effects on crop plants.

One interesting pattern that was revealed from the cladode leachate experiment is that proteoid roots were more abundant in *Grevillea* seedlings subject to litter treatments than bare soil and concentrated on the soil surface (fig. 6.18). Studies of Proteaceae have shown that proteoid roots can be induced by micro-organisms in the rhizosphere (Lamont, 1993) which suggests that *Gymnostoma* litter might also act as a source of micro-organisms. Alternatively, litter may act as a source of nutrients for proteoid root forming bacteria in the oxisol used in the experiment.

Measures of seed germination and seedling growth on treatments testing for the physical effects of litter reveal several patterns. It appears that the size of seed has a major influence on whether it remains on the surface of litter or is small enough (< 6 mm^2 area) to pass between cladodes and thereby descend to the organic soil matrix (fig. 6.22). Such a phenomena may explain why the understorey tall maquis on iron crust is largely composed of small seeded Myrtaceae, Cunoniaceae and Dilleniaceae. Larger seeds (eg: *Beccariella, Alphitonia, Acacia*) remaining on the litter never germinated while those placed below the litter germinated and showed slightly higher rates of survival than seedlings on bare ground subject to water stressed regimes (fig. 6.23). Under natural conditions, seed that fails to penetrate through litter might also be heavily predated on by birds, rodents and insects. Parotta (1995) found that small seeded bird dispersed species were heavily predated in Central American *Casuarina* plantations because seed failed to penetrate through litter. Hopkins & Graham (1987) also found high levels of predation in many large seeded rainforest species in Australia.

6.7 Conclusion

Several important processes have been revealed from measures and experiments presented in this chapter.

(i) Standing biomass increases with the development of successional communities on iron crust and hypermagnesian soil.

(ii) Litterfall provides increasing amounts of nutrients over time.

(iii) Biomass development is slow at early successional stages due to low N, P, K and Ca concentrations of ultramafic soils.

(iv) *Gymnostoma* plays a key functional role in successional development of tall maquis and forest stages by providing most (76%) of the nitrogen through atmospheric fixation via *Frankia*.

(v) Nutrient inputs to soil from litter decay in successional communities appear to be largely influenced by changes in abundance of *Gymnostoma*.

(vi) Leachates produced by slow *Gymnostoma* litter decay appear to have no effect on maquis plant growth. However deep litter beds may exclude many large seeded species by impeding seed passage.

Chapter 7

Plant growth on ultramafic substrates

7.1 Introduction

Mine wastes appear to present a number of problems for plant establishment and growth in addition to bare soil following fire. Revegetation work has focussed on using exotic and endemic ultramafic maquis species with the objective of initiating natural succession on mine sites (Cherrier, 1990; Jaffré & Rigault, 1991; Jaffré *et al*, 1994c; Jaffré *et al*, 1997; Sarrailh, 1997). However, preliminary observations revealed that many native and exotic species grew slowly (Jaffré & Rigault, 1991; Jaffré *et al*, 1994 c) possibly because plants were not tolerant of the climatic and edaphic conditions encountered on mines. This chapter examines how certain processes regarded as important in colonisation and succession on ultramafics affect plant growth on bare ultramafic soils and mine wastes.

The analysis of vegetation at Plaines des Lacs and Kouaoua used to develop the succession models in chapter 3, suggested that shade or litter generated by colonist vegetation favours certain species and excludes others. Shade and litter are strongly associated in colonist vegetation (refer to chapter 4) so it is necessary to adopt an experimental approach to determine their separate effects. Since litter may have a mixture of physical, chemical and biological effects on plant growth, it was considered desirable to also examine the effects of separately adding a nutrient source such as fertiliser. Hydrated lime was also used as a treatment in field experiments to determine whether raising soil pH and calcium availability alleviated potential imbalances or toxicities (eg: Ni, Mn) which might be limiting plant growth on ultramafic substrates (Hunter & Vergnano, 1952; Proctor & Cottam, 1982; Brooks, 1987; Nagy & Proctor, 1997 b).

Since mine wastes appear to present additional problems for establishment and growth compared with natural soils, the experiment was designed to compare adjacent mine waste, bare eroded oxisol, hypermagnesian soil and iron crust oxisol. The aim was to determine whether these different substrates affected plant responses rather than to characterise growth on each substrate. Accordingly contrasting sites were

Table 7.1: Habitat and successional status of species used in field experiments

Species	Oxisol	Hypermagnesian soil	Non ultramafic soil	Successional stage early	late
Gymnostoma deplancheanum	*			*	*
Gymnostoma chamaecyparis		*		*	*
Gymnostoma nodiflorum			*	*	
Grevillea exul var. rubiginosa	*			*	
Austrobuxus carunculatus	*	*			*
Carpolepis laurifolia	*		*	*	*

Table 7.2: Average initial height, number of leaves and shoot dry weight of species used in field experiments. *Gymnostoma nodiflorum* seedlings seedlings were 1 year old at the plantation stage except for those at the eroded oxisol site (**).

Species	Germination date	Height (cm)	No. Leaves	dry weight (g)
Gymnostoma deplancheanum	Jan-93	3.56 ± 1.06	3 ± 2	0.17 ± 0.05
Gymnostoma chamaecyparis	Jan-93	3.33 ± 0.75	3 ± 2	0.15 ± 0.03
Gymnostoma nodiflorum	Jan-92	17.23 ± 10.56	30 ± 12	0.73 ± 0.41
Gymnostoma nodiflorum **	Jan-91	28.05 ± 5.96	34 ± 11	7.72 ± 2.36
Grevillea exul var. *rubiginosa*	Feb-93	2.95 ± 0.83	7 ± 2	0.50 ± 0.05
Austrobuxus carunculatus	Jan-93	3.82 ± 1.14	5 ± 2	0.19 ± 0.04
Carpolepis laurifolia	Dec-92	6.06 ± 1.97	16 ± 4	0.47 ± 0.02

selected rather than a number of sites within each substrate type. Replication was made using a split plot design at each site. Soil types were selected to represent a range of disturbed ultramafic soil conditions encountered by plants colonising mines in New Caledonia. Six species were selected to represent a contrast between *Gymnostoma* species which are nitrogen fixing, and broad leafed species. Furthermore, these species were selected to represent plants naturally occurring on a range of ultramafic and other substrates (table 7.1).

7.2 Methods

7.2.1 Experimental design

Field experiments were set out to examine the separate and combined effects of four treatments, Shade (± shade cloth), Litter (± litter), Fertiliser (± fertiliser) and Lime (± lime) on the growth of six maquis species: *Gymnostoma deplancheanum*, *G. chamaecyparis*, *G. nodiflorum* (Casuarinaceae) *Grevillea exul* var. *rubiginosa* (Proteaceae), *Austrobuxus carunculatus* (Euphorbiaceae) and *Carpolepis laurifolia* (Myrtaceae)(fig 7.1). This design was repeated with slight variation at four Sites: an iron crust oxisol at Plaines des Lacs, and an eroded oxisol, a mine overburden and a hypermagnesian soil at Kouaoua. Field experiments were designed to provide enough statistical power and replication so that third order interactions could be examined between sites, species and treatment combinations.

The experimental design on the mine overburden, the eroded oxisol and iron crust oxisol consisted of all 16 treatment combinations in plots randomly located in each of two adjacent blocks at each site (fig. 7.2). Each treatment plot contained two individuals of each species that were randomly allocated positions. Growth parameters were averaged for these two plants; in a few cases the measures were based on a sole surviving individual.

Certain aspects of the design were considered unbalanced. The design was unbalanced at the species level by use of some *Gymnostoma nodiflorum* that were older than the other test species at some sites. The original test plants were taken by another researcher. The design was unbalanced at the site level because *Gymnostoma chamaecyparis* was not planted in the overburden mine overburden site because previous trials

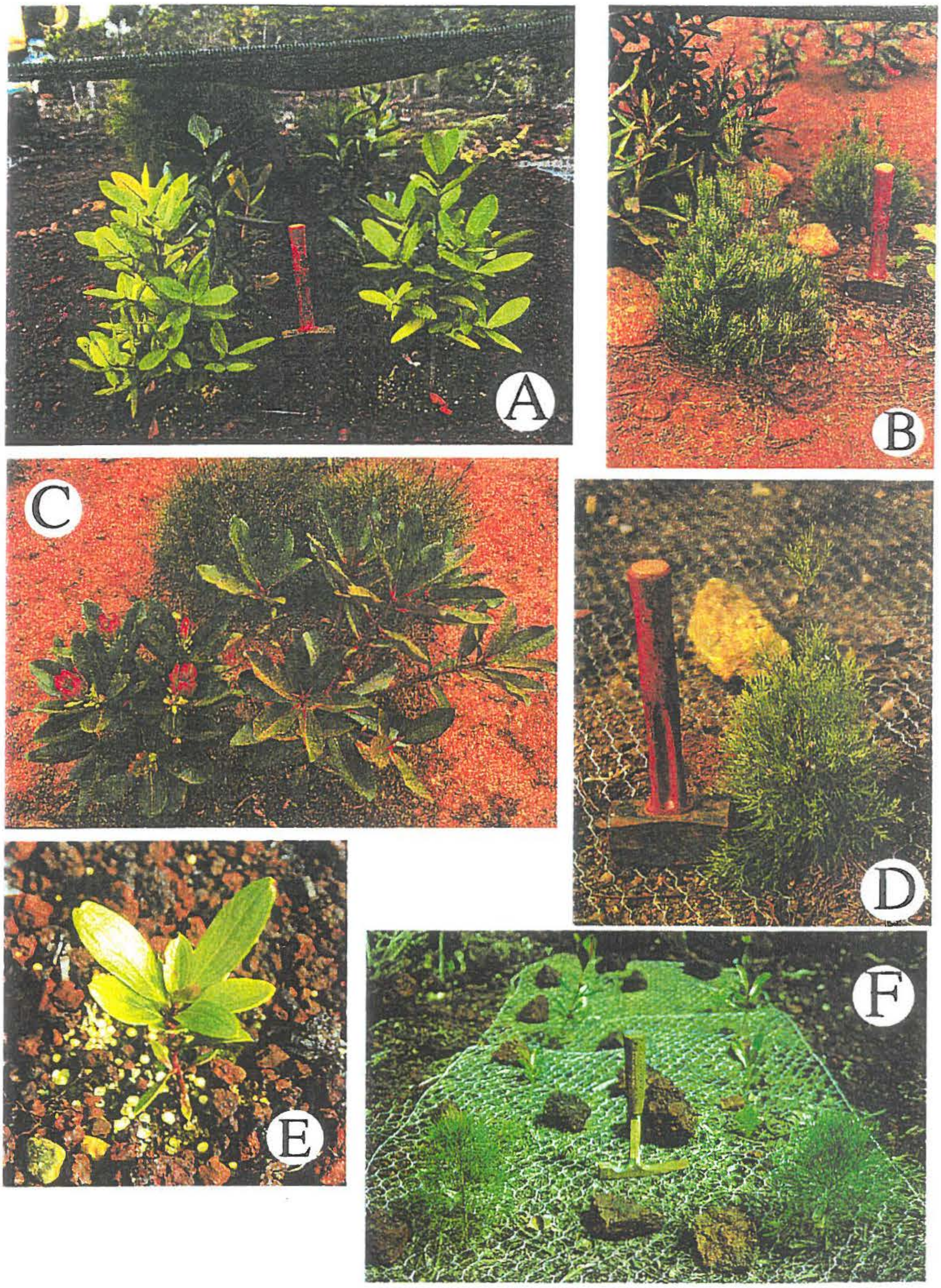


Figure 7.1 The endemic maquis species used on fueld experiments at Plaines des Lacs and Kouaoua. *Austrobuxus carunculatus* (Euphorbiaceae) seedlings aged 2 yrs on a fertiliser x shade treatment at the iron crust oxisol site (A). *Gymnostoma deplancheanum* seedling aged 2 yrs on a fertiliser x shade x litter treatment at the mine overburden site (B). *Carpolepis laurifolia* (Myrtaceae) seedlings aged 2 yrs on a fertiliser x litter treatment at the eroded oxisol site (C). *G. chamaecyparis* seedling aged 2 yrs on a litter treatment at the hypermagnesian soil site (D). *Grevillea exul* var.*rubiginosa* (Proteaceae) seedling aged 6 months on a fertiliser treatment at the iron crust oxisol site (E). *G. nodiflorum* seedlings aged 6 months on a litter treatment at the iron crust oxisol site (F).

Figure 7.2 General view of the field experiment on the mine overburden site showing arrangement of treatments, in particular shade and litter treatments. Seedlings are 2 yrs old. The field experiment on mine overburden covers an area of 1400 m.sq.

Figure 7.3 A general view of the arrangement of *Gymnostoma chamaecyparis* seedlings aged 2 yrs old on the hypermagnesian soil site at Kouaoua. Seedlings on the first back row are either on litter (left) or bare ground (right). Row two contains litter or bare ground, but with lime added. Row three contains litter or bare ground, but with fertiliser added. Seedlings in the front row are either on litter x fertiliser x lime (left) or fertiliser x lime (right).

suggested that it would die under these conditions. However, this species was examined by itself on a hypermagnesian soil. The design of the field experiment on hypermagnesian soil consisted of two adjacent blocks with 16 treatment combinations in each block (fig. 7.3).

7.2.2 Field experiment Sites

The iron crust oxisol site was selected at Creek Pernod (Lat 22° 11' 223", Long 166° 51' 117"; altitude 190 m a.s.l) to represent a relatively undisturbed substrate typical of mine prospecting roads and early post-fire disturbance. The experiment trial was established on an abandoned prospecting road that had been cleared of loose surface iron crust by bulldozers and was surrounded by tall maquis. This site rarely exceeded nine metres in width and consisted of large flat gravel pockets containing iron crust boulders and other breccia iron crust debris.

The mine overburden site (Lat 21° 26' 529", Long 165° 45' 525"; altitude 790 m a.s.l) was selected at Kouaoua to represent a surface substrate that had been completely altered by nickel ore extraction both chemically and physically. The experimental trial was established at Méa mine on an infill terrace that had been constructed in 1992 near Mt Réve. This level terrace consisted of a mixture of compacted B horizon clay and A horizon gravel that had been removed from eroded oxisol above weathered peridotite nickel ore bodies.

The eroded oxisol site and a hypermagnesian soil site were selected at Kouaoua to represent ultramafic mountain slopes that had experienced erosion of surface horizons. The eroded oxisol site (Lat 21° 26' 763", Long 165° 45' 285"; Altitude 700 m a.s.l) was established approximately 1 km from the mine overburden site on a level platform found in close proximity to forest on eroded oxisol. Much of the gravel from the platform had been scraped from the surface by bulldozers to expose a compacted clayey B horizon containing iron crust and peridotite debris. The hypermagnesian soil site (Lat 21° 26' 320", Long 166° 27' 21"; altitude 240 m a.s.l) was established on an abandoned road that had been constructed on a steep serpentinite outcrop below Méa mine. The surface of this field experiment was level and consisted of a shallow rocky A horizon of eroded hypermagnesian soil less than 20 cm deep that had been deposited on top of serpentinite rock.

7.2.3 Seedling propagation

All seedlings were established in a soil mixture composed of 1 part coarse river sand and 2 parts non ultramafic alluvial soil. Seedlings were kept in a shade house (30% transmission) prior to field trials and were watered twice daily. *Gymnostoma* seedlings were not deliberately inoculated with *Frankia*, but may have become infected from spores in the soil used for propagation. Unusually, large and small seedlings were excluded from the field experiment. Eight randomly selected seedlings were harvested from each species and oven dried for 48 hours at 105°C to obtain an average initial shoot dry weight for each species. Details of the initial height and shoot dry weight of test species are given in table 7.2. All seedlings planted on field experiments were approximately six months old except for *G. nodiflorum* seedlings which were 1.5 yr on the iron crust oxisol and mine overburden sites, and 2.5 yr on the eroded oxisol site.

7.2.4 Establishment of field experiments

Plants were established on field experiment plots in July 1993 except for *Gymnostoma chamaecyparis*. This species grew slower than the other species in the shade house and was planted in January 1994. Seedlings were planted in treatment plots at a spacing of 40 cm. Treatment plots were separated by 1 m of bare ground to minimise cross contamination of treatments.

7.2.5 Treatments

Litter treatments set out to mimic natural conditions in maquis. The litter was an equal mixture from beneath *Gymnostoma deplancheanum*, *G. chamaecyparis* and *G. intermedium*. Litter was air dried and sorted to remove branches and stones and then weighed into 3 kg portions. The litter portions from each species were mixed together and spread over each litter treatment plot to an average depth of 5 cm (3 kg m^2). Galvanised wire mesh was placed over litter treatment plots to ensure that litter remained around seedlings.

Based on the nutrient concentrations of *Gymnostoma* litter from successional communities, litter applications initially provided approximately 39 g of N, 0.3 g of P, 0.8 g of K, 2 g of Na and 32 g of Ca per plant.

Shade treatment plots were designed to mimic to light regimes experienced by seedlings underneath primary colonist trees and shrubs. Shade was provided by shade cloth (50% transmission) that was fixed to metal rods at 1 m above the soil surface and kept taut with cables that had been staked to the ground. Cyclone damage required replacement of some shade cloths. This treatment allowed some direct light penetration at lower solar angles-as observed beneath pioneer trees.

Seedlings on fertiliser treatment plots were supplied with 4.6 g (manufacturers recommended dose) of Osmocote™ slow release NPK fertiliser (15 - 5 –11) that was applied to soil at a 10 cm radius around each seedling at a depth of 0 to 5 cm. Fertiliser doses were reapplied to the soil surface at 4 month intervals.

Lime treatment plots were supplied with a hydrated lime dose [$Ca(OH)_2$] that was intended to raise soil pH by 0.5 to a depth and distance of 20 cm around each plant. The doses at each site were calculated by measuring the pH of solutions containing 20 g of soil : 50 ml of distilled water and increasing amounts of hydrated lime over a 3 day period (fig. 7.4). Seedlings on iron crust oxisol treatment plots were supplied with a 3.2 g dose of $Ca(OH)_2$ to raise the soil pH to 5.0. Seedlings at Kouaoua were supplied with 2.6 g $Ca(OH)_2$ to raise the soil pH around each plant to 6.0 on mine overburden, to 6.8 on eroded oxisol and hypermagnesian soil. Hydrated lime doses were initially thoroughly mixed in soil surrounding each plant to a depth of 10 cm. Lime reapplied at 4 month intervals at the surface to ensure that soil pH was raised by 0.5 for the duration of the experiment.

7.2.6 Measures of plant growth on field experiments

Stem height (cm) was recorded for all seedlings in July 1993, January 1994, January 1995 and July 1995. In August 1995, one plant from each species in each plot was harvested, from one side of the plot, leaving one replicate *in situ* for long term monitoring (not reported). These plants were harvested to obtain measures of relative shoot growth (g, g dry weight). Plant shoots were rinsed in tap water to remove dust, separated into their stem and leaf parts which were then weighed individually. Five grams of fresh leaf was sub sampled from plants grown on bare ground and litter for chemical analysis to determine foliar concentrations of N, P, K, Na, Mn, Ni, Ca and Mg (refer to Appendix 1 for techniques). The remaining stem and

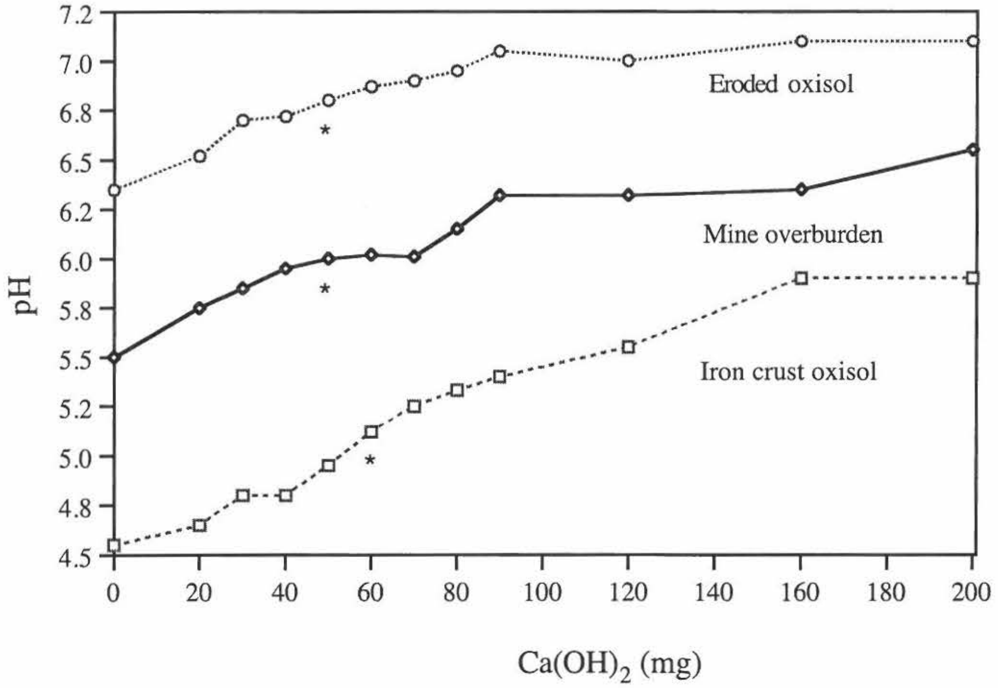


Figure 7.4 The effects of different amounts of hydrated lime [$Ca(OH)_2$] on the pH of soils from experimental sites after 3 days. The $Ca(OH)_2$ dose used to raise the pH by 0.5 at each site is indicated by *.

leaf material of each seedling was oven dried at 105°C for 48 hours to obtain the final total shoot dry weight (g) and leaf and stem dry weight (S_d, g). Relative shoot growth (g, g dry weight) was calculated from the final shoot dry weight (g) minus the average initial shoot dry weight (g) divided by the initial shoot dry weight (g).

Root harvesting was conducted on *Gymnostoma* species at all sites and broad leafed test species from one block on the eroded oxisol site to obtain measures of total plant dry weight (g) and root : shoot ratios. In most cases, only surface root material was removed. Harvested root systems were washed of all surface soil and then weighed (W_r, g, wet weight). The length of primary root material and the cross sectional area of primary roots (D, mm) were measured. Due to the rocky substrate it was not possible to extract all root material so an estimate was made of the fraction collected based on the diametre of roots at the limits of the sample. Estimated total root wet weight (R, g) and estimated total root dry weight (R_d, g) was calculated for harvested roots using the following equations.

$$R = 100 W_r D$$

where

$$D = D_r \, 0.7854$$

$$R_d = R S_d$$

The number and weight of *Frankia* nodules was recorded for each harvested *Gymnostoma* root system to obtain total *Frankia* nodule weight (g, wet weight) per plant.

7.2.7 Chlorophyll fluorescence measures at field experiments

Chlorophyll fluorescence was measured in December 1994 using a portable chlorophyll *a* fluorescence measuring system [Plant Efficiency Analyser (PEA meter), Hansatech Instruments Ltd., Kings Lynn, Norfolk, UK]. Measures of *Fv/Fm* and *Fo* (5.3.1.1) were recorded for fully expanded top and bottom leaves of all seedlings. Several morning fluorescence measures of seedlings on bare ground plots were repeated at midday at each site to determine whether plants were experiencing chronic or transient stress at each site. This indicated that measures were relatively constant during the day, so sampling could be conducted during the day. All plant leaves were dark adapted for a period of approximately 20 minutes using leaf clips. Several cladodes were placed within clips for *Gymnostoma* species to ensure that the entire surface was covered. Fluorescence measurements were made at full light intensity (100%: 1000 μmol quanta $m^{-2} s^{-1}$). Chlorophyll fluorescence measures were repeated in July 1995 on the current top and bottom fully expanded leaves.

7.2.8 Light & Temperature conditions experienced by seedlings

Light levels were examined on shade treatment plots and treatment plots without shade in January 1994, April 1994, August 1994, January 1995 and June 1995 during day visits at all sites. Measurements were made for 5 minutes at 9 am, 12 am and 3 pm using a LiCor light meter, then averaged over the day, to determine the daily light regime of photosynthetically active radiation (PAR) available to plants. Measures were recorded by placing the LiCor sensor on level ground in the center of shade treatment plots and on treatments plots without shade.

