THE OPEN-FOREST - 'TREELESS' PLAINS BOUNDARY ON

MELVILLE ISLAND, NORTHERN TERRITORY.

by

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DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except when due reference is made.

Bruce Wilson

ABSTRACT

The 'treeless plains' is a colloquial name given to low lying undulating areas on Melville and Bathurst Islands which support a variety of shrubland and low open-woodland plant communities. The major aim of this thesis is to describe the vegetation of the plains and elucidate which environmental factors are determining the vegetation patterning, particularly across the forest plains boundary.

Numerical classification of vegetation survey data is used to define seven plant communities on the plains and adjacent forests. These communities differ floristically and/or structurally to other northern Australian plant communities, and show similarities to vegetation which is classified under the general headings of 'heath' and 'savanna'. The major environmental correlate differentiating the treeless plains communities from each other is wet season inundation. Secondary variation within the plains vegetation and between the vegetation of the plains and adjacent open-forests is associated with changes in several inter-correlated edaphic factors, including texture and moisture.

Detailed descriptions of the vegetation patterning across forest plains boundary shows that there is an abrupt structural change, with a distinct 'ecotone' or 'transition' zone between the forest and the plains. This structural change is accompanied by a gradual or 'ecoclinal' shift in composition of the understorey. A parallel study of environmental factors showed a gradational change in conditions with the plains occurring on soils which are generally sandier, less fertile, drier and possessing higher water tables than adjacent forest areas, and other red earth soils supporting eucalypt forests and woodlands in northern Australia.

Eucalypt seedling growth was significantly retarded when subjected to flooding in pots, but the flooding tolerances of species tested did not

correspond to their relative ecological ranges observed in the field. It was concluded that the deep sandy soils on the plains drain excess water rapidly at the end of the wet season and thus do not maintain water tables at levels high enough to prevent tree growth even in very wet years.

Field measurements showed that although surface soil moisture levels on the plains were severely depleted during the dry season, there appeared to be adequate moisture at depth to support tree growth throughout the year. Field plantings and associated pot trials supported this contention by showing that seedlings could grow under conditions of higher moisture stress that those recorded in the field at the end of the dry season.

There were significant differences in levels of nutrients, particularly magnesium, calcium and aluminium, across the forest plains boundary. Pot trials showed that eucalypt seedlings grew slower in plains soils compared to forest soil and that the growth differential was not due to differences in mycorrhizal fauna. The growth of transplanted eucalypt seedlings appeared to be suppressed by the forest overstorey, possibly due to competition for moisture. Seedling growth rates increased with site moisture and nutrient status on the plains, although there was no evidence that additions of calcium and magnesium had a differential effect on seedling growth across the boundary.

It is suggested that the deep sandy soils of the plains have been subjected to heavy leaching of nutrients, which is a primary factor associated with changes in vegetation across the forest plains boundary. Fire is implicated as a secondary agent, interacting with the differential growth rates of the seedlings and suckers across the boundary to retard tree development and cause the sharp structural boundary. The dominant eucalypts in the area possess several characteristics, such as poor seed dispersal, sporadic germination and seedling development and

suckers with a low potential to develop into trees, which reinforce the fire-edaphic patterning.

The vegetation and environmental patterning across the forest plains boundary is discussed in relation to various models that have been used to explain the relationship between tree and grass growth, particularly with respect to tropical savanna vegetation.

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CHAPTER 1 INTRODUCTION

The 'treeless plains' is a colloquial name given to low lying undulating areas on Melville and Bathurst Islands, which support a variety of shrubland and low open-woodland[1] plant communities (Wells *et al.* 1978). The vegetation of the plains form a distinct boundary with the adjacent, more widespread tropical eucalypt open-forests, although there is no corresponding change in environmental factors apparent (Wells *et al.* 1978). Since 1975 about 2000 hectares of the plains have been cleared to allow the establishment of exotic pine plantations.

The forestry operations and general lack of knowledge of the ecology of the area provide the major impetus for this thesis. Thus a primary aim of this thesis is to describe the vegetation of the plains and surrounding open-forests and elucidate environmental factors associated with the vegetation patterns. The work is also relevant to the more general problem of the relationship between tree and grass growth in northern Australia and tropical regions of the world.