Day air + radiation temperature were measured on one open treatment and one shade treatment at the iron crust oxisol site from the 12th to the 14th of January 1994. This was carried out to describe temperature regimes experienced by seedlings underneath shade cloth and in exposed conditions during hot months of the year. Temperatures were recorded underneath shade cloth and on a treatment with no shade using a mercury bulb thermometer that was hung vertically approximately 10 cm above the ground. The temperature was recorded during the day at 2 hr intervals. The temperature underneath tall maquis was also examined over the three day period at similar time intervals.

Measures of iron crust and serpentinite rock surface temperature were recorded at midday using a thermocouple in December 1993.

7.2.9 Soil chemistry of treatment plots

In August 1995, soil was sampled from next to two plants on simple treatment plots to a depth of 10 cm at all sites to determine whether treatments amended soil properties. Soil samples were sieved through 2 mm mesh and oven dried at 40°C for 24 hours. A 20 g sub-sample was used to determine the pH of soil. The remaining soil sample was used for chemical analysis to identify total concentrations of N, P, K, Na, MN, Ni, Ca and Mg (Appendix 1).

7.2.10 Statistical analysis

To obtain normal residuals and homogenise variance, transformations were made to plant growth measures: ln height (cm), ln relative shoot growth (g, g dry weight), ln total *Frankia* nodule weight + 1 (g, wet weight) and $\log_{10}$ foliar concentration (ppm). Fv/Fm ratios of top and bottom leaves were averaged for each plant and transformed by taking ln $(0.96 - Fv/Fm)$.

Analysis of variance (ANOVA) stratified at the soil level (residual d.f. 6), plot level (residual d.f. 42) and species level (residual d.f. 240) was made on plant measures at the mine overburden, the eroded oxisol and the iron crust oxisol using Genstat 5. An ANOVA stratified at the plot level (residual d.f. 6) was made on *Gymnostoma chamaecyparis* seedling measures on the hypermagnesian soil.

A simple ANOVA was made on root and shoot measures of broad leafed species (JMP 3™) harvested from a single block on the eroded oxisol site to test whether there were significant difference in plant root : shoot ratios between species and between treatments containing fertiliser and non-fertilised treatments.

An analysis of variance was made on soil pH and total concentrations of N, P, K, Na and Ca from simple treatment plots at each site to test whether soil were significantly different between fertiliser, litter, lime and bare ground treatments at the end of the field experiment (JMP 3™). Total Mn, Ni and Mg concentrations in soil were omitted from the ANOVA because these elements were absent in treatment applications.

Results of soil chemistry and temperature effects of shade are presented first to describe the treatment effects on sites. ANOVA results of plant growth measures are presented second to describe how treatments affected species at sites. Effects are reported for the stratified ANOVA when both the probability was significant ($p < 0.01$) and variance ratio exceeded 5.0 for at least one time period.

7.3 Results

7.3.1 Effects of treatments on soil chemistry

The soil chemistry of bare ground, litter, lime and fertiliser treatments plots at each site are presented in table 7.3. The ANOVA revealed that total soil N and P concentrations were significantly higher on fertiliser treatment plots and total calcium concentrations were significantly higher on lime treatments than other treatments at all sites. Sodium concentrations were marginally higher in soil of litter, lime and fertiliser treatment plots than on bare ground on the iron crust oxisol site. The ANOVA did not reveal a significant difference in soil pH between lime and other treatment plots except on the mine overburden site. Soil pH of lime treatment plots at this site was significantly higher than bare ground. Soil pH on litter and fertiliser treatments showed considerable variation between sites. On oxisol sites, there was a tendency for litter and fertiliser treatment to raise soil pH to levels slightly greater than bare ground. In contrast the soil pH of fertiliser treatment plots on the hypermagnesian soil site was slightly less than bare ground.

7.3.2 Light and temperature environments on field experiments

Periodic measures of PAR at all sites indicate that direct solar radiation ranged from 70-90% during relatively cloud free days to 15-20% during foggy days. Low light levels associated with foggy conditions were more frequent on the eroded oxisol site at Kouaoua than at the other sites. Measures of light underneath shade cloth indicate that plants received 50-60% less PAR at midday than on bare ground.

Measures of air + radiation temperature on treatment plots at the iron crust oxisol site during cloud free days in January 1994 showed that shade cloth reduced ground temperatures by 5 to 10°C (fig. 7.5). Mid to late afternoon air temperatures were similar to those beneath the canopy of *Gymnostoma deplancheanum* and rarely exceeded 30°C on shade treatment plots. In contrast, bare iron crust were experiencing temperature in excess of 40°C. Thermocouple measures of iron crust rock, revealed that these dark surfaces reached a temperature of up to 60°C during days where the ambient air temperature was 30°C. Serpentinite rock under full sun reached temperatures of 72°C at ambient air temperatures, similar to those on iron crust.

Table 7.3: The analysis of variance on $\log_{10}$ transformed total concentrations (ppm) of N, P, K, Na and Ca, and pH of soil from bare ground, litter, lime and fertiliser treatment plots at field sites. Significance is indicated, $p > 0.05$ = ns, $p < 0.05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***.

				Treatment means (ppm)			
Total, ppm	r^2	v.r.	s.e.d	Bare	Litter	Lime	Fertiliser
Mine overburden							
N	0.66	7.87 **	215	631	1016	991	2034
P	0.80	16.38 **	42	122	111	144	464
K	0.24	1.24	30	129	49	97	105
Na	0.26	1.38	18	168	122	97	133
Ca	0.64	7.25 **	1887	302	282	10356	190
pH	0.54	4.71 *	0.12	5.40	5.38	6.20	5.75
Eroded oxisol							
N	0.73	10.83 ***	113	970	1032	810	1656
P	0.62	6.55 **	38	192	197	209	397
K	0.31	1.81	19	53	43	44	73
Na	0.02	0.06	17	118	117	123	127
Ca	0.70	9.53 **	1269	157	178	8002	257
pH	0.45	3.33	0.17	5.95	6.27	6.70	6.20
Hypermagnesian soil							
N	0.96	38.05 **	434	2872	3475	3025	9065
P	0.99	1936.12 ***	3	96	78	90	353
K	0.72	3.47	40	214	146	76	131
Na	0.45	1.10	43	314	230	285	333
Ca	0.92	17.21 **	228	1326	1152	2483	1179
pH	0.78	4.67	0.15	6.35	6.55	6.90	6.15
Iron crust oxisol							
N	0.78	14.48 **	433	534	1376	1363	4288
P	0.76	12.82 **	50	191	265	192	564
K	0.24	1.31	152	4	65	274	237
Na	0.56	5.18 *	41	69	235	279	243
Ca	0.87	28.52 ***	2205	82	323	23829	426
pH	0.46	3.38	0.18	4.57	4.92	5.37	5.15

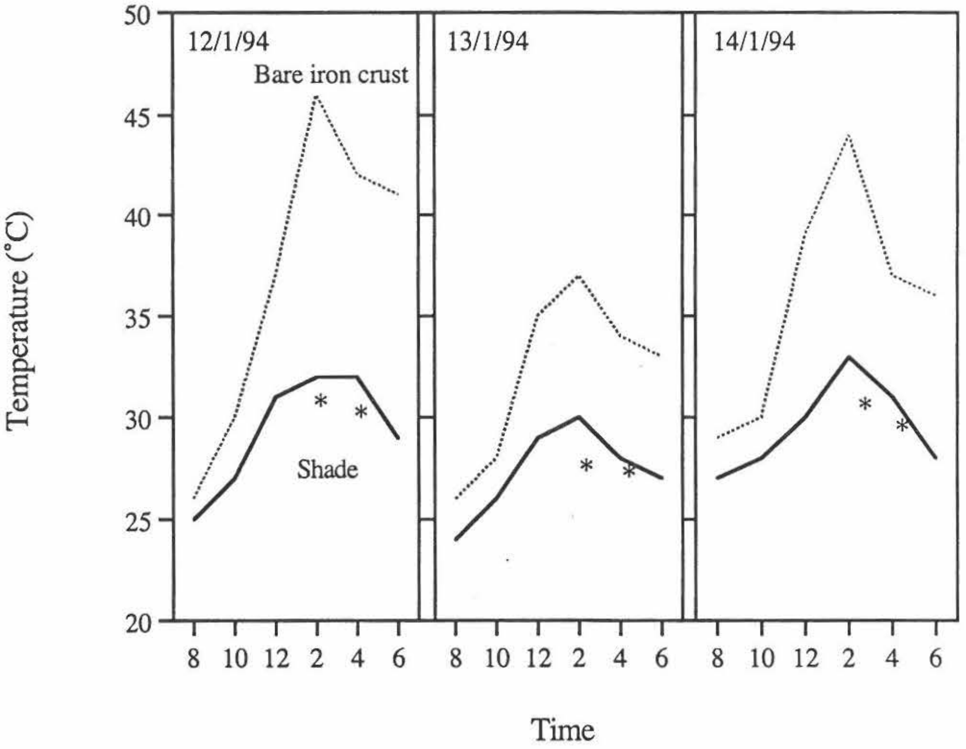


Figure 7.5 Mercury temperature at 10 cm above the ground on shade treatments and bare ground at the iron crust oxisol site. Measures were taken from the 12th to the 14th of January 1994. The temperatures recorded at 10 cm above the ground in tall maquis at 2 and 4 pm are given as *.

7.3.3 Seedling height

Analysis of variance of seedling heights showed a significant Fertiliser. Species interaction (fig. 7.6) and a significant Litter effect (fig. 7.7). Plants grew taller with fertiliser and litter than on treatments without fertiliser and litter, however there was considerable variation between species on fertiliser plots. *Gymnostoma* species grew much slower than broad leafed species on fertiliser treatment plots and *Gymnostoma nodiflorum* showed only marginal increase in height. *Carpolepis laurifolia* seedlings showed the greatest increase in growth on fertiliser treatment plots followed by *Grevillea exul* var. *rubiginosa* and *Austrobuxus carunculatus*. The ANOVA also revealed a significant Site.Litter.Fertiliser interaction (fig. 7.8) which indicated that plants grew taller on litter plus fertiliser treatment plots at the mine overburden site.

7.3.4 Relative shoot growth

The analysis of variance of relative shoot growth revealed a significant Litter (fig. 7.9), Fertiliser.Litter (fig. 7.10), Shade.Species (fig. 7.11) and Site.Fertiliser.Species interaction (fig. 7.12). In general, all species grew significantly faster on fertiliser plus litter combinations than on simple fertiliser and litter treatments. However, there was considerable variation between species and sites in relation to fertiliser treatment plots. Broad leafed species and *Gymnostoma deplancheanum* growth was marginally higher on fertiliser than treatments without fertiliser at the eroded oxisol and iron crust oxisol sites, and doubled in size on fertiliser treatments at the mine overburden site. *Gymnostoma chamaecyparis* grew much faster on the iron crust oxisol site than on other sites. *Gymnostoma nodiflorum* grew faster on fertiliser at the mine overburden and iron crust oxisol sites, but showed no response to fertiliser on the eroded oxisol site.

The Shade.Species interaction suggests that there was a significant variation in relative shoot growth between species with shade treatments. *Gymnostoma chamaecyparis* growth was significantly slower on shade treatments than on treatments without shade. Shade also had a marginally negative effect on *G. nodiflorum* and *Grevillea* relative growth. In contrast, *G. deplancheanum*, *Austrobuxus* and *Carpolepis* grew faster on shade treatments than on treatments without shade.

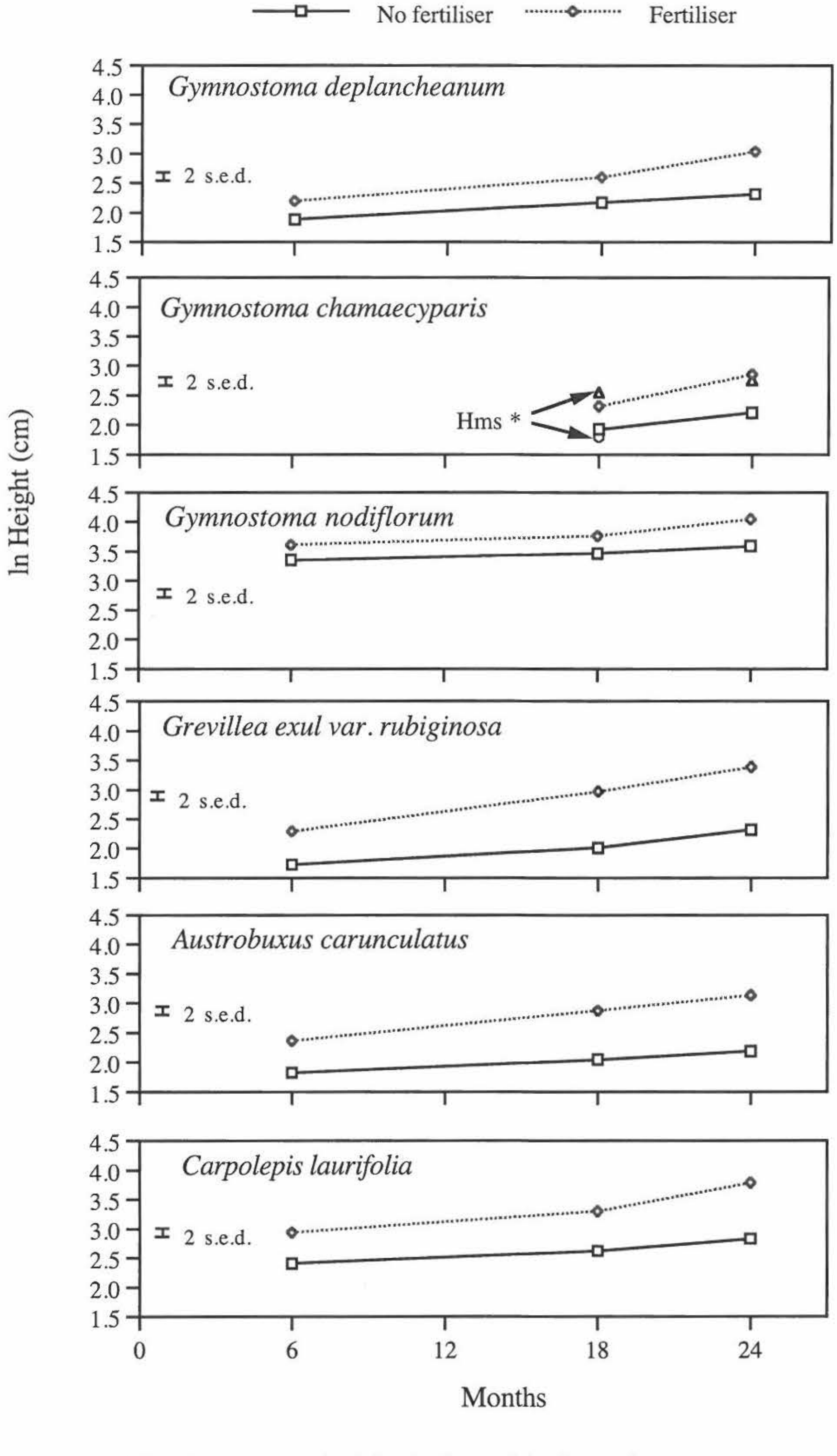


Figure 7.6 ln Average height (± 2 s.e.d.) of species on treatments with either no fertiliser or fertiliser after 6 months (v.r. = 8.27; $p < 0.001$), 18 months (v.r. = 19.63; $p < 0.001$) and 24 months (v.r. = 16.36; $p < 0.001$) at the iron crust oxisol, eroded oxisol and mine overburden Sites. The ln average height (± 2 s.e.d.) of *Gymnostoma chamaecyparis* seedlings at the hypermagnesian soil Site (Hms*) are after 18 months (v.r. = 29.45; p = 0.001) and 24 months (v.r. = 28.60; F prob.= 0.002).

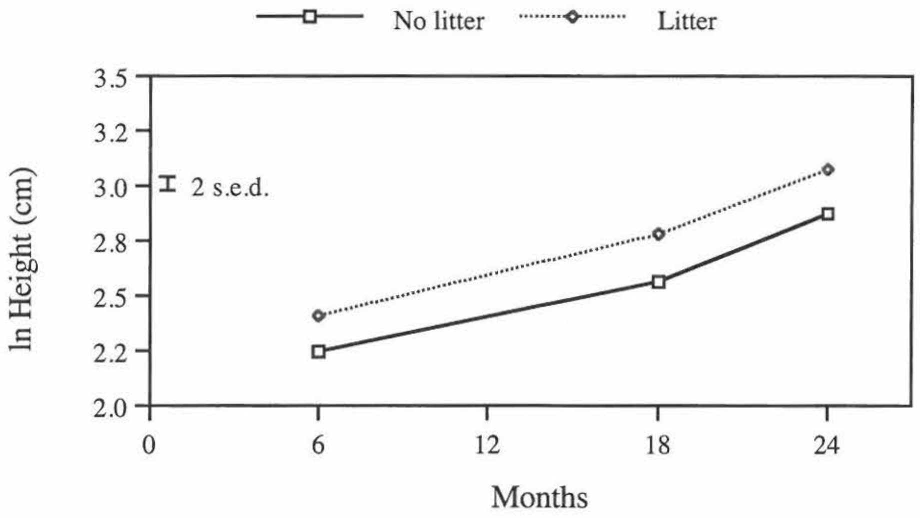


Figure 7.7 ln Average seedling height (± 2 s.e.d.) on no litter and Litter after 6 months (v.r. = 31.64; $p < 0.001$), 18 months (v.r. = 50.30; $p < 0.001$) and 24 months (v.r. = 36.49; $p < 0.001$) at the iron crust oxisol, eroded oxisol and mine overburden sites.

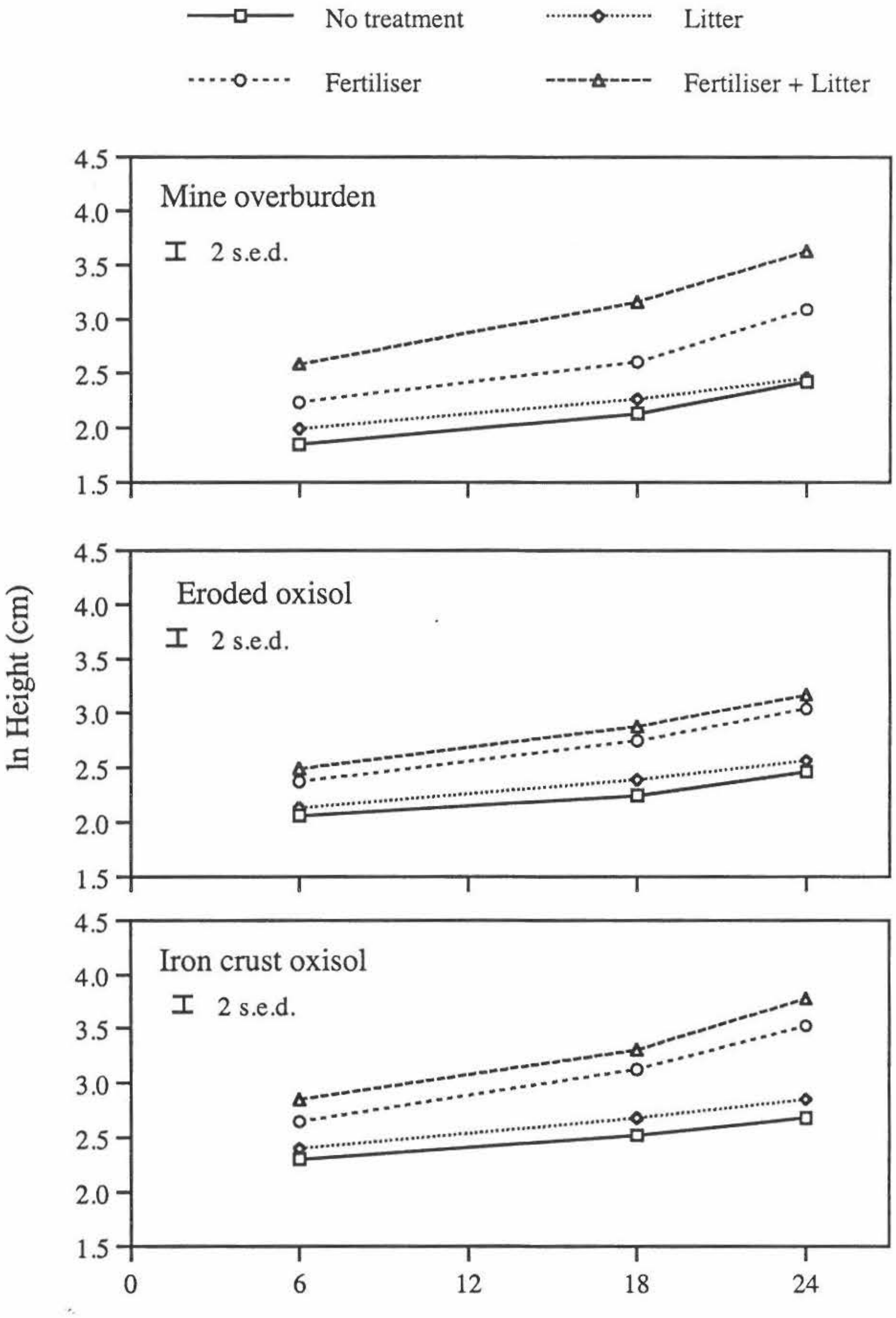


Figure 7.8 ln Average seedling height (± 2 s.e.d.) on no treatment, litter, fertiliser and fertiliser + litter treatment plots after 6 months (v.r. = 4.23; p = 0.046), 18 months (v.r. = 5.25; p = 0.024) and 24 months (v.r. = 9.29; p = 0.004) at the iron crust oxisol, eroded oxisol and mine overburden sites.

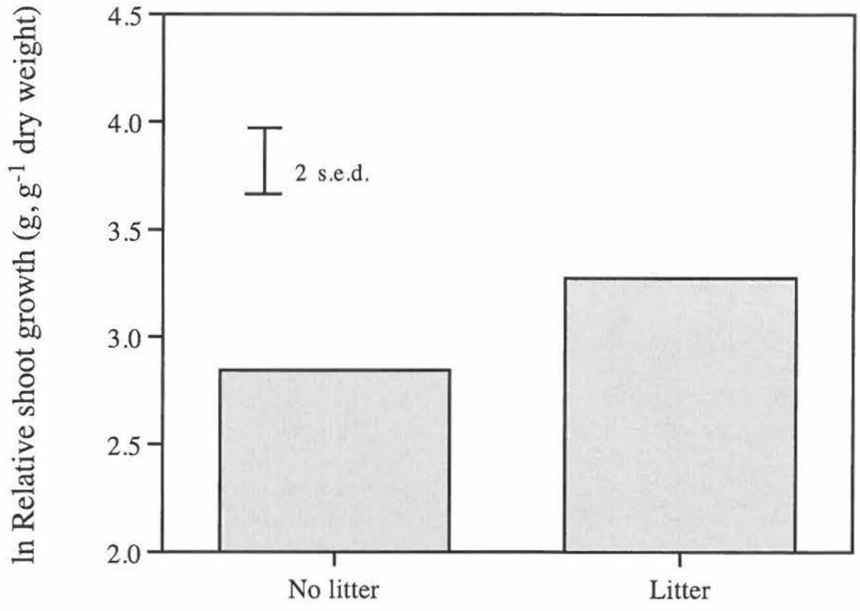


Figure 7.9 Average ln relative shoot growth (± 2 s.e.d.) of seedlings on no litter and litter (v.r. = 13.69; p < 0.001) at the iron crust oxisol, eroded oxisol and mine overburden aites.