The remainder of this introduction gives a regional perspective background to the Melville Island plains, including details on location, climate, soils, geology and vegetation, followed by a brief overview of tree versus grass growth and an outline of the thesis.

1.1 Regional context

1.1.1 Location and population

Figure 1.1 presents a map of Melville and Bathurst Islands showing their location relative to the rest of Australia. The Islands are some 7000 km²

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[1]Structural terminology follows Specht (1981) throughout.

.2

ARAFURA SEA

Pularumpi

Milikapiti

Yapilika

Rola Plains

Taracumbi

MELVILLE ISLAND

BATHURST ISLAND

Three Ways

Paru

Nguiu

Pickataramoor

0 5 10 15 km

TIMOR SEA

Forestry plantations

NORTHERN TERRITORY
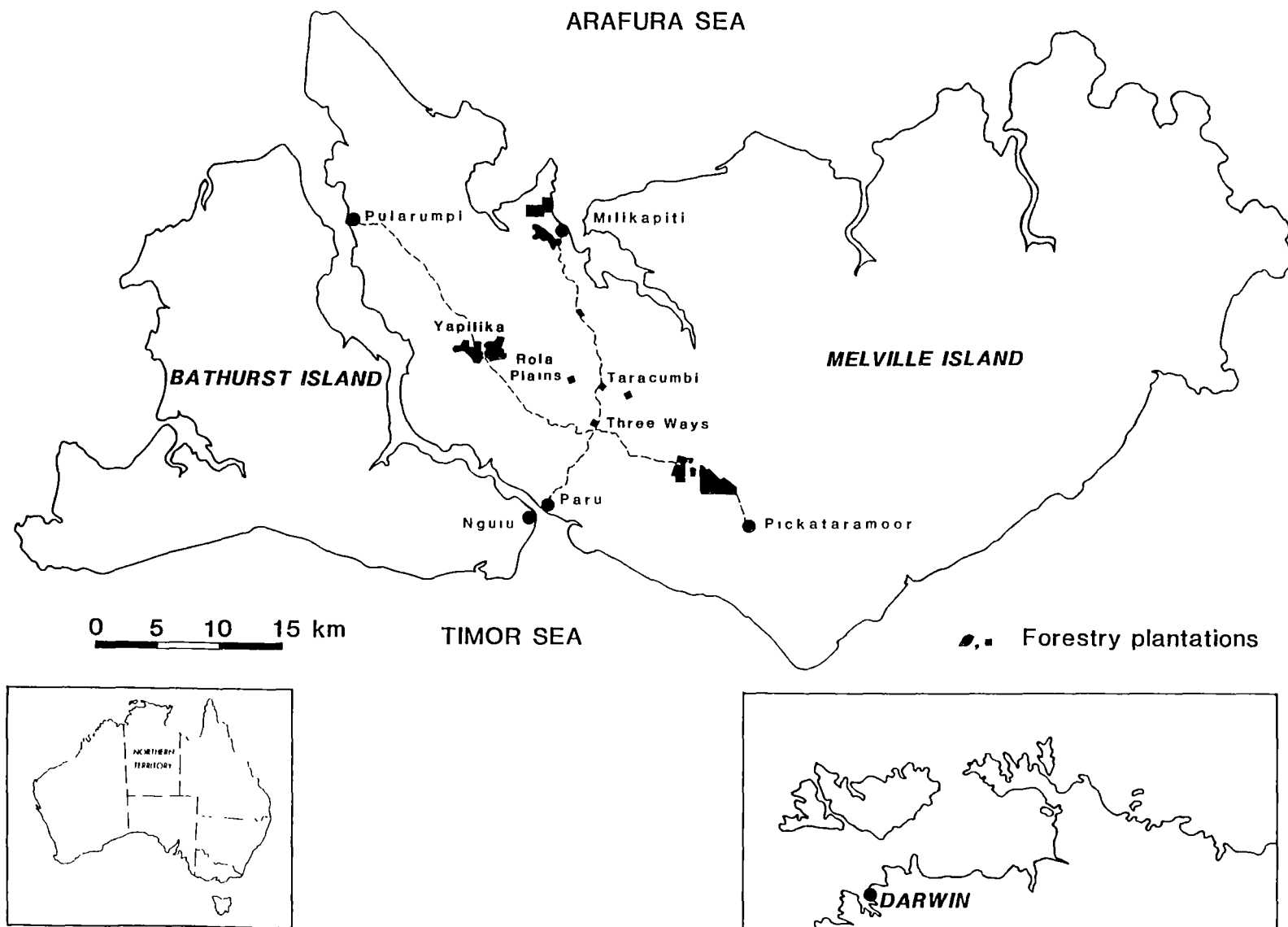
DARWIN

Figure 1.1   Location map of Melville and Bathurst Islands showing major place names.