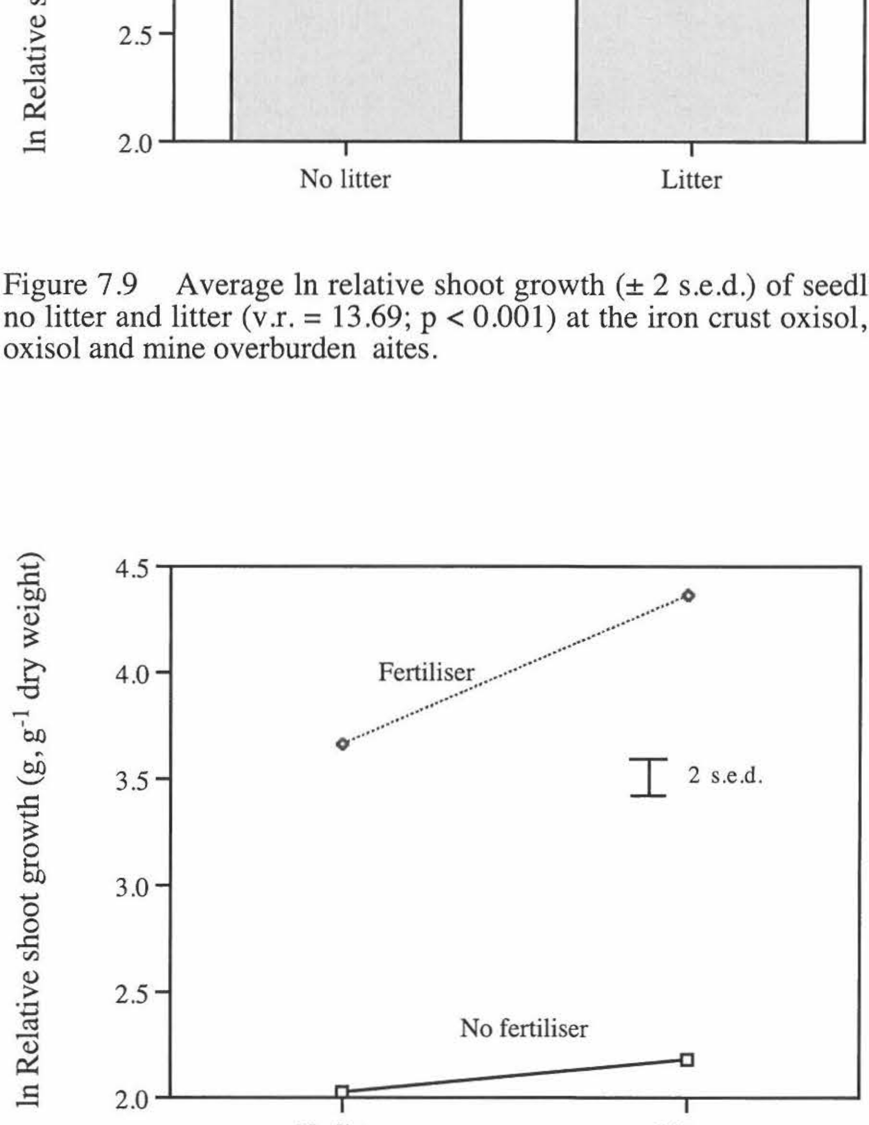


Figure 7.10 Average ln relative shoot growth (± 2 s.e.d.) of seedlings on no treatment, litter, fertiliser and fertiliser + litter (v.r. = 5.61; p = 0.023) at the iron crust oxisol, eroded oxisol and mine overburden sites.

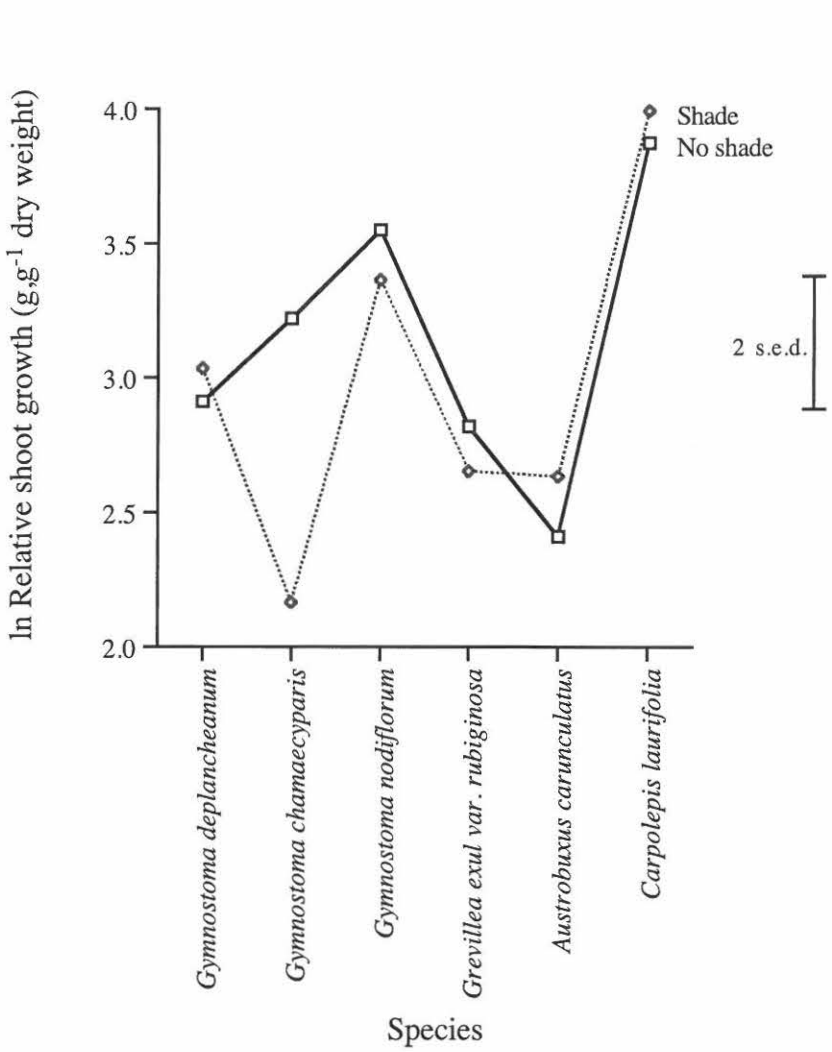


Figure 7.11 Average ln relative shoot growth (± 2 s.e.d.) of species on no shade and underneath shade (v.r. = 5.26; $p < 0.001$) at the iron crust oxisol, eroded oxisol and mine overburden sites. Note *G. chamaecyparis* was not present at the mine overburden site.

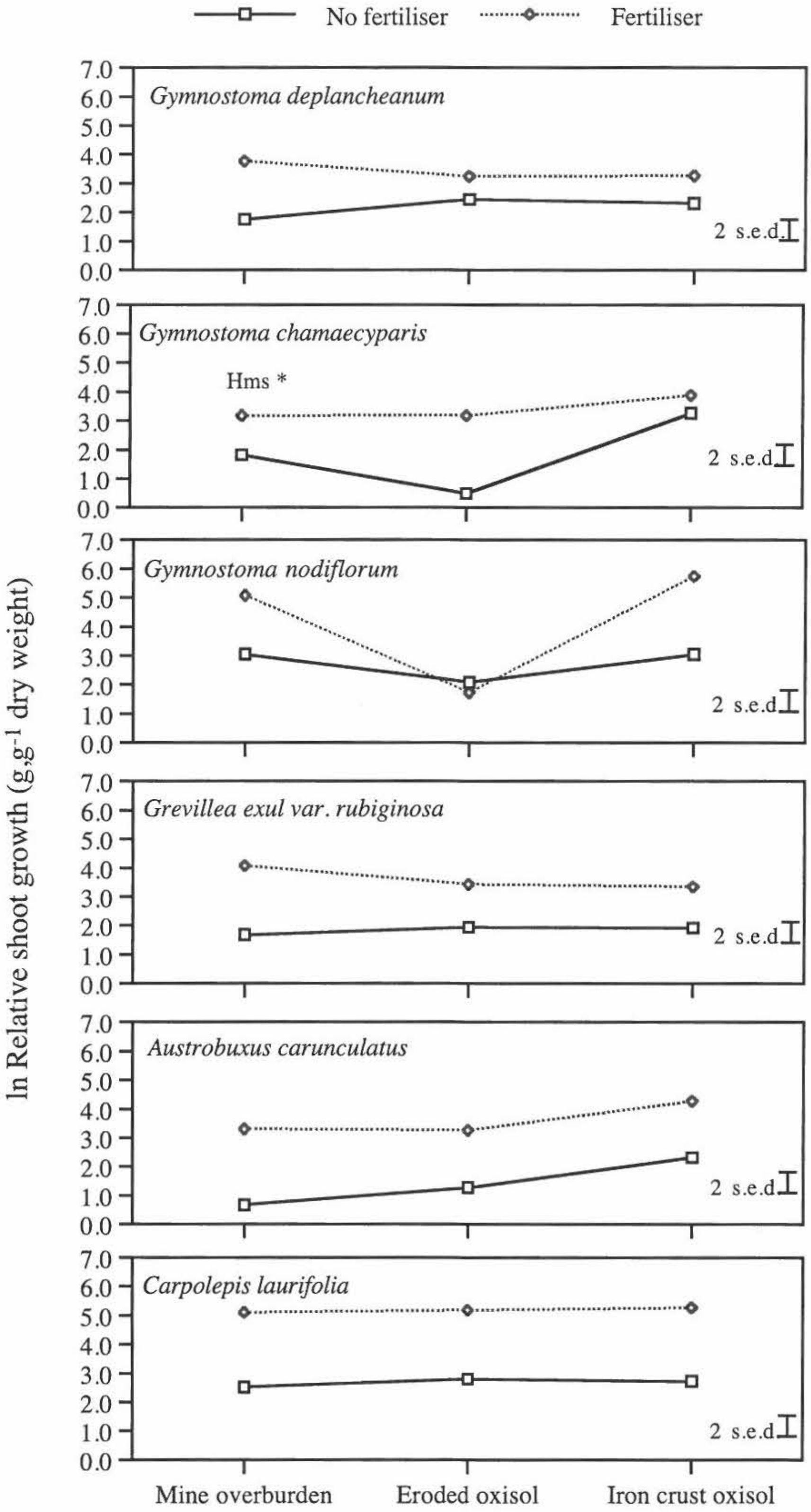


Figure 7.12 Average ln relative shoot growth (± 2 s.e.d.) of species on no fertiliser and fertiliser (v.r. = 6.96; $p < 0.001$) at the iron crust oxisol, eroded oxisol and mine overburden sites. The average ln relative shoot growth of *Gymnostoma chamaecyparis* at the hypermagnesian soil site (Hms*) is also given for seedlings on no fertiliser and fertiliser (v.r. = 23.14; $p = 0.003$).

7.3.5 *Gymnostoma* root : shoot ratios

The ANOVA of *Gymnostoma* root : shoot ratios showed a significant Fertiliser.Species interaction (fig. 7.13), Litter.Lime interaction (fig. 7.14) and a Shade.Lime interaction (fig. 7.15). This suggests the while root development in *Gymnostoma* species was relatively greater on bare ground than on fertiliser and litter, *G. chamaecyparis* root development was much greater on bare ground. Root development was significantly greater on lime and litter plots than on bare ground.

The ANOVA of root : shoot ratios of broad leafed species at the eroded oxisol site only indicated a significant Species interaction (fig. 7.15). Root development in *Grevillea* was less than in *Austrobuxus* and *Carpolepis*, and showed a trend that was similar to *Gymnostoma* Species whereby seedling root systems were more extensive on bare ground than on fertiliser. *Carpolepis* root weight was in general more than the other species. Measures of root length on the eroded oxisol site revealed that *Carpolepis* possessed a very extensive shallow root system that attained lengths of > 2 m (fig. 7.16).

7.3.6 Total *Frankia* nodule weight on *Gymnostoma*

The ANOVA of total *Frankia* nodule weight (+1) (g) showed a significant Site.Fertiliser.Species interaction (fig. 7.17) and a Lime.Species interaction (fig 7.18). In general, total *Frankia* nodule weight was higher on fertiliser treatment plots than on bare ground. However, there was considerable variation between species and sites. *G. nodiflorum* produced a larger weight of nodules with fertiliser, while the other species only showed a marginal response.

Gymnostoma nodiflorum produced significantly fewer nodules on lime. The other *Gymnostoma* species showed a slightly negative response to lime that wasn't significant.

7.3.7 Seedling mortality at field experiment Sites

Seedling mortality (table 7.4) was higher on the eroded oxisol site than at the other sites. In general all species showed higher mortality on treatment plots containing fertiliser. *Gymnostoma chamaecyparis* seedling mortality was high compared to all other species.

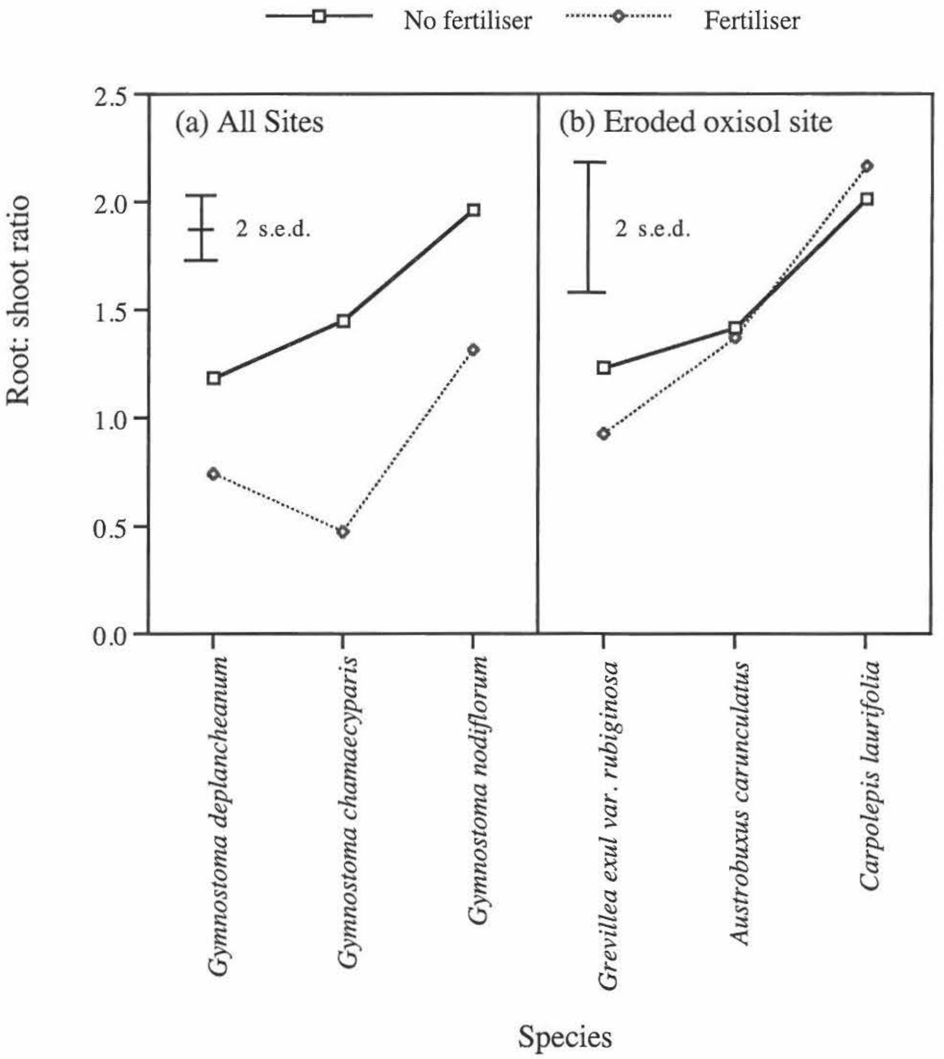


Figure 7.13 (a) Average root : shoot ratio of *Gymnostoma* Species on no fertiliser and fertiliser (v.r. = 6.37; p = 0.003) at the iron crust oxisol, eroded oxisol and mine overburden sites. The standard error of deviation of *Gymnostoma* root : shoot ratios is assymetrical. (b) Average root : shoot ratio (± 2 s.e.d.) of broad leafed species on treatments with and without fertiliser at the eroded oxisol site (v.r. = 5.92; p = 0.005).

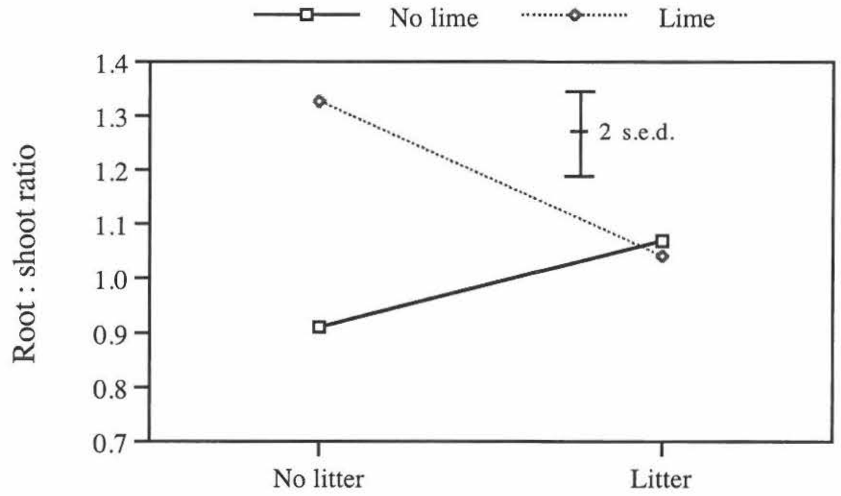


Figure 7.14 Average root : shoot ratio of *Gymnostoma* on no treatment, litter, lime andlitter + lime treatments plots (v.r. = 6.64; F prob. = 0.014) at the iron crust oxisol, eroded oxisol and mine overburden sites. The standard error of deviation is assymetrical.

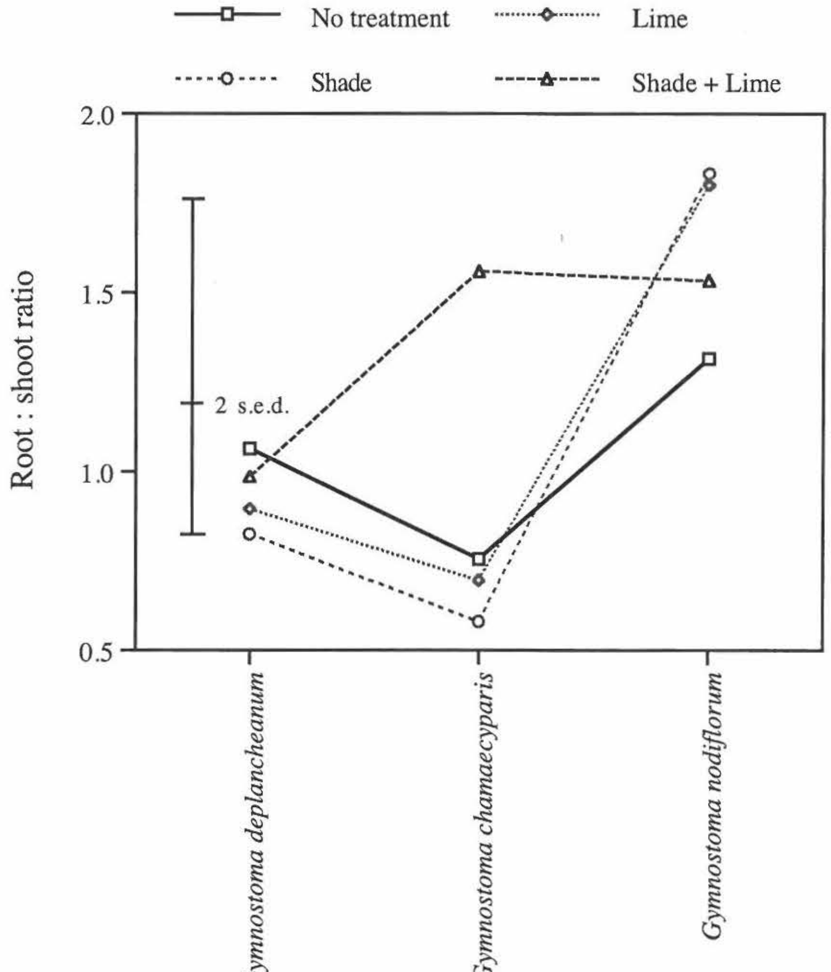


Figure 7.15 Average root : shoot ratio of *Gymnostoma* species on no treatment, shade, lime and lime + shade treatment plots (v.r. = 6.28; p = 0.003) at the iron crust oxisol, eroded oxisol and mine overburden sites. The standard error of deviation is assymetrical.

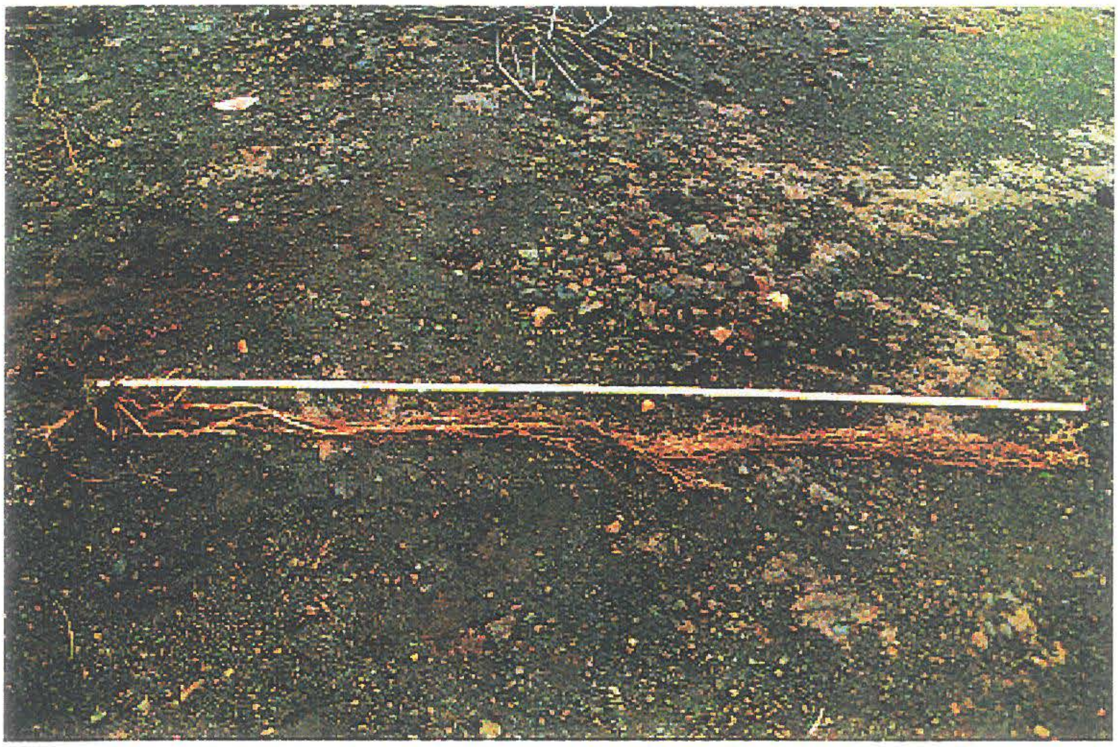


Figure 7.16 The root system of a 2 yr old *Carpolepis laurifolia* seedling harvested from a fertiliser x litter treatment on the eroded oxisol site at Kouaoua. The root system is 2 m long. Note that the eroded oxisol surface consists of compacted clay and contains only a thin layer of gravel.

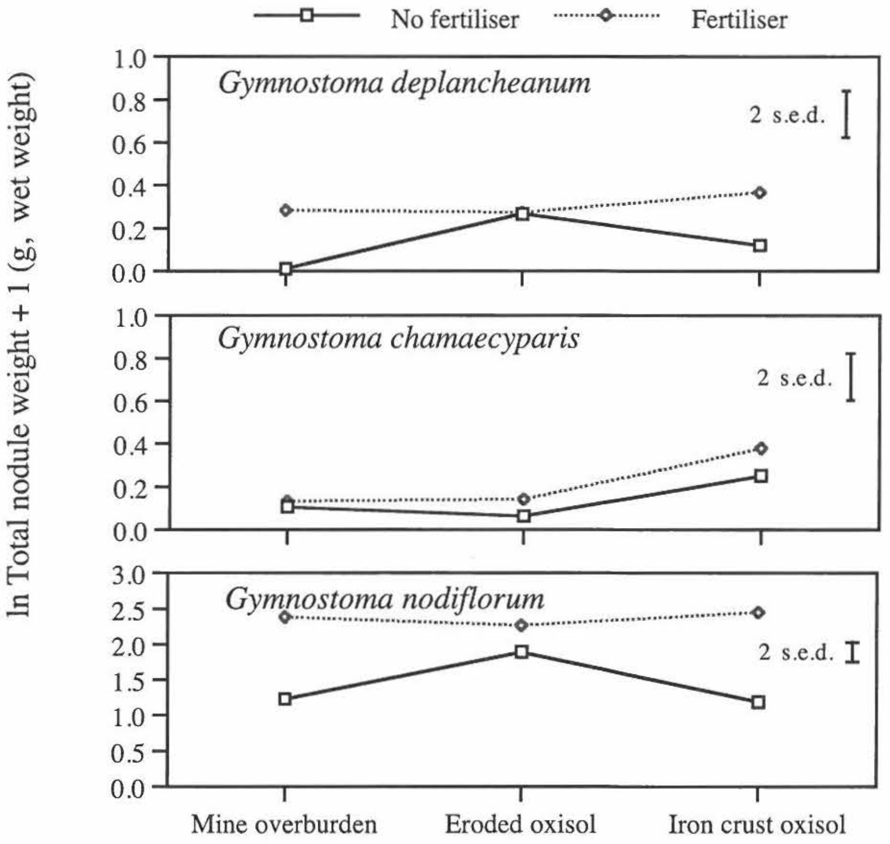


Figure 7.17 Average ln total *Frankia* nodule weight + 1 (± 2 s.e.d) of *Gymnostoma* species on no fertiliser and fertiliser (v.r. = 9.85; $p < 0.001$) at the iron crust oxisol, eroded oxisol and mine overburden sites.

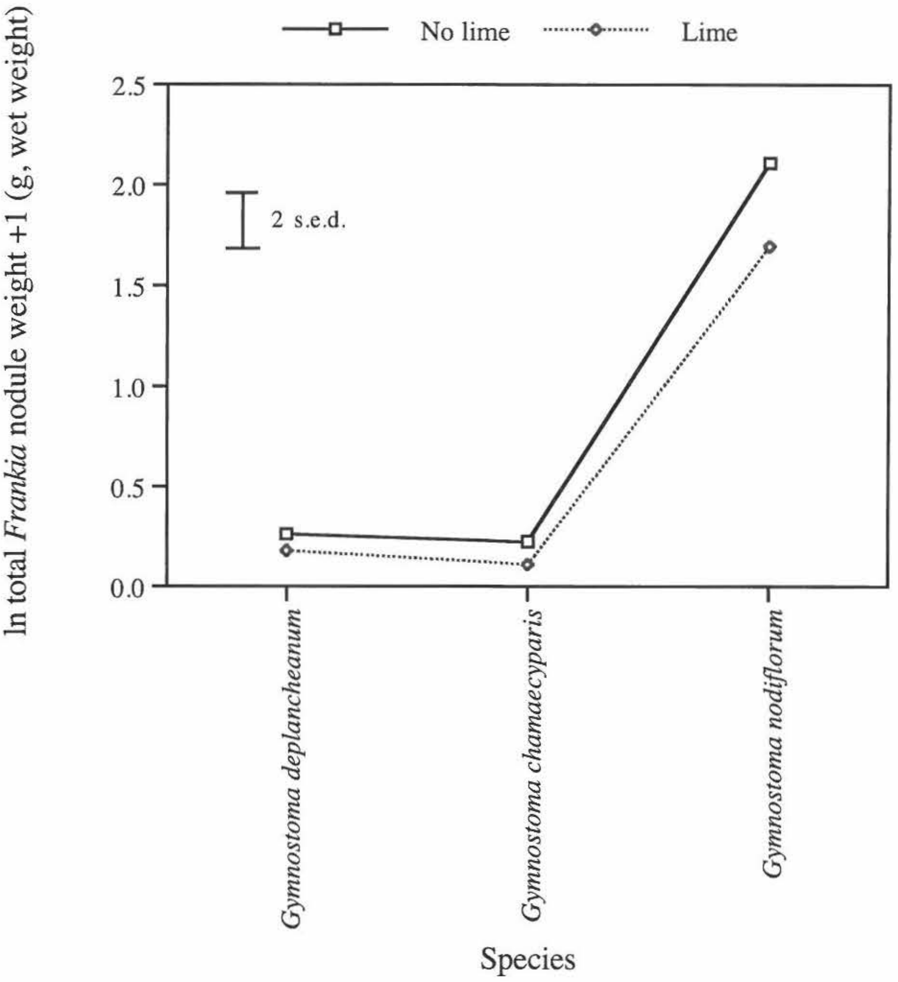


Figure 7.18 Average ln total *Frankia* nodule weight + 1 (± 2 s.e.d.) of *Gymnostoma* species on no lime and lime (v.r. = 5.87; p = 0.004) at the iron crust oxisol, eroded oxisol and mine overburden sites.

7.3.8 Chlorophyll fluorescence response of plants to treatments.

Chlorophyll fluorescence measures (fig. 7.19) indicate the *Fv/Fm* ratios of seedling leaves generally declined from early morning to midday and *Fo* values increased. However there was considerable variation between species, sites and days sampled. Fluorescence measures at the iron crust oxisol site and mine overburden site were conducted during relatively cloud free periods in December 1994. Chlorophyll in plant leaves became increasingly stressed by a combination of high light and substrate conditions at these sites evident from increasing *Fo* values. Furthermore, the *Fv/Fm* ratio of *Grevillea* leaves were consistently low for early morning and midday measures on the mine overburden site indicating that this species was experiencing chronic stress. Plants on the eroded oxisol Site showed only a marginal increase in *Fo* values and a slight reduction in *Fv/Fm* ratios at midday possibly because fog had reduced radiation levels on plots and therefore reduced stress to the photosynthetic apparatus of plant leaves caused by a combination of high light and substrate conditions.

The analysis of variance indicated that Shade, Fertiliser and Litter (fig. 7.20) had significant effects on the *Fv/Fm* ratio of seedlings at early stages of field experiments. Moreover, there were also significant differences in *Fv/Fm* ratios between Species (fig. 7.21). Fluorescence measures after 6 months showed that *Gymnostoma deplancheanum*, *G. nodiflorum* and *Grevillea exul* possessed relatively similar *Fv/Fm* ratios that were significantly higher than *Austrobuxus carunculatus* and significantly lower than *Carpolepis laurifolia*. *Fv/Fm* ratios of *Gymnostoma deplancheanum*, and *Austrobuxus carunculatus* seedlings showed a decline at the end of the experiment suggesting that these species were becoming increasingly stressed by the conditions at all sites. *Gymnostoma chamaecyparis* seedlings at the eroded oxisol site and iron crust oxisol site also possessed low *Fv/Fm* ratios at the end of the field experiment suggesting that this species may have been stressed by the conditions at these Sites. In contrast, fluorescence measures at the hypermagnesian soil site showed *G. chamaecyparis* seedlings possessed *Fv/Fm* ratios of 0.8 suggesting that seedlings were less stressed than at other sites. *Fv/Fm* ratios of *Gymnostoma nodiflorum*, *Grevillea exul* and *Carpolepis laurifolia* seedling increased over the same time period suggesting that they were becoming accustomed to conditions at all sites.

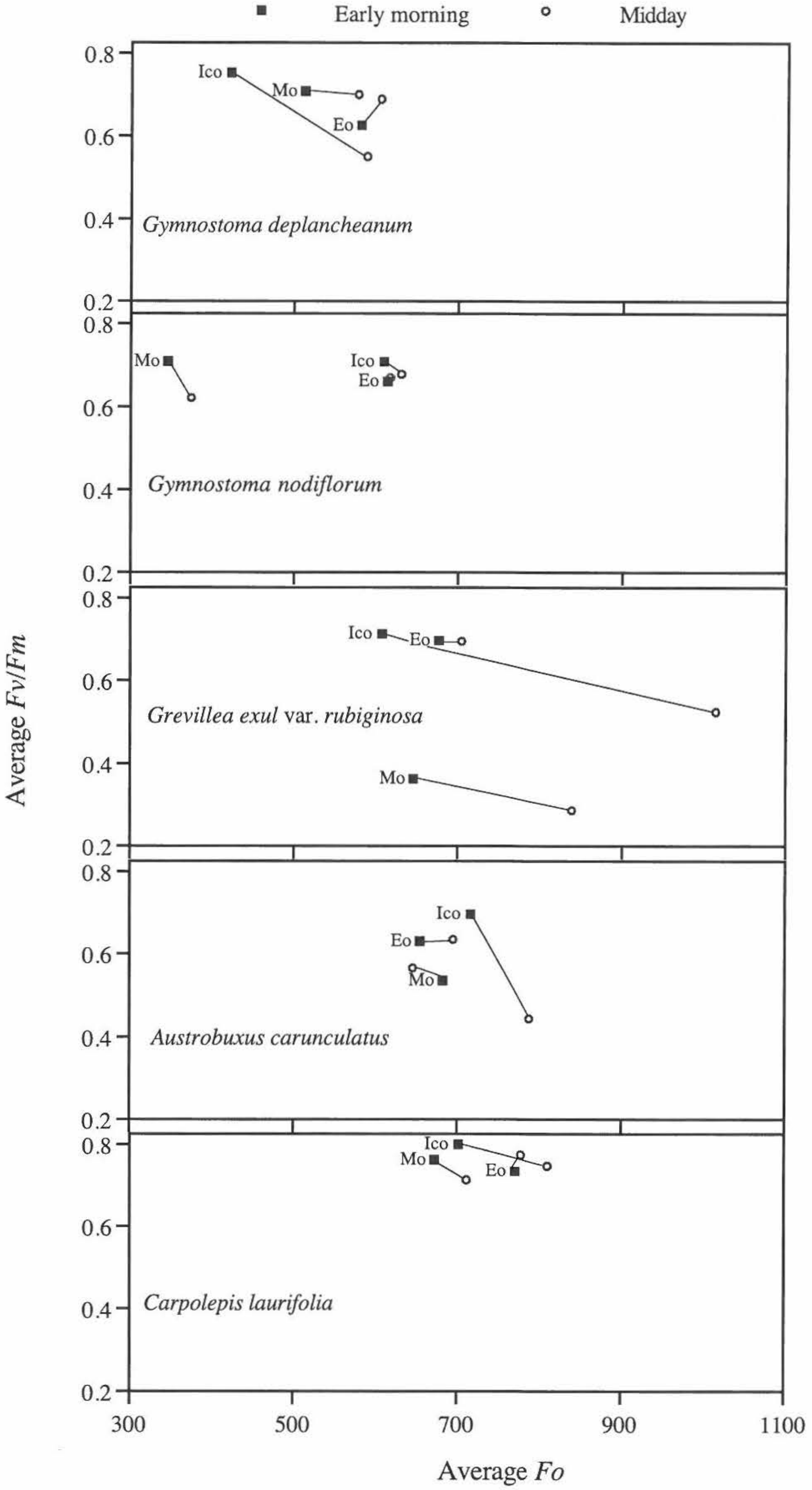


Figure 7.19 Average trends in *Fv/Fm* and *Fo* of species recorded during the early morning and at midday at the iron crust oxisol (Ico), eroded oxisol (Eo) and mine overburden (Mo) sites.

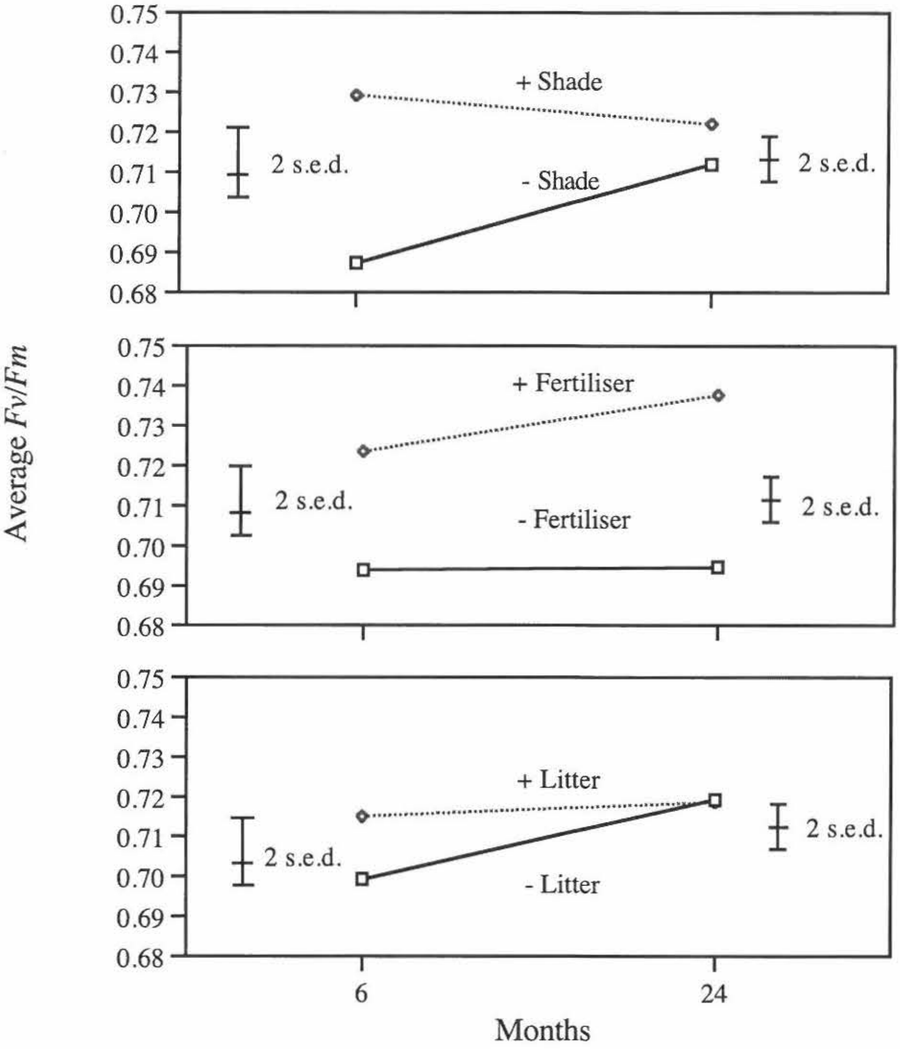


Figure 7.20 Effects of shade (top), fertiliser (middle) and litter (bottom) on the average *Fv/Fm* of seedlings after 6 months (Shade: v.r. = 52.03; $p < 0.001$; Fertiliser: v.r. = 25.98; p = < 0.001; Litter: v.r. = 11.02; $p = 0.002$) and 24 months (Shade: v.r. = 2.45; $p = 0.125$; Fertiliser: v.r. 45.27; $p < 0.001$; Litter: v.r. = 0.43; $p = 0.515$) at the iron crust oxisol, eroded oxisol and mine overburden sites. The standard error of deviation for both time periods is assymetrical.

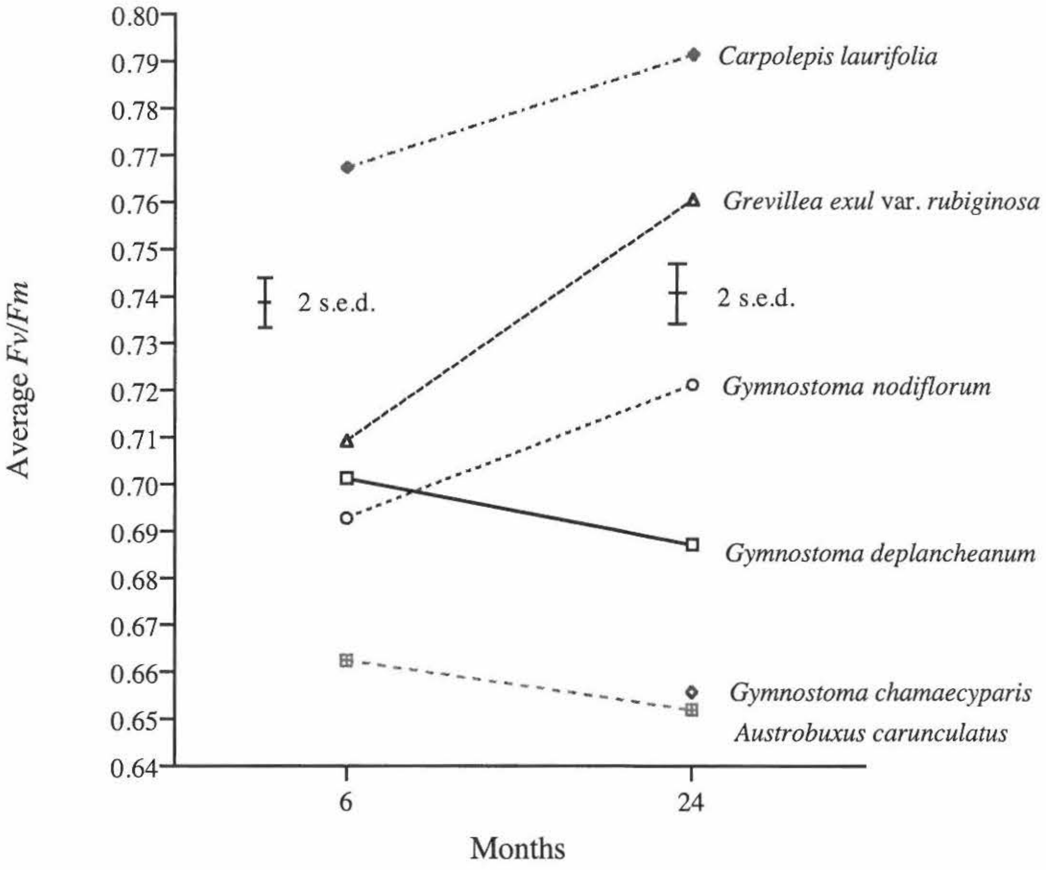


Figure 7.21 The average *Fv/Fm* of species at the iron crust oxisol, eroded oxisol and mine overburden sites after 6 months (v.r. = 66.10; $p < 0.001$) and 24 months (v.r. = 111.87; $p < 0.001$). The standard error of deviation for both time periods is assymetrical.

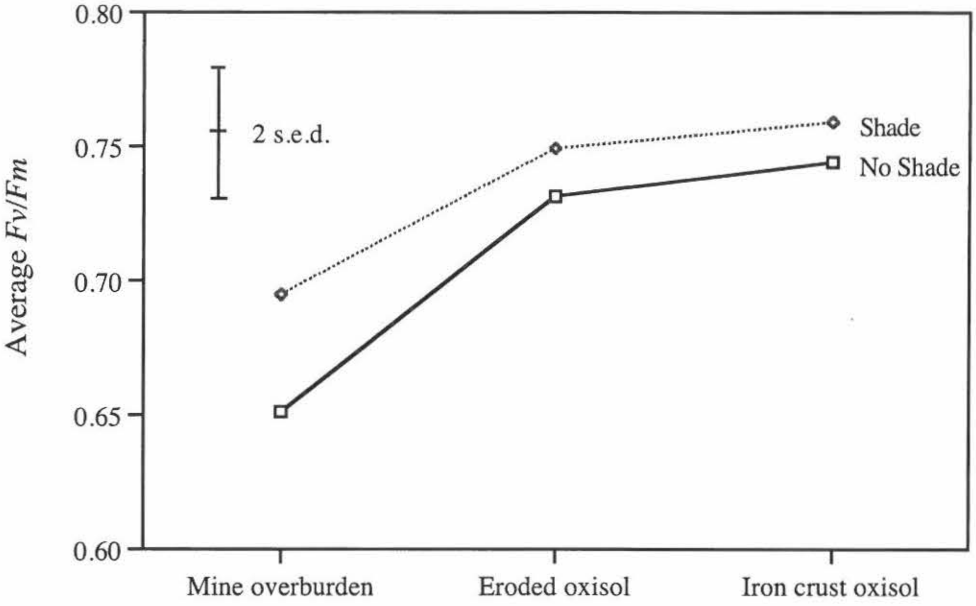


Figure 7.22 Average *Fv/Fm* of seedlings at the iron crust oxisol, eroded oxisol and mine overburden sites (v.r. = 8.83; $p < 0.001$) after 24 months. The standard error of deviation is assymetrical.

Table 7.4: Seedling deaths over the entire experiment of species on treatments plots with (n = 192) and without Fertiliser (n = 192) at each site.

	Mine Overburden			**Eroded oxisol**			**Iron crust oxisol**		
	Fertiliser	Other	Total	Fertiliser	Other	Total	Fertiliser	Other	Total
Gymnostoma deplacheanum	1	0	2%	1	0	2%	3	0	5%
Gymnostoma nodiflorum	1	0	2%	3	0	5%	0	0	0%
Grevillea exul var. *rubiginosa*	1	0	2%	6	0	9%	3	0	5%
Austrobuxus carunculatus	1	0	2%	0	1	2%	3	0	5%
Carpolepis laurifolia	0	0	0%	3	0	5%	0	0	0%

	Hypermagnesian soil			**Eroded oxisol**			**Iron crust oxisol**		
	Fertiliser	Other	Total	Fertiliser	Other	Total	Fertiliser	Other	Total
Gymnostoma chamaecyparis	8	8	25%	10	7	27%	5	2	11%

Significant treatment effects at the mine overburden site, the eroded oxisol site and the iron crust oxisol site suggest that seedlings on shade, fertiliser and litter treatment plots had much higher Fv/Fm ratios than on treatments without shade, fertiliser and litter at early stages of the experiment. Fertiliser continued to have a significantly positive effect on Fv/Fm ratios of seedling leaves at the end of the experiment. In contrast, litter and shade were no longer having a significant effect on the photosynthetic efficiency of seedling leaves at the end of the experiment. A significant Site. Shade interaction (fig. 7.22) at the end of the experiment suggests that the Fv/Fm ratio of plant leaves were lower on shade than on treatments without shade, but showed significant variation between sites arising from different climate conditions during measuring periods. Fluorescence measures at the iron crust and eroded oxisol sites in July 1995 were conducted under relatively overcast weather that may have alleviated plant stress from a combination of high light and substrate conditions. In contrast, fluorescence measures at the mine overburden site were conducted under high light conditions that generated a significant difference between shade and treatments without shade.

7.3.9 Plant : soil element ratios

The $\log_{10}$ ratio of foliar : soil element concentrations were calculated for bare ground and litter treatment plots to give an indication of plant uptake relative to the soils. Figure 7.23 indicates that N, P, K, Na and Ca concentrations are higher in species leaves than in the underlying soil. In contrast plant : soil ratios indicate that foliar concentrations of Ni, Mn and Mg are lower than in soil (fig. 7.24).

7.4 Discussion

The field experiments address how certain processes affected plant growth on different types of bare ultramafic substrate. The emphasis of the first part of the discussion is on describing the site conditions and how factors regarded as being important such as shade and litter influenced plant growth on bare ultramafic surfaces. The second part of the discussion focuses on how mine revegetation treatments such as fertiliser and lime applications affected the growth of maquis species.