in area and located about 40 kilometres north of Darwin, between latitude 11° and 12° south. The islands are populated by about two thousand people concentrated in the towns of Milikapiti, Pularumpi and Nguiu. Most of the people on the islands are from the Australian aboriginal 'Tiwi' tribe. Hence the islands are commonly referred to as the Tiwi Islands.

1.1.2 Climate

The Tiwi Islands are located within the climatic region referred to as the monsoonal or wet-dry tropics. This region is characterised by a distinct summer wet season and consistently high maximum temperatures all year round. The portion of the Northern Territory that falls within this region (within about 400 km from the coast) is colloquially referred to as the 'Top End', a term which will be used through this thesis.

Mean maximum temperatures in the Top End vary between about 31°C in July and 34°C in November (Darwin Bureau of Meteorology, various stations). Hours of daylight vary throughout the year by only 1.5 hours (McAlpine 1976). Most of the annual rainfall in the region occurs over the months December to March (the 'wet' season) while the months June to August are virtually rainless (the 'dry' season). The total amount of rainfall in one season (June - May) is reliable although its distribution is variable, particularly in the dry (June - August), late wet (April - May) and early wet (September - November) periods (Taylor & Tulloch 1985). Thus it is generally considered that, the direct effects of temperature and light are non-limiting to biological growth in the region, while the amount and distribution of rainfall are critical (Fitzpatrick & Nix 1970, Nix 1983).

Rainfall and temperature figures for Darwin, Pularumpi and Yapilika are shown in Table 1.1. The mean annual rainfall on Melville Island is over 1900 mm, which is substantially higher than the 1660 mm which falls annually in Darwin. Table 1.1 also shows that the area around Yapilika

Table 1.1 Rainfall statistics for Darwin, Pularumpi and Yapilika

Various stations
Mean monthly falls
(mm)

Station	N	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
Darwin	45	1	6	18	72	142	224	409	355	316	99	17	2	1661
Pularumpi	22	4	9	36	82	208	304	426	372	402	105	17	8	1975
Yapilika	7	1	8	44	149	178	257	366	377	289	129	97	6	1901

Pularumpi
Monthly falls for duration of study.
(mm)

Year	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
1985-86	0	0	5	110	279	150	643	171	178	105	52	13	1706
1986-87	45	30	7	197	94	563	247	94	93	123	97	1	1591
1987-88	0	0	2	531	574	352	33	335	214	123	22	0	1574

receives more rainfall than Darwin in the dry and late wet season. This is due to the catabatic thunderstorm activity, which is responsible for the arrival of the wet season across the middle of the Tiwi Islands about a month earlier than on the mainland of the Top End (Keenan *et al.* 1989). The period over which field work for this thesis was carried out, 1985 to 1988, was drier than average. The wettest and driest seasons on record at Pularumpi occurred in 1974/75 (2500 mm) and 1985/86 (1400 mm) respectively.

1.1.3 Vegetation

The structure and morphology of the vegetation of Top End generally reflects the seasonal nature of the climate of the region. Trees are generally evergreen although deciduous and semi-deciduous species are common components of the vegetation. Many ground layer species are annual or have perennial underground stems with annual aerial parts. Typically the ground layer of the vegetation is dominated by tall (> 0.5 m) tussock grasses with a scattering of shrubs and forbs. Much of the ground layer desiccates in the annual dry season when it is often consumed by low intensity fires (Haynes 1985).

The native vegetation of Melville Island has been described in the course of various studies (Stocker 1966, Van Cuylenberg & Dunlop 1973, Wells *et al.* 1978, Fensham 1990). In broad terms the vegetation of the Tiwi Islands is similar to that of the balance of the Top End in that eucalypt open-forests dominate, with eucalypt woodlands, mixed woodlands, mangroves, mixed-species closed-forests, grasslands and *Melaleuca* forests and woodlands occurring to greater or lesser extents depending on soil type.