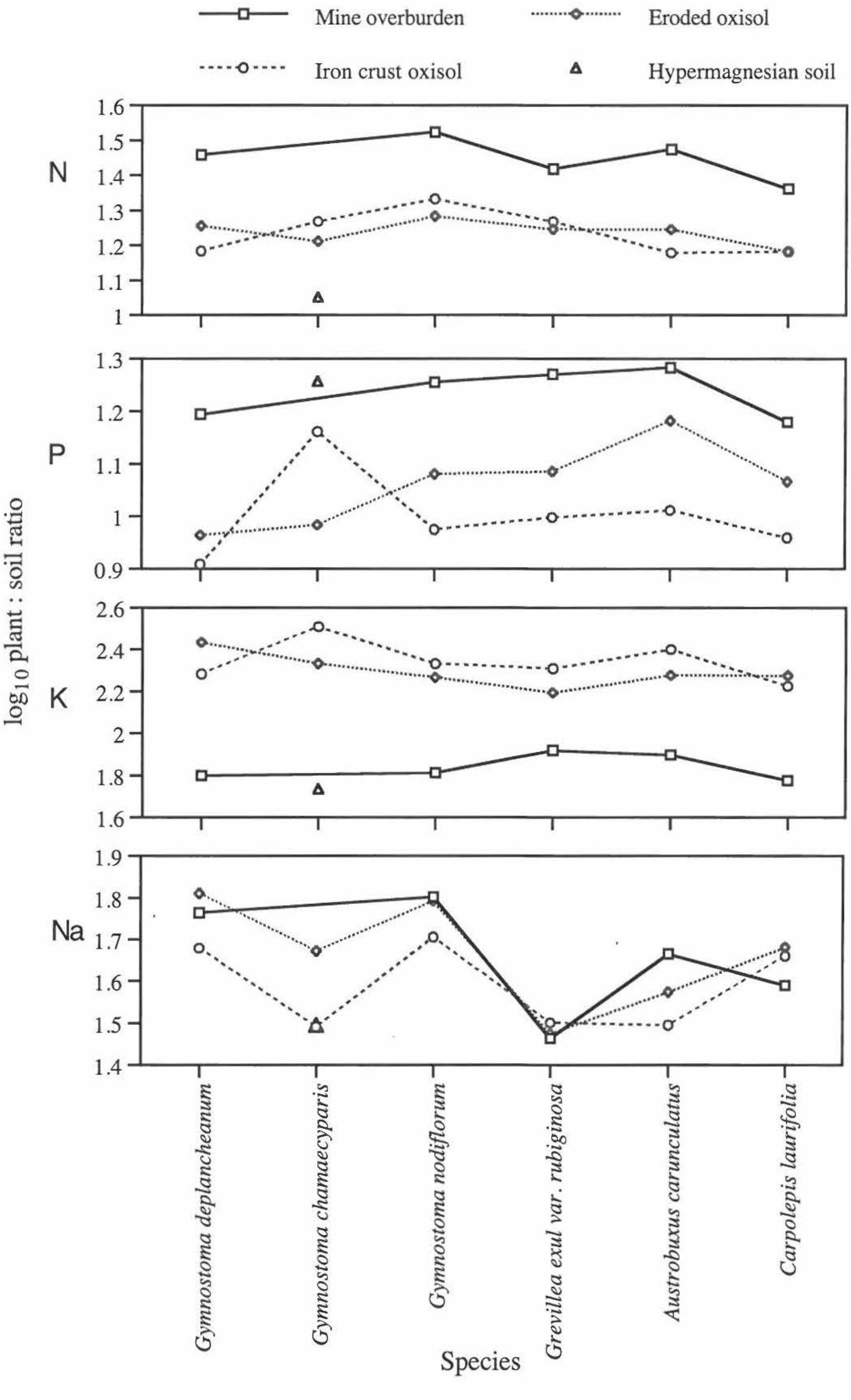


Figure 7.23 $\log_{10}$ Average plant : soil ratio of total N, P, K and Na of species on bare ground + litter treatment plots at the iron crust oxisol, eroded oxisol, mine overburden and hypermagnesian soil sites.

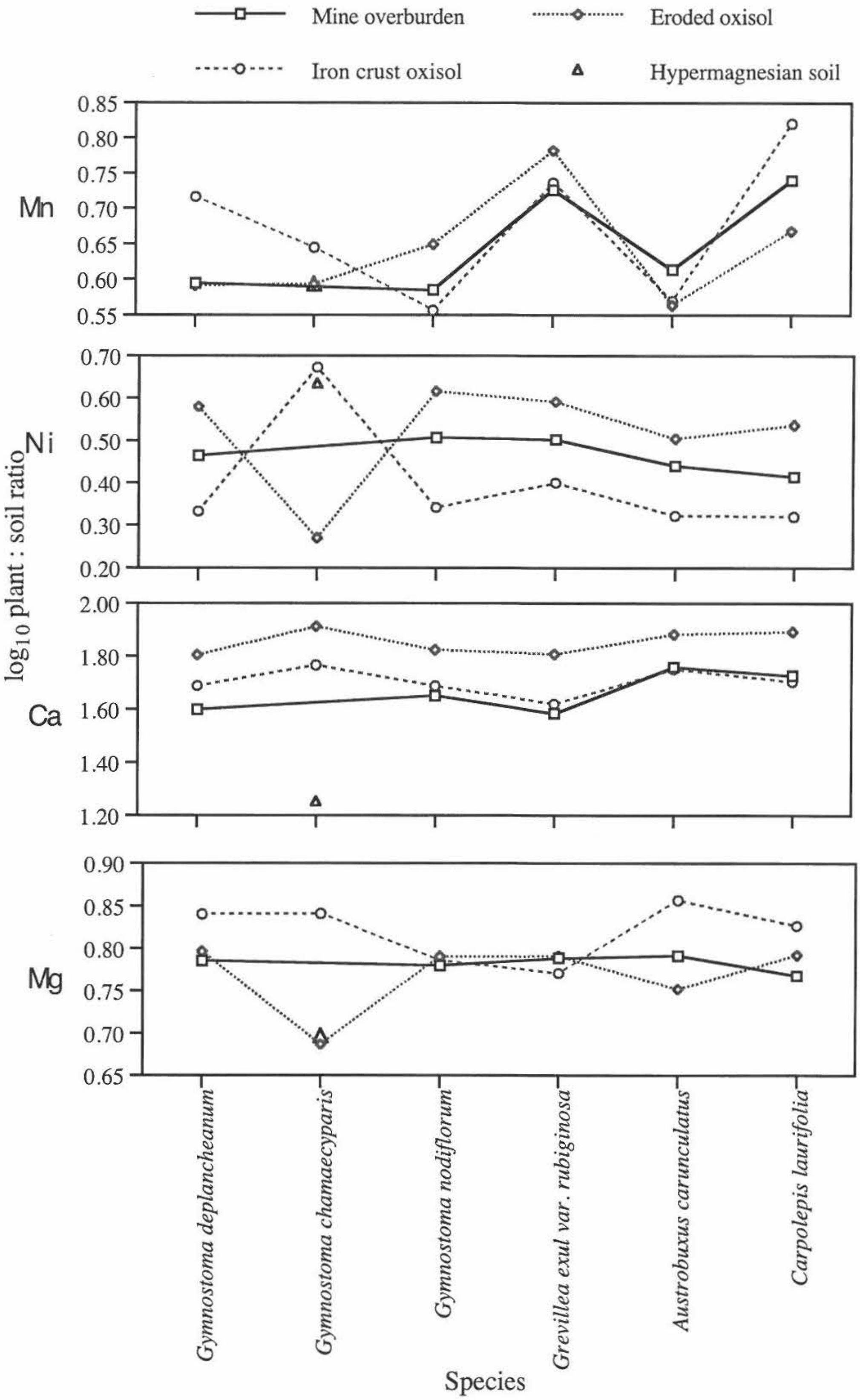


Figure 7.24 $\log_{10}$ Average plant : soil ratio of total Mn, Ni, Ca and Mg of Species on bare ground + litter treatment plots at the iron crust oxisol, eroded oxisol, mine overburden and hypermagnesian soil sites.

7.4.1 The environment of bare ultramafic substrates

Field sites experienced weather conditions ranging from rain deficits in late 1993 (July to December) when rainfall was below monthly averages to torrential rain (341 mm at Kouaoua, 399-1056 mm at Plaines des Lacs in 48 hours) and high wind speeds (120 km hr^{-1}) associated with cyclone Rewa (3-5/01/94). Light environments differed with high altitude Sites at Kouaoua experiencing more frequent fog. Measures of temperature 10 cm above bare ground indicate that seedlings were experiencing temperatures in excess of 40°C on cloud free days. Surface temperatures of serpentinite were high compared to iron crust and probably reflect a combination of high light effects and low soil moisture conditions of hypermagnesian soil at Kouaoua (Rigault *et al*, 1996).

Soil surveys indicate that there were major differences in physical and chemical soil properties between experimental sites (table 2.2) that may directly affect plant growth and indirectly impact on the properties of litter, lime and fertiliser. Hydrological properties of soils at the iron crust oxisol site, the hypermagnesian soil site potentially favoured greater root development because of the loose soil structure containing large pore spaces. Conversely, the high porosity of these substrates may have stressed drought sensitive species. Measures of hydraulic conductivity indicated that the eroded oxisol site contained large pore spaces and were therefore free draining. In reality free draining soil properties were limited to a shallow gravelly horizon < 10 cm deep. The underlying B horizon consisted of colluvial debris and compacted clay that potentially retained moisture for longer periods (table 2.1), but also experienced waterlogging during heavy rain. Similar clayey structural properties were recorded at the mine overburden site. Hydraulic conductivity measures indicate that pore spaces in this clayey substrate were very small and saturated rapidly causing water to descend at depth very slowly. This slow water movement may suggest that soil moisture levels were higher than at other sites. However under heavy rain, low porosity also led to frequent waterlogging that may have restricted root activity.

Field sites generally contained much lower concentrations of N, P, K Na and Ca than in the underlying soil of surrounding vegetation (fig. 6.2 a, b). Soil Ni, Mn and Mg concentrations at the mine overburden site were exceptionally high compared to the other sites and adjacent eroded oxisol.

Plant : soil element concentration ratios of N, P, K, Na, Mn, Ni, Ca and show considerable variation between sites and species (figs. 7.23 & 7.24) that may reflect differences in physiological allocation between species and element availability in substrates. However several generalisations can be made between sites assuming that foliar concentrations provide a rough indication of element absorption from the soil. Plant : soil ratios of N and P are higher on the mine overburden site than other Sites. In contrast, plant : soil ratios of K are lower on the mine overburden Site than the other Sites. Plant : soil ratios of nickel and calcium are higher at the eroded oxisol Site than at the other Sites. Plant : soil ratios of Na, Mn and Mg show considerable variation between Species and between Sites.

7.4.2 Effects of Shade

Plants on bare ground often experienced photoinhibition during cloud free days at early stages of the experiment. Low *Fv/Fm* ratios and high *Fo* values recorded on plants at midday are indicative of photoinhibition (fig. 7.19). Photoinhibition is both a symptom and a cause of plant stress and arises when plants are unable to overcome photodamage from high light environments or avoid damage through photoprotection. Photoinhibition results in an overall reduction in photosynthetic activity (Osborn, 1994; Raven, 1995). Stress to photosynthetic mechanisms may inturn raise respiration and reflect a plants inability to cope with other factors such as limited nutrient availability (Raven, 1995). In most cases, seedlings recovered from high light conditions during periods of reduced solar radiation. However certain species at the mine overburden site exhibited chronic photoinhibitive stress suggesting that photosynthetic mechanisms were severely damaged by site conditions.

Shade cloth reduced solar radiation and temperatures to levels that were similar to that underneath trees in adjacent maquis (fig. 7.5). This had a significant effect on seedlings at early stages of the experiment by raising *Fv/Fm* ratios (fig. 7.20). High *Fv/Fm* ratios are characteristic of a greater photosynthetic efficiency and a reduction in transpiration suggesting that shade reduced plant stress due to site conditions. Fluorescence measures at the end of the experiment indicated that shade was no longer having a major effect on seedlings. Taller species (*Gymnostoma nodiflorum*, *Grevillea exul* var. *rubiginosa* and *Carpolepis laurifolia*) showed an increase in *Fv/Fm* at the end of the experiment suggesting that they had become accustomed site conditions (fig. 7.25). In contrast, *Austrobuxus* showed a decline in *Fv/Fm* ratios possibly because the site conditions were unsuitable

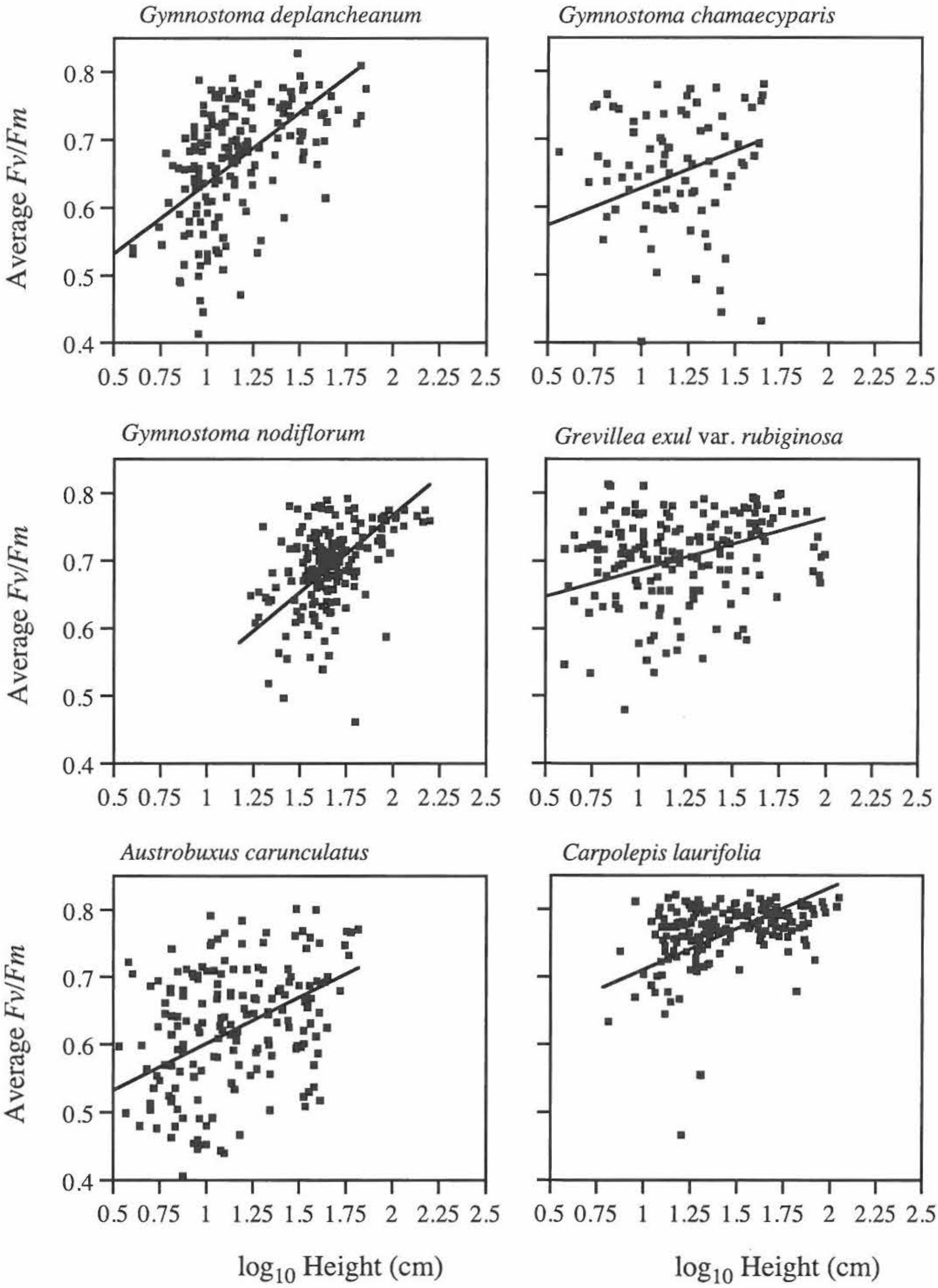


Figure 7.25 Average *Fv/Fm* plotted against $\log_{10}$ height of species after 24 months for all sites except the hypermagnesian soil site. Trends are indicated by linear regression lines.

for this late successional forest species. *Gymnostoma deplancheanum* seedlings were relatively small compared to the other species at end of the experiment and showed a decline in *Fv/Fm* ratios probably due to continued stress from a combination of climatic and substrate conditions at sites. Fluorescence measures at the end of the experiment indicate that *G. chamaecyparis* seedlings were stressed by conditions at the oxisol sites but not at the hypermagnesian soil site.

The shade treatment had no significant effects on seedling growth in most species, but had a significant negative effect on relative shoot growth of *G. chamaecyparis*. This negative effect is likely to have been partly driven by the poor development of this species at the eroded oxisol site.

7.4.3 Effects of Litter

Litter provided higher amounts of N (39.34 g) and lower amounts of P (0.26 g) and K (0.76 g) than fertiliser. This organic medium decayed to produce a coarse humus that potentially decreased soil moisture evaporation by reducing the penetration of solar radiation (refer to chapter 6). Soil nutrient analysis indicate that N concentrations underneath litter at the end of the experiment were low compared to fertiliser, but higher than bare ground (table 7.3). This suggests that N may have been largely bound up with cladode lignin (Constantides & Fownes, 1994) and therefore released at much lower rates than fertiliser. P, K, Na and Ca concentrations were similar to bare ground suggesting either that these elements were leached or absorbed by plants.

Fluorescence measures indicate that *Fv/Fm* ratios were significantly higher for seedlings on litter than for seedling with no litter after 6 months (fig. 7.20). This suggests that seedlings overcame photoinhibitive stress of high respiration and photodamage by obtaining moisture and nutrients from litter. Root : shoot ratios indicate that *Gymnostoma* root systems were more extensive on litter than on treatments without litter possibly in response to a combination of greater soil moisture and low nutrient availability (fig. 7.14). Low nutrient release from litter decay resulted in plants generally being smaller than on fertiliser but twice as large as plants with no litter in terms of height (fig. 7.7) and relative shoot growth (fig. 7.9). Similar positive plant growth responses to litter have been documented by Ahlgren & Ahlgren (1981), Fowler (1988), Molofsky & Ausperger (1992) and Parotta (1995). Furthermore, litter is widely used in degraded ecosystems as an organic source of nutrients that may also potentially act as a mulch providing better moisture conditions for plants (Sanchez, 1976; Bradshaw, 1983).

Measures of plant growth indicate that seedlings were significantly larger on fertiliser.litter combinations than on individual fertiliser and litter treatments (figs. 7.8 & 7.10). One possible explanation for this apparent growth response on fertiliser.litter combinations is that the mulch effect of litter increased the release of nitrogen, phosphorus and potassium from fertiliser treatments. Alternatively, fertiliser applications to moist litter environments may have generated suitable conditions for micro-flora and fauna that resulted in a greater release of N, P, K and Ca from cladode litter decay. Soil moisture varied between sites according to different structural properties and potentially may have also influenced rates of litter decay by micro organisms and nutrient release. Plants on the mine overburden site were significantly larger on litter.fertiliser combinations than at other sites possibly because higher soil moisture ensured greater nutrient release from fertiliser and N availability from litter through rapid decay.

Another probable outcome of greater root development on Litter treatments is that there may have been greater competition between species for either moisture or nutrients. This notion has also been proposed by Nagy & Proctor (1997 b). Root competition may have a major influence on seedling densities underneath primary colonists. However according to Fowler (1988), the positive effects of seedling aggregation on microsites containing litter far outweigh the negative effects of competition among these plants.

7.4.3 Effects of Lime

Lime was applied at relatively low doses compared to agricultural trials on oxisols in New Caledonia (Edighoffer, 1991) to ensure that plant roots were not damaged by the caustic properties of calcium hydroxide (von Uexkull, 1986). Lime was initially applied to a depth of 10 cm and then applied to surface soil to avoid disturbing roots. These applications resulted in a significant increase in soil calcium concentrations and raised soil pH by 0.5 and in some cases by 1.0 (table 7.3). Surface soil pH exceeded 6 at all sites except for the iron crust oxisol site. One negative effect of surface applications was that lime tended to concentrate in surface horizons. This potentially produced a false indication of actual soil calcium concentrations and pH.

Plants that had received lime showed no increase in height and relative shoot growth. Furthermore, the ANOVA didn't show a significant difference in *Fv/Fm* ratios between plants with and without lime which suggests that lime had no effect on plant growth. This finding is consistent with Soane & Saunder (1959) who demonstrated that lime had no effect on crop yields on serpentinite soils in Zimbabwe possibly because other factors were limiting growth. However, this finding goes against numerous studies which have shown that applications of lime to ultramafic soil increased growth of native (Nagy & Proctor, 1997 b) and crop species (Hunter & Vergnano, 1952; Proctor & Cottam, 1982; Wallace, 1989).

Root : shoot ratios of *Gymnostoma* seedlings indicate that root systems were significantly larger on lime than on treatments without lime (fig. 7.14). Furthermore, total *Frankia* nodule weight (+1) in *Gymnostoma nodiflorum* seedlings was significantly lower on lime treatments than on treatments without lime and showed a reduction in *G. deplancheanum* and *G. chamaecyparis* seedlings (fig. 7.18). Such growth and micro-flora responses to lime may be interpreted as an over-liming effect. Similar plant responses to over-liming have been reported on acidic mine tailings (Costigan *et al*, 1982) and tropical lateritic soils (Sanchez, 1976; von Uexkull, 1986; Aitken *et al*, 1997), and arise when lime application raise the pH of only the topsoil (von Uexkull, 1986). This may restrict root growth to this zone and therefore cause plants to not fully utilise moisture and nutrients in the subsoil (von Uexkull, 1986). Localised increases in calcium and pH around roots may also precipitate phosphorus into insoluble calcium phosphate in acidic oxisols (Sanchez, 1976; Haynes, 1982) and reduce the availability of potassium (Magdoff & Bartlett, 1980) causing a reduction in shoot growth and the development of extensive root systems (von Uexkull, 1986). Inhibitory effects of lime induced reductions in phosphorus availability have also been shown to affect *Macadamia* seedlings by reducing proteoid root abundance (Aitken *et al*, 1997). Costigan *et al* (1982) indicated that inhibitory effects of lime on phosphorus availability caused major reductions in the abundance of nitrogen fixing *Rhizobium* on *Trifolium repens* resulting in a decline in growth. This suggests that lime potentially had a negative effect on *Gymnostoma* seedling growth by reducing the amount of phosphorus available for *Frankia* activity (Diem & Arahou, 1996). Alternatively, the decline in total *Frankia* weight (+1) may have arisen in response to the caustic properties of $Ca(OH)_2$.

7.4.4 Effects of Fertiliser

Applications of slow release fertiliser resulted in a significant increase in soil nitrogen and phosphorus concentrations. Plants grew much larger (figs. 7.6 & 7.12) than on all other treatments except for litter. fertiliser combinations where litter had an additive effect by increasing nutrients and moisture (figs. 7.8 & 7.10). Similar positive growth responses to fertiliser have been reported on nutrient deficient mine sites (Liston & Blakwill, 1995; Redente & Richards, 1997; Sarrailh, 1997) and ultramafic outcrops (Hunter & Vergnano, 1952; Proctor & Cottam, 1982; Brooks, 1987; Koide & Mooney, 1987; Nagy & Proctor, 1997 b).

Chlorophyll fluorescence measures indicate that plant *Fv/Fm* ratios were significantly higher on fertiliser than on non-fertiliser treatments (fig. 7.20). High *Fv/Fm* ratios suggest that plants responded positively to fertiliser in terms of photosynthetic efficiency possibly by alleviating stress through increased nutrient absorption. Growth measures of *Gymnostoma* seedlings indicate that increased nutrient availability of fertiliser treatments resulted in a significant decrease the root : shoot ratio (fig. 7.13). These roots systems contained significantly more *Frankia* nodules than seedlings on non-fertiliser treatments. Increases in total *Frankia* nodule weight (+1) may infer a correlation with plant size (fig. 7.17). Conversely, *Frankia* development responded to an increase in phosphorus, and showed greater development irrespective of potentially negative effects of added N (Dommergues, 1995). This hypothesis is consistent with studies of *Gymnostoma papuanum* (Racette *et al*, 1990) and *Casuarina* spp. (Redell *et al*, 1997; Yang *et al*, 1997) which showed that increased P availability favoured *Frankia* development.

Plants showed considerable variation in fertiliser response between species and sites in terms of relative shoot growth. Species effects are likely to have been driven by differences in how species allocate nutrients used in carbon fixation to leaf, stem, root development and plant reproduction. Species relative shoot growth responses to fertiliser appear to be also influenced by site conditions. Measures of relative shoot growth in terms of height are presented in figure 7.26 for species used in field experiments and other revegetation trials (Sarrailh, 1997) in New Caledonia. They suggest that low altitude native species and exotics are generally slower growing on high altitude mines than at coastal sites. These changes in height between sites are unlikely to be driven solely by altitudinal changes in atmospheric pressure, but instead may be related to the suitability of climate (fig. 2.4) and substrate conditions (table 2.2) which vary with altitude (Latham *et al*, 1978; Jaffré, 1980; Jaffré *et al*, 1994 c).

Another pattern evident from the Site. Fertiliser. Species interaction is that serpentinite species (*G. chamaecyparis, Austrobuxus carunuclatus*), non-ultramafic species (*G. nodiflorum*) and oxisol species found on other soil types (*Carpolepis laurifolia*) generally showed a much stronger growth response to fertiliser than species restricted to oxisols (*Gymnostoma deplancheanum, Grevillea exul*). Such fertiliser driven differences in growth have also been observed between oxisol and exotic species on oxisol overburden in southern New Caledonia (Cherrier, 1990).

There are several possible explanations for this apparent difference in growth between non-oxisol and oxisol species. Serpentinite species showed a greater growth response to fertiliser than oxisol species because plants may have been less constrained in terms of nutrient assimilation by magnesium availability of oxisols which is low compared to serpentinite soils. Serpentinite species may have responded favourably to the phosphorus concentrations of oxisols which are slightly higher than on serpentinite, and were more effective at assimilating P through VAM associations not found in *G. deplancheanum* seedlings (Amir *et al*, 1997; Amir & Pineau, 1998).

Non-ultramafic *Gymnostoma nodiflorum* showed no response to fertiliser at the eroded oxisol site. One possible explanation for this lack of response is that seedlings were more mature than at other sites and possessed well developed root systems at the plantation stage which became root bound in compacted clay layers that were widespread at the eroded oxisol site. In contrast, *G. nodiflorum* seedlings showed a large growth response on fertiliser plots at the mine overburden site and iron crust oxisol site that may have arisen because plants were older than other species and therefore potentially experienced less stress at these sites. Furthermore these species also possessed VAM associations and more abundant *Frankia* development than other *Gymnostoma* species.

One hypothesis put forward by Snaydon & Bradshaw (1969) is that there is a genetic basis for differences in plant responses to nutrient availability. In the case of the species examined at field sites, *Gymnostoma nodiflorum* and *Carpolepis* are possibly genetically predisposed to fast

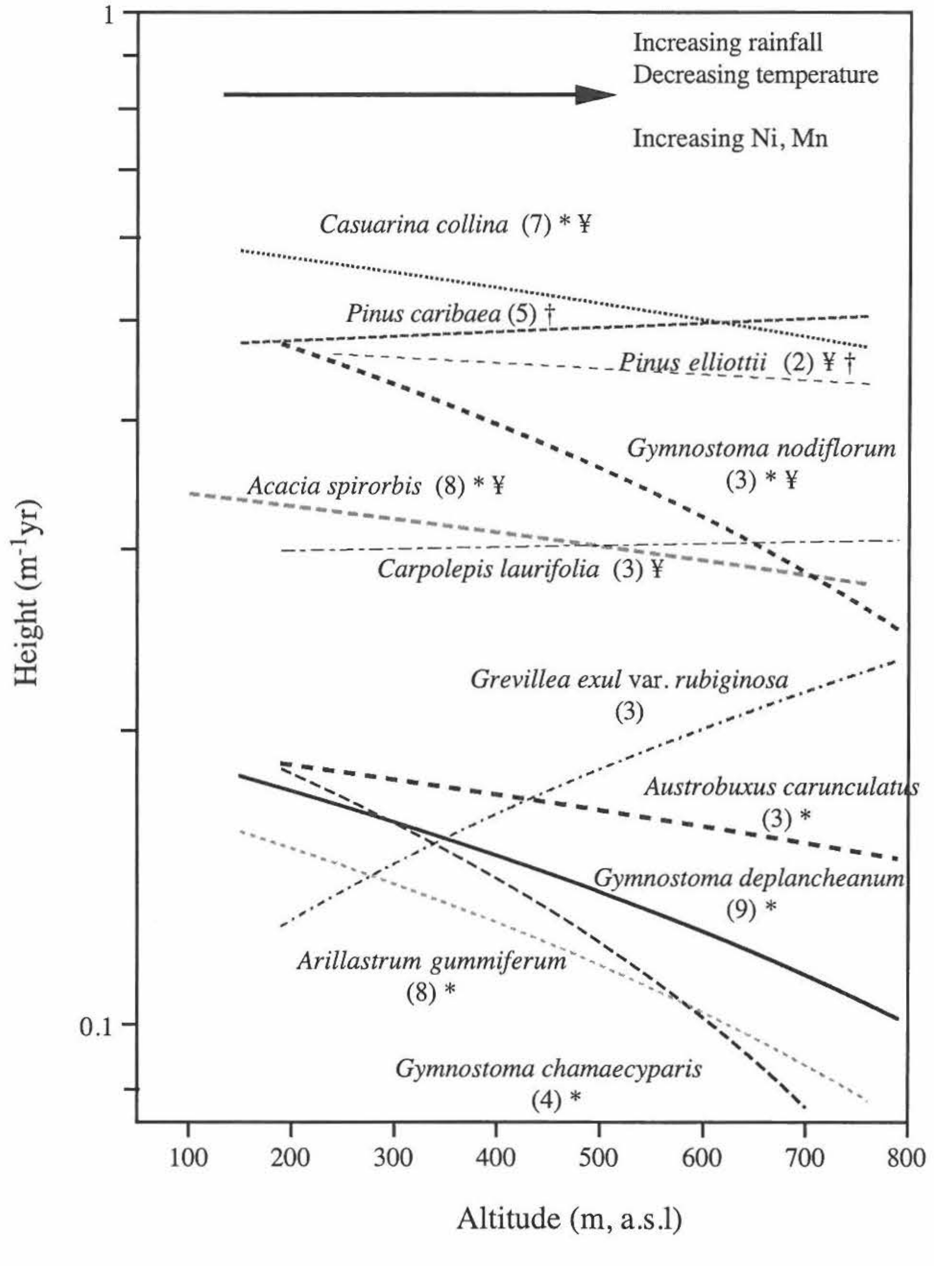


Figure 7.26 Height (m^{-1}yr) of species used in revegetation trials on mine sites at different altitudes in New Caledonia (ref: Cherrier, 1990; Sarraih, 1997, and present study). All species recieved fertilisers. Trends are shown by fitted splines. Low altitude species (< 300 m a.s.l) are indicated by the symbol *. Non-ultramafic and ultramafic species found on other substrates are indicated by the symbol ¥. Exotic species are indicated by the symbol †. Height trends for species with less three values should be treated with caution.

growth in response to sudden decrease in nutrient availability associated with disturbance in their native habitats. *Carpolepis* frequently colonises land slips in rainforest. One apparent adaptive trait of *Carpolepis* which probably enabled its rapid growth on field experiments was its extensive shallow root system that acquired nutrients over a larger area than other species. Conversely, *Gymnostoma deplancheanum*, and *Grevillea* are possibly genetically predisposed to slow growth and survival on nutrient poor oxisols and therefore showed a much slower growth response when nutrients are added. This genetic predisposition to slow growth in oxisol species raises several important issues concerning species selection for revegetation and the potential catastrophic effects of exotic species invasion of ultramafic plant communities from revegetated land.

7.4.5 Use of fertilisers in revegetation of nickel mines

The current focus of large scale revegetation programs in New Caledonia has been to use large initial doses of fertiliser or manure to stimulate growth in fast growing native species such as *Casuarina collina* and *Acacia spirorbis*, and exotics such as *Pinus caribaea*. (Cherrier, 1990; Sarrailh, 1997). Slow release fertiliser applications at field sites provided substantially lower amounts of N (4.2 g), P (1.4 g) and K (3.0 g) per plant than on other trials (Cherrier, 1990). In the case of *Gymnostoma deplancheanum*, low P amendments on fertiliser treatment plots at the iron crust oxisol site yielded a significant growth response that was similar to plantations of this species on iron crust overburden that had received much higher concentrations of P (Cherrier, 1990) (fig. 7.27). This suggests that only small repeated amounts of fertiliser are required to achieve significant growth responses in many maquis species. Furthermore, much of the excess phosphorus is likely to have been immobilised by iron on oxisols due to their high negative charge (Sanchez, 1976; Brooks, 1987). In contrast, excess amounts of other plant nutrients such as nitrogen, potassium and calcium are potentially available to other plants and possibly generate within stand competition between plants.

One additional source of competition for slow growing ultramafic species on revegetation trials at mine sites is from exotic weeds originating either from soil containing plants or from manure applications. Exotic weed invasions on high altitude mine sites have usually been localised and short lived possibly because weed species are intolerant of high nickel, manganese and magnesium concentrations (Jaffré *et al*, 1994 c). However at low altitude areas, where Ni, Mn and Mg concentrations are low and

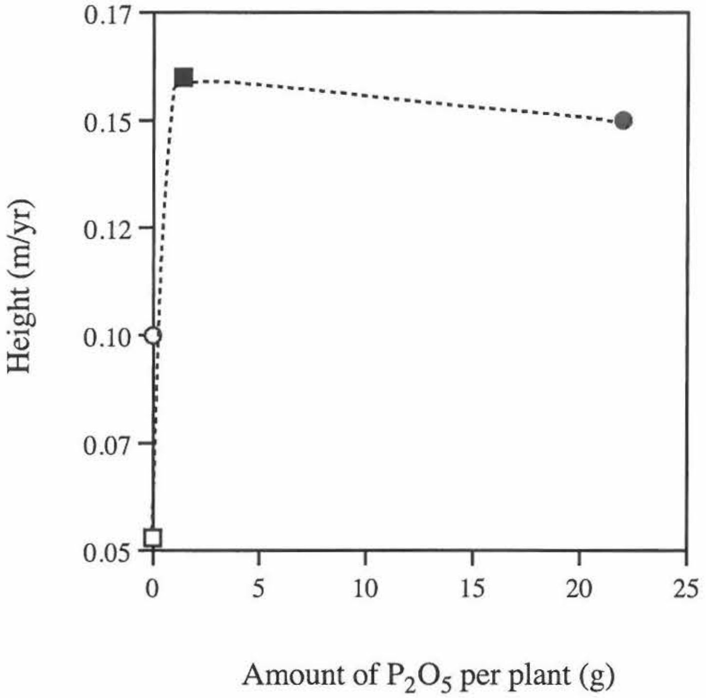


Figure 7.27 Height growth ($m^{-1}yr$) of *Gymnostoma deplancheanum* seedlings supplied with approximately 1.4 grams of P at the iron crust oxisol site (solid square) and 22 g of P at Grand Lac trial site (solid circle) compared to seedlings recieving no P amendment (hollow symbols). Line indicates the general trend in relative growth of *Gymnostoma* with increasing P_20_5.

warmer climatic conditions are more favourable for growth, fast growing weeds have the potential to directly affect surrounding vegetation by growing faster than ultramafic species. Rapid weed growth was observed at early stages of field experiments on fertiliser treatments at all sites and was particularly apparent at the iron crust oxisol site. Weed species originating from non-ultramafic alluvial soil that contained test plants rapidly colonised fertiliser amended soil, and in some cases had progressively expanded out where litter had been applied. Fast growing rhizomatous *Pilea microphylla* (Urticaceae) often surrounded *G. deplancheanum, G. chamaecyaparis* and *Grevillea exul*, and possibly led to higher mortality of these species on fertiliser treatments at field sites (table 7.4). Isolated clumps of *P. microphylla, Desmodium* sp. (Fabaceae), *Mimosa pudica* (Mimosaceae) and *Trifolium* sp. (Fabaceae) continued to persist at all sites at the end of the experiment possibly because residual N and P were high enough to sustain growth. These species may have also developed a tolerance to elevated concentrations of metals at the field sites at Kouaoua. The notion of resistance of plants to toxic metals is well documented in literature on mines (Cox, 1980; Bradshaw & Chadwick, 1980; Bradshaw, 1987; Brooks, 1987; Sumner & Naidu, 1997) and potentially posses a major threat to slow growing diverse ultramafic vegetation in New Caledonia. Weed invasion on mines has recently been reported to have serious effects on surrounding high conservation value vegetation in Australia and in most cases has required quite costly schemes of eradication (Panetta & Groves, 1990).

7.5 Conclusion

Field experiments indicate that slow maquis growth on bare ground arises essentially from a combination of open environment effects and limited nutrient availability. Shade generated by primary colonists is important for early seedling survival by reducing moisture loss through raised transpiration associated with photoinhibition. An important source of moisture on bare ground is provided by primary colonist litter which retains moisture in organic material and by reducing evaporation of soil moisture. Plant growth on litter is slower than more conventional fertiliser techniques possibly because litter decay is slow and releases limited amounts of N, P and K. Plants respond to the moist conditions by developing extensive root systems to scavenge nutrients over a large area of litter. This may generate competition between plants underneath primary colonists. However, the benefits of slight increases in nutrient availability and raised soil moisture possibly outweigh negative aspects of aggregating.

Application of fertiliser to maquis plants results in a major increase in shoot growth and reduction in root development to the area where nutrients are applied. Maquis species are slower growing on fertiliser amended ultramafic soil than non-ultramafic species possibly because they are genetically predisposed to the low nutrient supply of ultramafic soils. However, it appears that only small fertiliser doses are required to achieve a major growth response. Fertiliser applications resulted in a significant increase in total *Frankia* weight probably in response to slight increases in P. In contrast, *Frankia* nodulation appears to have decline on lime treatments either because of direct effects of caustic $Ca(OH)_2$ or the reduction in P availability arising from over-liming.

Chapter 8

General discussion & conclusion

This thesis has focussed on (i) determining whether changes in certain vegetation patterns on ultramafics in New Caledonia are successional and how certain processes (ii) change along the apparent chrono-sequences and affect (iii) plant establishment and (iv) growth. This chapter has been separated into four sections. The first section provides a general overview of succession and evaluates findings on ultramafic successional vegetation presented in this thesis. The second section describes how certain processes affect plant colonisation, and assesses whether metal toxicity and nutrient deficiency influence plant growth on bare ultramafic ground. The third section will raise several issues concerning the origin of plant adaptations to ultramafic soils in New Caledonia and how they have impacted on vegetation patterns. The fourth section presents recommendations for revegetation work on nickel mines based on findings presented in this thesis.

8.1 Are vegetation patterns successional?

8.1.1. Succession

Succession refers to non-cyclic changes in population and community composition over time (Whelan, 1995). These changes are associated with a series of complex processes which are often difficult to define, but generally can be sub-divided into four categories. One cause initiates the succession by producing a bare area, another selects the population, a third determines the sequence of stages, and a fourth stabilises the development (Guttierrez & Fey, 1980). Such changes in populations follow different successional pathways depending on the severity to which the original community is damaged. In vegetation systems, primary succession is initiated by a large scale disturbance (glacier movement, volcanic eruption, open cut mining) which results in the death of above and below ground plant parts of the original community, and relies on colonisation from surrounding areas through propagules (Del Moral *et al*, 1995). Secondary succession in plant communities is initiated by a disturbance such as fire, cyclone and agriculture, and results in the removal of aerial plant parts of the original community. Vegetation development along the secondary succession pathway may originate from seed banks, live rootstocks and seedfall from surrounding vegetation (Fox & Fox, 1986).

Qualitative studies of the processes governing primary and secondary succession patterns have produced a wide range of models with varying degrees of applicability due to the long time scales associated with vegetation changes (McCook, 1994). The earliest 'relay floristics' model of Clements (1938) is a sequential floristics model whereby early dominant species modify the environment making it less favourable to themselves but suitable for latter invaders. This unidirectional model will eventually result in climax formations if no other disturbances disrupt the vegetation. Since colonisation is dependent on complex factors such as dispersal, plant life cycles and the suitability of disturbed substrates for colonisation, Egler (1954) proposed an 'initial floristic composition' model in which the species that survive the disturbance are the first colonisers. Unlike Clements, the conditions produced by early colonists in Eglers model don't facilitate later invaders, and the processes of later succession are largely dependent on life histories.

Drury & Nisbet (1973) proposed a model similar to Egler whereby the patterns of abundance after disturbance, involves a sequence of species with different growth cycles for a given site. Succession patterns in this model are correlations between stress tolerance, growth rate, size, life cycle and seed dispersal (Drury & Nisbet, 1973). Connell & Slatyer (1977) expanded on models by Clements (1938), Egler (1954) and Drury & Nisbet, 1973) and proposed a three way model in which early colonists will either inhibit, have no effect or facilitate later invaders. The basis of facilitation, inhibition and tolerance concepts are qualitative observations. They imply that early colonists will have a net outcome on later invaders, and the interactions between early species may have both a facilitation and inhibitory effect on later species (Connell *et al*, 1987).

This thesis argues that the maquis formations containing *Gymnostoma* represent a secondary succession vegetation that eventually develops into forest and possibly rainforest through a process of facilitation (Connell & Slatyer, 1977). Part of the successional pattern is known to be post-fire and is based on reports of fires, changes in the demography, floristics and age of fire sensitive species presented in chapter 3. These changes to vegetation patterns alter light regimes and nutrient cycling processes which in turn facilitate the eventual entry of a later successional

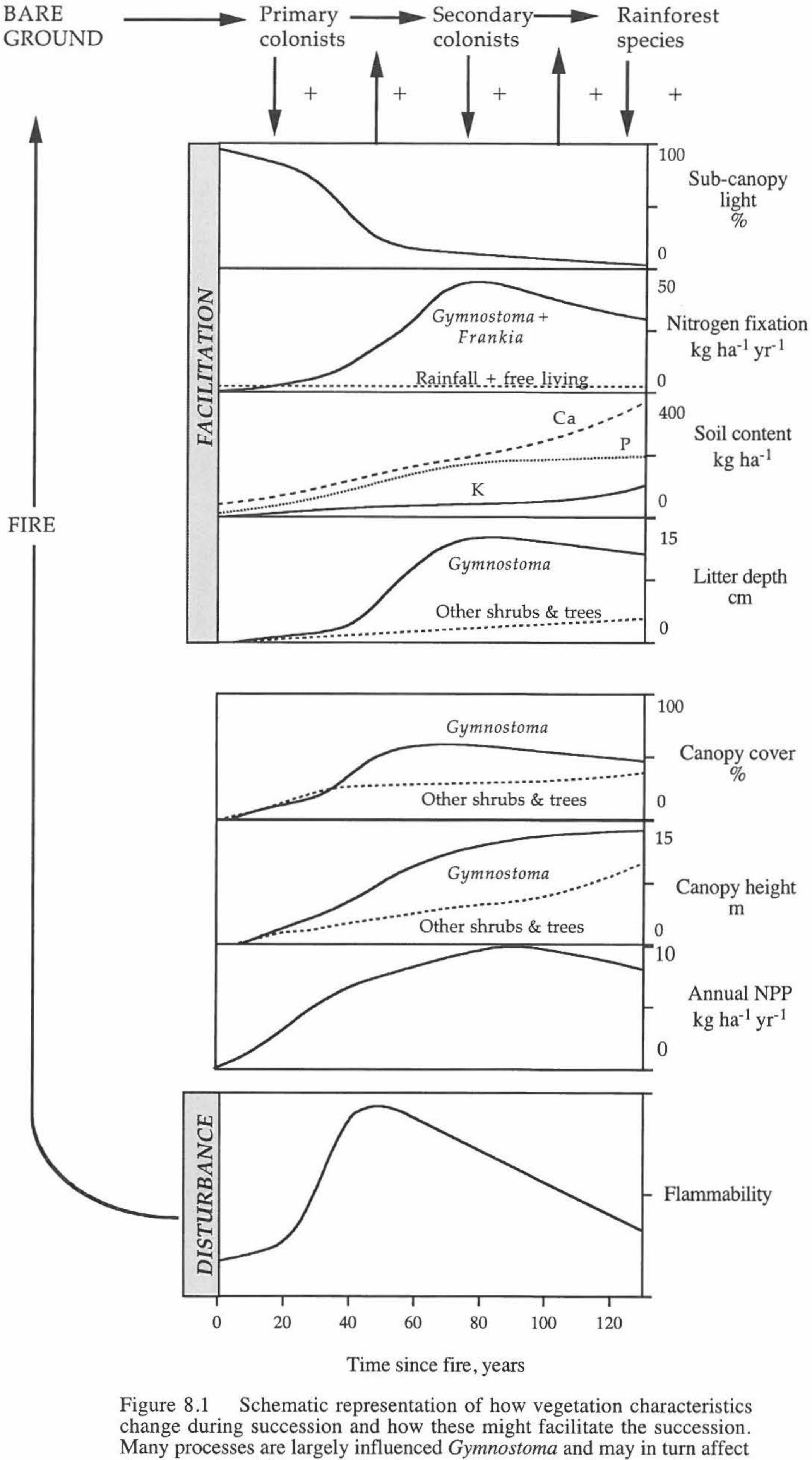


Figure 8.1 Schematic representation of how vegetation characteristics change during succession and how these might facilitate the succession. Many processes are largely influenced *Gymnostoma* and may in turn affect the degree to which vegetation is susceptible to disturbance such as fire. Arrows indicate vegetation contributions to processes during the facilitation succession.

group (fig. 8.1). However, other processes such as variations in climate, topography and hydrology seem to be also influencing vegetation patterns possibly by either directly impacting on floristic populations, or indirectly modifying the susceptibility of plant communities to fire. The issue of how processes other than fire have influenced successional patterns will be discussed in later sections.

An important issue that has been raised at several occasions in this thesis, is the role of substrate nutrient availability on rates of successional development. Substrate effects have often been attributed a minor role in vegetation succession in temperate and tropical regions, because the nutrient status of soil remains high following the disturbance (Guttierrez & Fey, 1980; Reiners, 1981; Brown & Lugo, 1990). However, in New Caledonia, the low nutrient status of the ultramafic substrates exerts a major influence on early successional stages causing these communities to develop at a rate which is much slower than other secondary communities in tropical regions (Brown & Lugo, 1990).

8.1.2. Post-fire vegetation succession on ultramafics in New Caledonia

The post-fire open maquis stage consists of a core group of primary colonists composed of secondary succession species originating from rootstocks and seed banks, and primary succession species from seedfall. These colonists are either short lived or persist and facilitate the succession. Measures of light regimes in chapter 5 indicate that light levels are very heterogeneous in post-fire open maquis and range from high light regimes which may rapidly dry fuel, to shady conditions underneath colonist shrubs. Seedlings suffer photoinhibition under high light environments, which may especially reduce the survival of late successional shade tolerant species. Nutrients such as N, P, K and Ca are limiting in these habitats resulting in low annual net primary production. Litterfall is low and localised near colonists and results in a patchy mixture of highly flammable vegetation separated by bare ground. Thus, the early successional stages may be relatively free of subsequent fires. On hard iron crust and serpentinite, this early fire free stage may last decades, while on eroded oxisol it may take as little 2-3 years for the connectivity of the fuel to rise to about 50% cover and sustain fires.

Gymnostoma deplancheanum and *G. chamaecyparis* colonise successional vegetation through abundant seed fall. This seedfall develops into isolated trees which represent a minor component (about 25-30%) of the first shrubby phase. However, *Gymnostoma* appears to have a dominant influence on the succession of later maquis phases due to its nitrogen fixing *Frankia* association (Jaffré *et al*, 1994 b). This potentially contributes to its relatively rapid establishment such that it forms a nearly pure but open canopy 5-7 m in height in tall maquis after 50-70 years. Measures of the nutrient dynamics in iron crust communities (chapter 6) indicate that *Gymnostoma* also provides an important source of N to the succession that is accumulated in vegetation biomass and soils over time. Litterfall in the later maquis phase is largely composed of *Gymnostoma* cladodes which decay slowly to form an organic soil horizon that raises the N, P, K and Ca content of soil. However, slow *Gymnostoma* litter decay may physically restrict the establishment of large seeded species and therefore favour the development of a tall maquis understorey composed of small seeded Myrtaceae, Cunoniaceae and Euphorbiaceae (chapter 6). Light level measures in chapter 5 reveal that *Gymnostoma* canopy permits about 10-25% light penetration in later maquis phases which may facilitate the establishment of a variety of late successional species, possibly by shielding them from deleterious photoinhibitory processes (chapter 5) while allowing sufficient light for moderate growth rates. However, shade cast by *Gymnostoma* trees seems to be insufficient to reduce evaporation and causes continuous litter in later maquis phases to remain dry and highly flammable.

Eventually, broad-leaved forest trees such as *Arillastrum* may colonise and, as these replace *Gymnostoma*, reduce light levels to about 2-10% in the understorey (chapter 5). This apparently suppresses regeneration by most of the primary colonists, including *Gymnostoma*. Furthermore, deep shade cast by a broad-leaved canopy and understorey species appears to decrease evaporation of fuels resulting in a reduction in flammability. The decline in *Gymnostoma* abundance in later forest stages also results in a change in nutrient cycling regimes from slow decay of nutrient poor litter to rapid decay and release of nutrients from rainforest biomass (chapter 6). These forest stands are invaded by rainforest species, though no stands which had reached a rainforest dominated canopy were observed on survey areas at Plaines des Lacs and Kouaoua. Sources of later successional species are limited to the localised forest and rainforest stands in fire protected topography. These are typically several kilometres apart and this may be constraining succession (chapter 3). However, according to pollen sediment records, rainforest may eventually establish in areas occupied by maquis (Hope, 1996; Hope & Pask, 1998).

Post-fire successional communities on ultramafics outlined in this thesis might apply to other maquis formations (Jaffré, 1980) on rocky habitats in New Caledonia, except for maquis on foggy mountain summits and permanent swamplands (Jaffré, 1980; 1995) where moist conditions are unfavourable for fire. Furthermore, these ultramafic successional communities appear to share certain patterns with post-fire heathlands and forest in Australia, in particular those containing *Casuarina* (Specht *et al*, 1958; Hueneke, 1976; Withers & Ashton, 1977; Fox & Fox, 1986, 1987; Hobbs & Atkins, 1990). Australian heathlands are initially composed of resprouters, seeders which develop into a shrubby vegetation cover (Specht, 1981; Whelan, 1995). *Casuarina* establishes on certain heathlands often immediately after fire from seed released from dehiscent woody fruits (Specht *et al*, 1958; Christensen *et al*, 1981). This seed release results in massive regeneration of *Casuarina* that may eventually develop into a dominant canopy species producing shade and deep litter that may exclude other species and itself (Hueneke, 1976; Withers, 1979). Deep litter beds are highly flammable, and fires in these formations may result in localised elimination of *Casuarina* (Johnson & Purdie, 1981).

8.2 Are models accurate at predicting vegetation change after fire?

8.2.1 Successional models of ultramafic communities

Vegetation surveys at Plaines des Lacs and Kouaoua set out to determine whether changes in vegetation were successional. Fire records at Plaines des Lacs provided limited information on the extent of vegetation burnt, so it was therefore decided to base the investigation of plant succession on qualitative records of vegetation structure, assuming that this would develop at rates that coincided with fire events from records. The notion of changes to vegetation structure is fundamental to models proposed by Connell & Slatyer (1977) and have net effects on species composition (Connell *et al*, 1987). Vegetation structure at 88 sites was used to construct a succession index using PCA ordination. For iron crust communities, the succession index explained for 80% of the variation of the MDS floristic data. Furthermore, other forms of evidence (changes in abundance of fire tolerant and sensitive species) supported that fire disturbances were a main cause of the patterns.

The succession index explained for less of the variation in MDS floristics for communities at Kouaoua. The low correlation suggests that this technique was possibly too simplistic for investigating succession from vegetation structure and floristic of a limited number of sites sampled over a small area and highlighted local and regional scale effects. Post-fire succession was therefore inferred from changes in abundance of fire tolerant species and the abundance of burnt standing plant material. Furthermore, the technique of comparing structural change with floristic variation was unable to reveal key floristic associations at Plaines des Lacs and Kouaoua. This was instead determined by measuring the population structure of communities.

The Plaines des Lacs and Kouaoua are heterogeneous landscapes which support maquis on plateaus and slopes, and forest types in moist valley bottoms and summits. Rainforest in valley bottoms at Plaines des Lacs and summits at Kouaoua frequently showed no trace of fire either as fire scarred trees or charred remains. This potentially suggests that distribution and abundance of late successional species may actually reflect a pattern associated with more favourable hydrological environments (Jaffré, 1996). Moister conditions of valley bottoms and cloudy mountain tops may also reduce the incidence of fire independent of conditions produced by late successional forest types. This interpretation is likely to be also applicable to serpentinite forests in valley bottoms at Kouaoua.

8.2.2 Transition matrix model

Transition matrix models presented for successional vegetation communities in chapter 3 predict vegetation change over time. After fire, vegetation progresses according to changes in fire frequency and flammability. It is a robust predictor of general vegetation change in relatively uniform environments containing mixed successional vegetation such as iron crust at Plaines des Lacs. An important pattern revealed by the model is that flammability raises to a peak then declines. The model is very sensitive and indicates that slight shifts in fire frequency for time scales encompassing the peak frequency will result in maquis developing into forest or forest reverting to maquis. This sensitivity to slight changes in fire frequency has important implications in terms of interpreting the time scales of palaeo-ultramafic vegetation shifts in New Caledonia (Hope, 1996; Hope & Pask, 1998) and suggests that a climate change need only shift fire frequency slightly to cause a major change in vegetation.

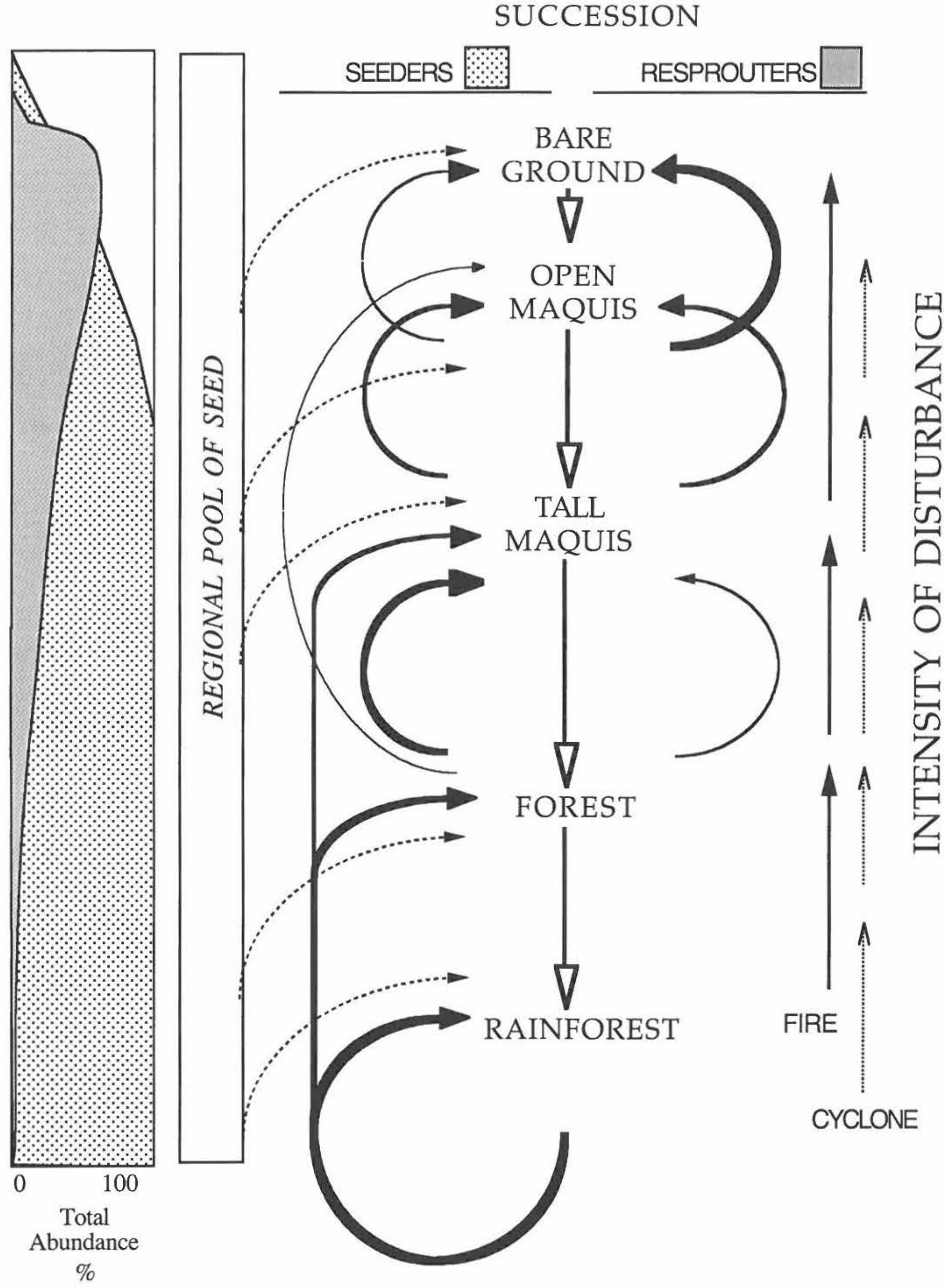


Figure 8.2 Total abundance of seeders and resprouters in successional vegetation subject to varying degrees of disturbance intensity. Descending arrows (hollow) show succession. Ascending curved arrows (solid) show contribution of seed or resprouters from each stage to post-disturbance succession. Cyclone damage to rainforest is largely recolonised from rainforest seeders. In contrast, fire will revert rainforest to earlier successional vegetation containing fewer rainforest seeders. Fire in forest will revert vegetation back to earlier successional vegetation containing an increasing proportion of resprouters and a decreasing number of forest and rainforest seeders. Fire in tall maquis will revert vegetation to an open maquis containing an equal proportion of seeders and resprouters. Seeders are from tall maquis and forest. Fire to open maquis will revert vegetation to bare ground containing abundant resprouters and few seeders. Regional seed sources contribute to disturbances at all successional stages.

The limitations of the model is that is doesn't deal with species change and assumes a spatially uniform mosaic environment in terms of topography, substrate properties and fire risk. It also assumes that fires revert vegetation back to the initial stage, and that some maquis, forest species and rainforest colonists are always available. In reality, successional vegetation types will respond differently to fire depending on their structural and floristic composition which varies with climatic, substrate and topographic position. Maquis is likely to revert to an initial post-fire flora dominated by resprouters (Jaffré *et al,* 1998 a). In contrast, late successional formations are unlikely to revert to an initial maquis stage because of the near absence of resprouters and will probably contain a mixture of species arising from seed banks and surrounding vegetation (fig. 8.2). Under the actual high fire frequencies rainforest seed sources have been largely eliminated from areas of uniform topography by fire (eg: iron crust plateaus at low altitude plateaus; open valley bottoms) and successional vegetation is likely to develop into *Arillastrum* or *Gymnostoma* forest instead of mixed rainforest.

Several changes could be made to improve the accuracy of predictive models of vegetation succession on ultramafics in New Caledonia. A spatially explained landscape model with estimated soil and microclimate properties at a resolution of approximately 10-50 pixels could be used to link vegetation development with landscape variation. Modelling at the landscape level would allow examination of (i) rates of vegetation development differ, (ii) flammability varies with landscape position and (iii) ignition responses vary in relation to surrounding vegetation. It would also establish that colonisation is dependent on prior vegetation and adjacent vegetation. Integrating landscape heterogeneity may also tend to make some of the landscape more susceptible or less susceptible to fire and under-estimate the persistence of formations such as rainforest gullies.

8.3 What is limiting colonisation?

Mining and fire cause extensive damage to soils and vegetation of ultramafic ranges in New Caledonia and may impact on coastal and inland catchments below the area of direct disturbance by increasing sedimentation and pollution arising from erosion (Bird *et al,* 1984). The area of direct disturbance presents various problems for plant growth which vary according to the degree of disturbance (Jaffré *et al,* 1994 c). Vegetation clearance results in a sudden increase in solar radiation that raises soil temperatures and evaporation. Soil surfaces are exposed to precipitation resulting in channel erosion from rain splash and experience higher wind conditions. Nutrient cycles are also disrupted with vegetation removal resulting in the creation of a nutrient depleted habitat. In areas where erosion from mine prospecting or fire has removed surficial organic material and root systems, infiltration rates of gravelly oxisol are very high and may generate water stress conditions for plants even after high rainfall. Conversely, areas where oxisol physical properties have been completely altered by mining through removal and compaction of oxisol into overburden waste terraces, plants may frequently experience waterlogged conditions.

Surveys of plant colonisation on the iron mine at Prony indicate that approximately 90% of the mine surface has remained devoid of vegetation since abandonment 30 years ago. Much of the plant establishment is in areas of remnant iron crust (retain root stocks and seed banks) and along vegetation margins (fig. 8.3). The lack of colonisation on other parts of the mine has arisen for two reasons. (i) Many species are dispersal limited and are, therefore, unlikely to colonise far from residual vegetation. (ii) Suitable crevice sites which may trap seed have been removed from much of the mine surface and replaced with a gravel plain that provides little micro-topographic resistance to windy conditions. Such colonisation constraints have important implications for revegetation as the extent and type of clearance at Prony is similar to many mines at higher altitudes. From a successional perspective, the apparent dispersal limitation of maquis species may infer that after large fires, colonisation from seedfall inputs is likely to be limited, and rates of post fire establishment will therefore largely depend on the abundance of resprouters.

The early successional stage of maquis following mining is composed of isolated primary colonists that support much of the subsequent secondary colonist establishment from seedfall. Seedling survival underneath primary colonists and in crevices is much higher than on bare ground highlighting the importance of these habitats providing shade, litter and potential sources of symbiotic mycorrhizae and bacteria. It also reflects that bare ground environments are unsuitable for plant growth.

Plants on bare ground generally experience photoinhibition which is both a symptom and a cause of plant stress. Low Fv/Fm ratios and high Fo

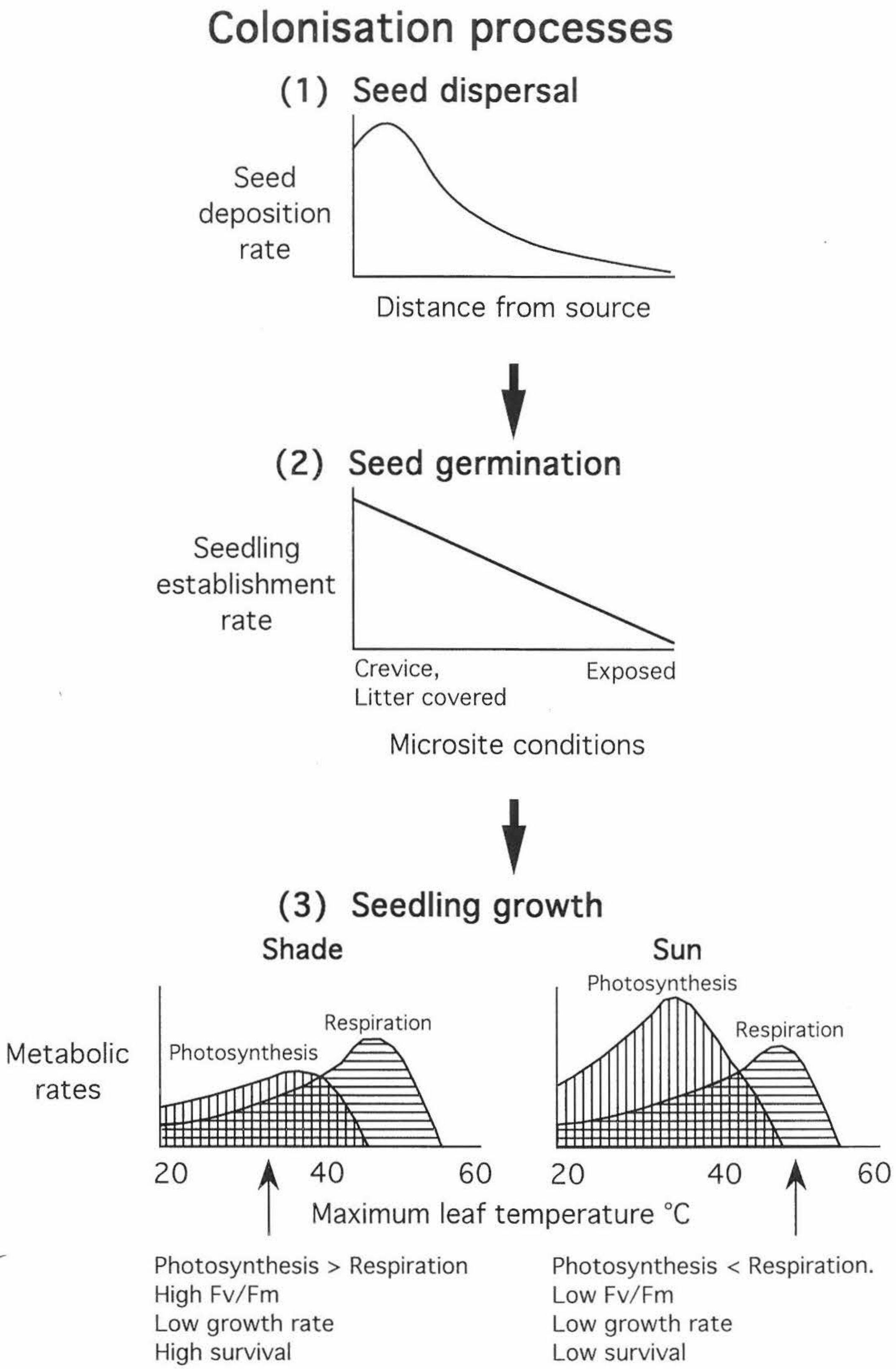


Figure 8.3 Colonisation processes affecting seedling establishment and survival on bare ground of mine sites.

values indicative of photoinhibition arise when plants are unable to overcome photodamage from high light environments resulting in an overall reduction in photosynthetic activity. Stress to the photosynthetic apparatus and high leaf temperatures may in turn raise respiration and reflect a plants inability to cope with other factors such as limited nutrient and moisture availability.

Field experiments at Kouaoua and Plaines des Lacs indicate that processes affecting plant growth underneath primary colonists vary in their importance depending on the stage of seedling development. At early stages, shade has an important direct impact on seedling survival by reducing photodamage and respiration caused by high solar radiation and high temperatures. This reduction in photosynthetic stress may indirectly increase survival by allowing seedlings to allocate more resources into developing root systems to overcome stress from nutrient and moisture limitations. At later stages of plant growth, high Fv/Fm ratios and low Fo values of plants under shade and full sun infer that seedlings overcome the problems of bare ground environments by adjusting growth according to the environmental conditions associated with bare ground.

Primary colonists accumulate nutrients through sorption and fixation from soil and atmospheric sources, and release it in litterfall. Measures of *Gymnostoma* litter nutrient content on field experiments indicate that inputs of P and K were low compared to other forms of nutrient amendment such as fertiliser, but higher than bare ground and potentially represent an important source for both plants and associated micro-flora. Litter may also increase plant survival by ensuring that moisture levels remain higher than bare ground around seedling roots (chapter 6). Raised moisture and nutrient availability on seedling growth may potentially outweigh negative effects caused by increased root competition created by greater seedling abundance (Fownes, 1988). However, in situations where seedling densities exceed the capacity of nutrient and moisture sources provided by litter, there is the possibility of higher rates of mortality (Lamont *et al*, 1993).

Field experiments indicate that seedling growth rates are much lower on litter (x 2) than with fertiliser (x 10-20) applications which suggests that the slow development of early maquis stages essentially arises because nutrient sources from litterfall and soil are limiting. Plant growth measures in glasshouse and field trials indicate that plants respond to low nutrient availability and moist litter conditions by allocating more resources to root development. Furthermore many maquis species form mycorrhizael (Amir *et al*, 1997; Amir & Pineau, 1998) and cluster root forming bacterial associations that may enhance nutrient sorption from bare ground and litter (Lamont, 1993). A notable example of bacterial associations is the substantial increase of proteoid roots on *Grevillea* watered with litter leachates.

8.4 To what extent is toxicity and nutrient deficiency an issue in plant growth on ultramafic soils ?

Studies of ultramafic vegetation frequently report on the floristic and physiognomic contrasts between ultramafic floras and adjacent vegetation on other substrates (Whittaker, 1954; Kruckeberg, 1954; Walker, 1954, Wild, 1965; Proctor, 1971; Proctor & Woodell, 1975; Jaffré, 1980; Brooks, 1987; Proctor, 1992; Baker *et al*, 1992). These patterns have usually been addressed with reference to the unusual soil properties of ultramafics and how they affect plant growth of native ultramafic species and agricultural crops found on non-ultramafic soils.

8.4.1 Ca : Mg ratio imbalance

The Ca : Mg ratio imbalance of ultramafic soils, in particular serpentinite, is frequently cited as a main causal factor limiting plant establishment from adjacent soil types in temperate and tropical zones (Whittaker, 1954; Kruckeberg, 1954; Walker, 1954; Proctor, 1971; Proctor & Woodell, 1975; Jaffré, 1980; Veltrup, 1981; Proctor & Cottam; 1986; Brooks, 1987, Baker *et al*, 1992; Proctor & Nagy, 1997 a). Toxicity from a Ca : Mg ratio imbalance arises in ultramafic environments because Ca supply in soils is insufficient to regulate excessive Mg uptake by plants (Walker *et al*, 1955; Proctor, 1971; Jaffré, 1980). Non-ultramafic plants such as crops, often experience cellular damage from Ca : Mg ratio imbalances (Veltrup, 1981). This damage is apparent as a reduction in root development that may also lower a plants tolerance to heavy metal toxicity (Ni, Mn, Co and Cr) and the scarcity of nutrients and moisture (Foy *et al*, 1978; Baker *et al*, 1990; Uren, 1992; Anglone *et al*, 1993). In contrast, most ultramafic plants have evolved mechanisms that maintain a favourable Ca : Mg ratio by preferentially absorbing Ca relative to excluded Mg (Jaffré, 1980, Proctor, 1992). However, these mechanisms of exclusion may break down at high Mg availability resulting in toxicity (Baker, 1981).

Vegetation surveys at Kouaoua indicate that the floristic similarity between eroded oxisol and serpentinite communities is weak (14% of species shared). Similar floristic patterns have also been reported at the base of the Boulinda and Koniambo ranges (Jaffré, 1974; Jaffré & Latham, 1974). This would suggest that eroded oxisol species are intolerant of the extreme Ca : Mg imbalance of serpentinite soils arising from high exchangeable magnesium. Alternatively, floristic differences may also reflect that dispersal limitations, climate and other soil properties such as lower P concentrations are excluding eroded oxisol species from colonising serpentinite.

Field experiments indicate that the serpentinite species *Gymnostoma chamaecyparis* grow larger than *G. deplancheanum* on iron crust oxisol. This apparent difference raises an important issue concerning what is limiting serpentinite species colonising oxisol. A possible explanation for the current absence of serpentinite species from iron crust is that serpentinite habitats are spatially distant from iron crust and are therefore unlikely to colonise. There may be several explanations for the absence of serpentinite species on adjacent eroded oxisol. (i) Serpentinite species may be dispersal limited and therefore unlikely to establish in surrounding eroded oxisol. (ii) Serpentinite species may be out-competed by faster growing woody-sedge maquis species that are tolerant of higher amounts of available Ni and Mn in eroded oxisol.

8.4.2. Heavy metal toxicity

Heavy metal toxicity arising from high concentrations of Ni, Mn, Co and Cr is often mentioned as a major factor limiting plant establishment on ultramafics (Brooks, 1987; Baker *et al*, 1992). Heavy metals such as nickel often exert negative effects on non-ultramafic plant growth that are often similar to those arising from an Ca : Mg imbalance (Foy *et al*, 1978; Heickel *et al*, 1989, Huillier & Eigenhoffer, 1996; Huiller, 1997). In contrast, most ultramafic plants have evolved strategies that reduce metal toxicity by either (i) accumulating these metals in plant parts as neutralised forms, or (ii) regulating metal uptake according to levels in the soil, or (iii) excluding high soil concentrations (Baker, 1981; Brooks, 1987; Baker *et al*, 1990).

Metal tolerance mechanisms operate in plants depending on the availability of heavy metals (Brooks, 1987, Magrath & Smith, 1990, Anglone *et al*, 1993). Heavy metals are generally more available to plants if organic chelates which transport metals between the soil root interface are abundant and soil pH is less than 6 (Foy *et al,* 1978; Romney *et al,* 1981; Brooks, 1987; Uren, 1992; Becquer *et al,* 1995). Oxisols derived from peridotite weathering of ultramafic ranges in New Caledonia often posses low pH and high organic levels which would suggest that heavy metal availability is high and might therefore exert an effect on plant growth (Latham *et al,* 1978; Jaffré, 1980). Plant : soil ratios from field experiments indicate that Ni foliar concentrations generally correspond with the availability of this element in soil. Foliar Ni concentrations are lowest in plants on acidic iron crust oxisol where Ni is less abundant and highest on eroded oxisol containing higher amounts of residual organic material. Mine overburden material has much higher concentrations of Ni than adjacent oxisol but is less allocated to plant leaves than on the eroded oxisol site, possibly because organic conditions necessary for their transport and accumulation in plant parts (Uren, 1992; Becquer *et al,* 1995) are absent in mine overburden. This possibly infers that heavy metal toxicity is unlikely to be a major factor influencing plant growth on mines. However, the presumption that high metal toxicity doesn't affect ultramafic plants in New Caledonia should be treated with caution as the argument is based only on heavy metal uptake in plant leaves. Studies of fruit tree growth on ultramafic soils in New Caledonia have reported that certain species show a reduction in fruit yield (Edighoffer, 1997). This may be a response to low nutrients. Conversely in may also reflect a heavy metal toxicity response in plants. The notion that heavy metal toxicity affects plant fecundity might also apply to native ultramafic vegetation, but requires further investigation, especially on mine sites, as there is no data to support this argument.

Heavy metal tolerance appears to be more common and widespread in New Caledonian ultramafic species than in temperate serpentinite communities, and reflects the longer association of this floras with ultramafic substrates under relatively stable tropical conditions (Jaffré *et al,* 1987). In most cases, the evolution of tolerance mechanisms has allowed ultramafic plants in New Caledonia to colonise a wide range of ultramafic substrates by excluding or accumulating and neutralising several metals without toxic effects (Jaffré, 1980; Rigault *et al,* 1997). This plasticity in metal tolerance may potentially explain the strong similarity between eroded oxisol and iron crust oxisol floras which share 50% of their species (fig. 8.4) but contain different amounts of Ni, Mg, and Mn in underlying soil.

Nickel hyper-accumulation probably represents the most advanced stage of metal tolerance mechanisms (Lee *et al,* 1977, Jaffré *et al,* 1976, Jaffré,

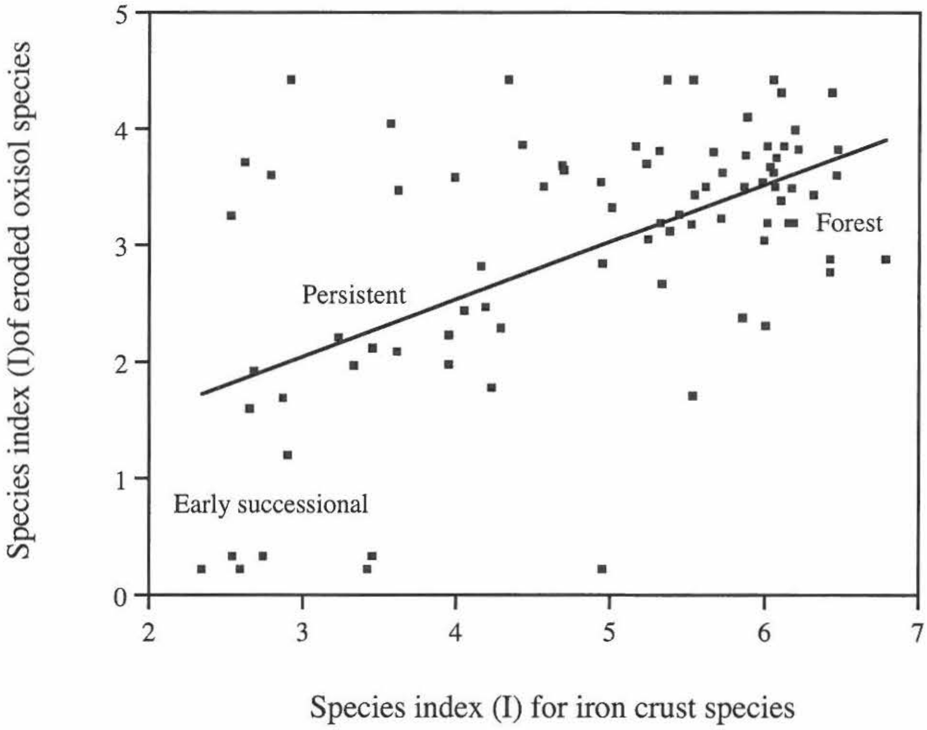


Figure 8.4 Species index scores (I) for taxa found on iron crust at Plaines des Lacs and eroded oxisols at Kouaoua. Fitted spline shows the trend for species groups between communities. Note that some species were assigned very different values at the two sites.

1980, Baker *et al*, 1990, Reeves, 1992). This mechanism is restricted to a few rainforest species that are often abundant on nickel rich eroded oxisol alluvium in rainforest valleys either because other species are unable to grow or there are better at competing for resources (Jaffré & Veillon, 1991). These species are unlikely to be suitable for early stages of mine revegetation because they require forested conditions (eg: deep shade, high nutrients & moisture) that are absent on mines.

More recently, studies of metal accumulating plants have suggested that such mechanisms might serve to deter herbivory (Noell & Morris, 1997; Balkwill & Burt, 1997). This idea requires further work, but potentially may be applicable to New Caledonian nickel hyper-accumulators and possibly explain why certain forest species are non-sclerophyllous.

8.4.3 Low nutrient soils and sclerophylly

Sclerophylly (leaf hardness) and xeromorphy (hard, drought resistant leaves) are foliar adaptations of perennials which have apparently evolved to deal with water stress and nutrient deficiency in soils (Specht & Rundel, 1990) and potentially herbivory (Coley *et al*, 1985). Sclerophyllous plants generally conserve nutrients by retaining their leaves over several seasons, and the trade-off of sclerophylly includes reduced rates of photosynthesis (Lambers & Porter, 1992). The scarcity of N and P in the soil also generates plastic responses in plants such as a reduction in internode length, which affects the height of the plant, and a reduction and hardening of leaves (Beadle, 1966, 1968).

Nutrient deficient substrate conditions suitable for sclerophyll evolution are widespread on ultramafics. They appear to have favoured stunted taxa compared to adjacent vegetation on nutrient rich soils. In the Malesian and Pacific floras, sclerophyllous Myrtaceae, Casuarinaceae, Euphorbiaceae, Epacridaceae, Rutaceae and Guttifereae are often a dominant component of ultramafics (Wild, 1965; Fox *et al*, 1971; Proctor *et al*, 1988, 1989, Jaffré & Veillon, 1990; Proctor, 1992; Cole, 1992; Jaffré *et al*, 1994a, Jaffré & Veillon, 1995). They are also found in Australia, Africa and South America (Fox, 1994) suggesting an ancestral Gondwanan origin.

Field surveys of successional communities at Plaines des Lacs and Kouaoua indicate that much of the early and later successional maquis phases is largely dominated by sclerophyllous Myrtaceae, Casuarinaceae, Euphorbiaceae, Epacridaceae and Guttifereae (figs. 3.3, 3.15 and 3.22). Taxa belonging to these families are abundant in later forest and rainforest stage which would suggest that much of the successional flora is tolerant of nutrient limitations. However the understorey of rainforests also contains non-sclerophyllous large or soft leaved rainforest taxa belonging to Cyatheaceae, Lindseaceae, Gleicheniaceae, Rubiaceae, Sterculiaceae, Lauraceae and Violaceae. Non-sclerophyllous rainforest taxa have been reported by Jaffré & Veillon (1991, 1995) as abundant in many New Caledonia rainforests, and may reflect more favourable nutrient conditions of surface soils. Alternatively, it may also reflect that non-sclerophyllous species occur in landscape positions with a more favourable hydrology.

According to Jaffré (1996) changes in hydrological conditions of ultramafic ranges in New Caledonia appear to have generated several vegetation patterns. (i) *Melaleuca quinquenervia* savanna grassland on clayey coastal sediments show an abrupt decline at the base of ultramafic ranges that coincides with the appearance of shallow free draining eroded oxisol. These gravelly slope sediments may experience longer periods of solar radiation that raise the frequency soil moisture evaporation and favour a drought tolerant woody sedge maquis. (ii) Maquis formations may inturn be replaced by less drought adapted forest and rainforest at the base of valleys that accumulate edaphic moisture from the surrounding slopes of the catchment and experience shorter periods of solar radiation that may raise evaporation (Jaffré, 1996). Changes in soil hydrology have also been proposed as a major causal factor influencing plant distribution between non-ultramafic and ultramafics in tropical and temperate regions (Brooks, 1987; Proctor, 1992).

8.5 Evolution of the maquis flora

New Caledonia separated from eastern Australia as an arc fragment during the late Cretaceous and carried with it a subset of Gondwanan flora. The gradual obduction of a Pacific peridotite sheet over much of the main island in the late Eocene had two major effects on the flora. (i) It probably eliminated some of the ancestral flora and (ii) generated a variety of ultramafic substrates under high light environments. This transition from ancestral Gondwanan to barren peridotite habitats potentially constrained the number of taxa capable of establishing and radiating into different ultramafic habitats. One group that is likely to have been favoured by these new substrate environments are sclerophyllous taxa that had already undergone species radiation in Tertiary Gondwana to form rainforest types and "heath-forest" (Heidewald) on soils of marginal fertility (Specht, 1981). Slow growth and leaf retention by these sclerophyllous taxa presumably resulted in the production of a nutrient poor litter that became flammable under dry open canopy conditions as currently witnessed in many heathlands (Fox, 1994). Raised fire frequencies during dry periods in the Tertiary may have resulted in species selected for fire tolerance (Jackson, 1968; Recher & Christensen, 1981; Kemp, 1981).

Fire has evidently been a factor shaping the vegetation in the Quaternary long before human arrival (Hope, 1996; Hope & Pask, 1998) and may have influenced the evolution of the flora during the Tertiary. Surveys at Plaines des Lacs and Kouaoua indicate that maquis 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 (eg. *Gymnostoma, Arillastrum, Grevillea, Tristaniopsis*), though the protection may not be sufficient for these to be classified as bradysporous. Some early successional fire tolerant genera, eg. *Babingtonia, 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 b; 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 b).

8.6 Revegetation and management of revegetated ultramafics. Implications of current practices and recommendations

Active and abandoned mines cover extensive areas of New Caledonia and have been the focus of revegetation operations since the 1970s. Revegetation has aimed at rapidly establishing vegetation to reduce erosion and to provide conditions that allow adjacent vegetation to establish or the eventual integration of commercial timber species such as *Pinus caribaea, Arillastrum gummiferum,* and *Agathis lanceoloata.* These trials have often been unsuccessful either because plants have not survived, or not provided conditions necessary to allow colonisation from adjacent vegetation or have required applications of large amounts of fertiliser which represents an additional cost. These apparent limitations raise several important questions. Why has revegetation failed? and what are the conditions needed for plants? These issues are particularly important because abandoned mines cover a much larger area of ultramafics than active ones and no longer provide a revenue that could be used in extensive revegetation operations. These abandoned mines and vegetation destruction from fire pose immediate environmental problems in terms of active erosion and the long term consequences on catchment health.

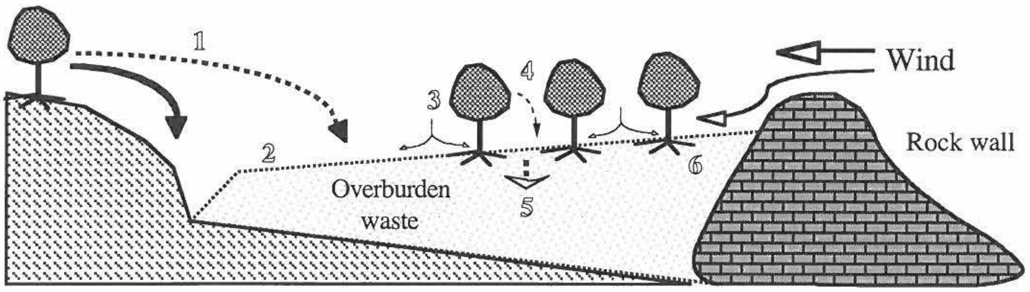
Surveys of vegetation after fire and mining disturbance indicate that primary colonist development is slow to develop into maquis because certain conditions are limiting colonisation. The most apparent constraint to colonisation from surrounding vegetation is that most species are dispersal limited and decline in abundance away from undisturbed seed sources. Many of these seeds fail to colonise bare ground because of the absence of crevices which could provide shade and potentially funnel nutrients necessary for seedling growth. The absence of crevices on abandoned mine sites at Prony is particularly apparent and results in the development of clumps of vegetation in areas of remnant rocky ground that may be spatially distant from adjacent vegetation and therefore largely remain as isolated pockets (chapter 4). These isolated primary colonists support much of the subsequent secondary colonist establishment emphasizing the importance of processes such as a greater area of shade and a supply of nutrients on seedling survival and succession. Shade provided by crevices or primary colonists is important at early stages of seedling survival and reduces damage caused by excess transpiration, high light and other environmental conditions of bare ground (high temperatures).

Revegetation with plantations of *Pinus caribaea* (from Cuba and Honduras) or native *Acacia spirorbis* and *Casuarina collina* are often devoid of colonists underneath trees and on bare ground between trees (Jaffré *et al* 1994 b). This absence of colonisation from surrounding vegetation may reflect dispersal limitations or unsuitable substrate properties for seedling growth. Alternatively, it suggests that the physical compaction of mine overburden is constraining colonisation by eliminating crevices and their micro-habitats. A possible solution to this problem (fig. 8.5) would be to mechanically rip the surface perpendicular to the slope to a depth of 1 m or place rock debris containing crevices and seed banks on the surface. Ripping would also reduce waterlogging by increasing the porosity of surface clays, thus allowing roots to develop. Such mine practices for revegetation are used in many parts of the world (Williamson *et al*, 1982; Ward, 1997). Revegetation in ripped areas should focus on tree planting close to adjacent vegetation margin to expand the area of suitable primary colonist habitats to within seedfall distance in order to reduce dispersal limitation effects. Broadcast seeding techniques could be used in remote ripped areas of mine platforms and steep slopes to establish an initial cover of woody species that would naturally be thinned through competition and eventually provide shrubs and trees.

The issue of species selection for revegetation will depend on the objectives of land-use after the mine has been abandoned and may consist of the introduction of commercial timber species or the re-establishment of a vegetation similar to surrounding areas. Ultramafic *Gymnostoma* species grow much slower than non-ultramafic *Casuarina collina*, but may potentially serve as a nurse species for succession processes by providing an important source of nitrogen through fixation. Furthermore, *Gymnostoma* along with most maquis species have evolved a wide range of tolerance mechanisms to heavy metals and an imbalance in the Ca : Mg ratio. Negative aspects of *Gymnostoma* litter on seed penetration could possibly be solved by mixing plantations with other primary colonists which show abundant regeneration (*Alphitonia, Longetia*) or increasing the spacing between trees. From a silvicultural perspective, *Gymnostoma* could also planted as a windbreak allowing the establishment of wind sensitive timber species. Casuarinaceae species are widely planted in the tropics to provide an important source of charcoal because of their high wood density (Midgley *et al*, 1983; NRC, 1984). *Gymnostoma* posses similar wood properties and could be used for charcoal if the focus of revegetation is to generate some form of eventual economic return.

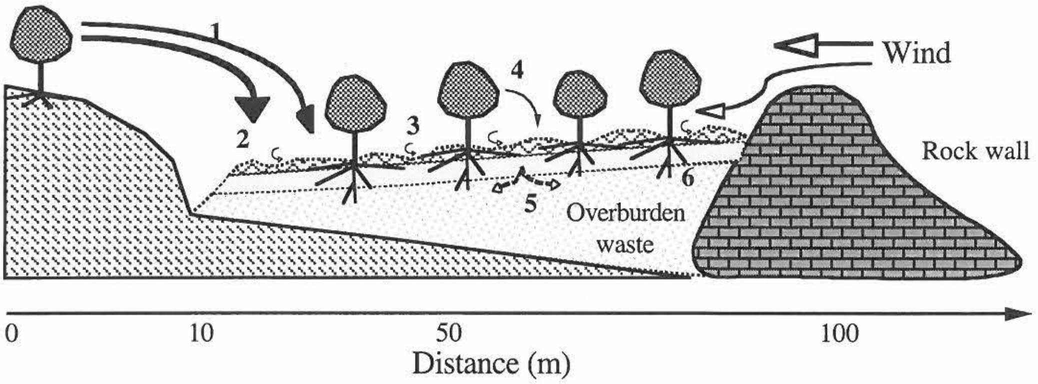
Slow growth of exotic species on nickel mine sites arises from combination of low nutrients, a Ca : Mg ratio imbalance and high concentrations of heavy metals. Reduced exotic plant growth has usually been alleviated by adding large amounts of fertiliser. Field trials indicate that maquis growth is slower than exotics with fertiliser. However, only

Current pattern of revegetation/colonisation on mine sites



1. Seed fall dispersal limited -tree planting distant from vegetation.
2. Compacted clay - crevices absent.
3. Smooth clay surface show no resistence to wind sheer and surface runoff - seed transported from site before germinating.
4. Shade and nutrients between trees sparse.
5. Clay compaction causes more frequent waterlogging.
6. Poor root development in compacted clays - more susceptible to tree fall during cyclones.

A possible solution for revegetating mine overburden



1. More colonisation from seedfall by reducing distance between adjacent vegetation and planted trees containing suitable habitats.
2. Mechanical ripping of compacted clay or placement of rocky overburden (saprolite, iron crust) on surface increasing the number of crevice seed traps containg shade and nutrients.
3. Rocky ripped surface provides micro-topography reducing wind sheer allowing seeds to remain in crevices.
4. More seedling establishment between trees.
5. Mechanical ripping increases drainage.
6. Greater root development reducing treefall during cyclones.

Figure 8.5 Schematic representation of current problems facing revegetation of mine overburden terraces in New Caledonia using direct planting techniques (top) and possible solutions; reduced spacing, ripping, top-dressing with rock overburden (bottom).

low fertiliser doses are required to show a growth response. This has important economic advantages for revegetation by reducing the high cost of initial large fertiliser doses. Fertiliser additions may have indirect positive effects on *Gymnostoma* growth by stimulating greater *Frankia* development, thereby potentially raising nitrogen fixation. Fertiliser applications might therefore solve problems of plant growth on mines. However fertiliser applications may potentially have negative effects in terms of establishing a rapid cover to reduce erosion.

Field experiments indicate that root : shoot values for *Gymnostoma* were low suggesting that root development concentrated around the nutrient source. From a revegetation perspective, the poor localised root development may potentially increase erosion between plants and raise susceptibility of plants to being uprooted during cyclones. This may potentially be solved by using other forms of nutrients such as maquis litter or hessian material, that provide a low nutrient source and retain soil moisture thus stimulating root development over a larger area.

Another negative effect of fertiliser is that faster growing weeds may invade revegetation areas resulting in the rapid development of flammable biomass (Panetta & Groves, 1990). Exotic grasses such as *Imperata cylindrica* have been shown to reduce tropical forest regeneration by raising vegetation flammability (Wibowo *et al*, 1996). This species was observed to have invaded plantations in southern New Caledonia and may pose a serious threat to rare endemic gymnosperms that are restricted to a few fire protected riverbank sites (Veillon, 1993; Gargomini *et al*, 1996; Mittermeier *et al*, 1996; Jaffré *et al*, 1998 b) by raising the flammability of surrounding vegetation. Jaffré *et al* (1998 a) reported that abandoned *Pinus caribaea* plantations in the same region had also affected native ultramafic vegetation by developing into dense populations that excluded maquis species, thus reducing the species diversity of these formations. Abundant fuel production by pines favoured the maintenance of a pyric succession in maquis containing pine invasions. Similar *Pinus* invasions have also been reported to adversely affect ultramafic plant communities in Mediterranean regions (Chiarucci & Dedominicis, 1995).

Revegetation of the mine waste and the iron crust overburden, may proceed along a successional path as outlined in this thesis, however, attention must also focus on fire management or the succession may be curtailed at the early maquis stage. More importantly, a high fire frequency is likely to prevent the development of later forest stages. Emphasis on establishing fire breaks in appropriate locations may allow stands to pass through the highly flammable maquis phase. Without such care, this unique endemic flora and vegetation may be threatened.

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Appendix 1

Soil physical properties

Soil structure

Soil physical properties were measured for eight samples from field experiment sites (chapter 7) using a 10 cm diameter soil auger. Sampling was spaced at 5 m intervals and consisted of coring to a depth of 7-10 cm. Bulk density (g, cm^{-3}) and soil porosity (% by volume) was calculated for the volume of soil removed from each hole (Landon, 1991). A replacement method (Landon, 1991) was used in conjunction with the auger method to obtain a more accurate measure of bulk density because surface soils frequently contained large amounts of coarse gravel that gave an overestimated value for weight. This technique consisted of completely filling auger holes with a known weight of oven dried fined grained beach sand. The remaining sample of sand was then weighed to determine the bulk density of the filled hole. Soil material removed using the soil auger was oven dried at 105°C for 24 hours and weighed to obtain the soil water content (%). This material was then sieved to determine the percentage of coarse (> 2 mm) and fine (< 2 mm) material.

Hydraulic conductivity

The hydraulic conductivity of iron crust oxisol, eroded oxisol, mine overburden and hypermagnesian soil was measured using a triple disc infiltrometer (T.R.I.M.S.) (Vauclin & Chopart, 1990). Measurements were made using the large (250 mm diameter) and medium discs (80 mm diameter) to obtain an average rate of infiltration. For iron crust oxisol, hydraulic conductivity measures were taken at three different pressures (0.5, 5 and 15 hPa) which correspond to pF values of between 0 and 1.2 (Bourdon *et al*, 1997, Duvig *et al*, 1998). Measures using both discs were carried out eight times on each soil type. A sample of soil was removed from underneath the infiltrometer before and after the measurement and oven dried at 105°C for 24 hours to determine saturation capacity of each soil type. The saturation capacity and time scale measures of infiltration were then used to calculate the hydraulic conductivity and macro pore size using equations given in Smettem & Clothier (1989).

Appendix 2

Soil and plant chemical properties

Organic carbon was calculated for soil samples by measuring weight loss from samples heated to 500°C in a muffle furnace for 24 hours.

Soil and plant samples were analysed for total nitrogen and phosphorus using an Auto-analyser Mk 2. The Kjeldahl method was used for determining total nitrogen and the Olsen method was used for determining total phosphorus (Rayment *et al,* 1992). Total N and P were measured for 0.5 g samples of soil and 0.2 grams of foliar material. Total potassium, sodium, calcium, magnesium nickel, iron and manganese in soil (0.2 g) and plant samples (0.15 g) were analysed with an atomic absorption spectrometer (Varian II) using techniques given in Rayment *et al* (1992).

Techniques used to measure extractable Na, Ca, Mg, K, NO_3, NH_4 and PO_4 in soil samples (5 g) are also given in (Rayment *et al,* 1992).