However, there are several features of the vegetation of the Tiwi Islands, apart from the treeless plains, which differentiate it from that of the

adjacent mainland. The open-forests tend to be slightly taller and denser than mainland counterparts. In addition to the ubiquitous open-forest species *E. miniata* and *E. tetrodonta*, the Tiwi Island open-forests are co-dominated by *E. nesophila* (Melville Island Bloodwood). The later species is restricted on the mainland to localities such as Cobourg Peninsula (NT), Mitchell Plateau (WA) and Cape York Peninsula (QLD).

On salt water creeks to the north of Yapilika, the palm *Nypa fruticans* grows amongst mangrove trees. This palm is widespread in parts of Asia but in Australia is restricted to areas which receive the right mix of salt and fresh water, such as in the Cobourg and Cape York Peninsulas. The Tiwi Islands possess a high density of rainforest patches compared to other areas of the Northern Territory (Russell-Smith 1991). These rainforests are the most species rich in the Northern Territory and are floristically distinct from their mainland counterparts (Russell-Smith 1991).

1.1.4 Geology, topography and soils

Melville and Bathurst Islands (hereafter referred to as the Islands) are characterised by low relief with undulating laterite rises and dissected plateaux (Hughs 1976). The areas of highest relief reach a maximum elevation of about 80 metres above sea level and are remnants of a Tertiary land surface formed after the deposition of the Van Diemen sandstone (Hughs 1976). Drainage on the islands is generally to the north, from a plateau scarp which run in an east west band along the southern half of the islands. Colluvium and extensive sandplains have built up over the northern part of the island as a result of erosion from the Tertiary surface. The treeless plains occur where colluvium overlies a distinct, older Cretaceous geological formation of mudstone, siltstone and sandstone (Hughs 1976).

All soil profiles on the Islands are strongly weathered (Wells *et al.* 1978). Soils on the Islands are dominated by deep red and to a lesser extent, yellow and grey, earths (Wells *et al.* 1978). Such soils are predominant over about 17% of Australia (Anon 1985), particularly in the higher rainfall regions of the Northern Territory (Day & van Cuylenberg 1988) and northern Australia (Anon 1985). Red earths are generally characterised by non-calcareous profiles with weakly differentiated horizons, massive structure, earthy fabric and gradational textural changes down the profile (Isbell & Smith 1976, Coventry *et al.* 1983). Profiles of these soils are generally deep, ranging from 3 to 20 metres plus (Isbell & Smith 1976, Williams and Coventry 1979, Coventry & Williams 1984).

Ironstone gravels are often present in red earths, sometimes abundant and scattered over the soil surface (Isbell & Smith 1976). These gravels may be the result of formation *in situ* caused by fluctuating water tables during the process of laterisation (Coventry *et al.* 1983). Mottled horizons are often present which are similar to the pallid zone of a lateritic profile (Isbell & Smith 1976). Such soils may be referred to as 'lateritic' red earths, although the term laterite has a wide and confusing usage (Paton and Williams 1972).

In preliminary resource surveys of the Yapilika area, van Cuylenberg & Dunlop (1973), Wells & van Cuylenberg (1978) and Wells *et al.* (1978) have described the soils under the treeless plains and adjacent open-forests as deep sandy red/yellow earths or earthy sands. In a subsequent brief study, Wells (1976) found no apparent changes in soil morphology or chemistry associated with the boundary between the plains and surrounding open-forest, although Bevege (1981) suggested that more detailed analysis may reveal nutrient differences.

1.1.5 Fire

The annual desiccation of the understorey herbaceous layer of the open-forests and woodlands of the Top End provides a ready source of fuel, and fire is almost an annual phenomena in the region. There is evidence that lightning is an important ignition source in the late dry season (Bowman *et al.* 1988a) and may have been so before the coming of man. Aboriginal people are likely to have been the major ignition source since their arrival in Australia (Haynes 1985) *c* 40 000 years ago. Haynes (1985) suggests that Aboriginal burning practices may have been tailored to optimise vegetation and habitat management. Present day Top End burning regimes appear to be broadly similar to pre-European times, although fires may burn slightly later in the year and thus be hotter (Press 1987, 1988). Fire is often invoked as a major issue concerning the vegetation ecology and management of the area (Bowman 1988), although there is still much debate about the specific effects of fire on vegetation structure and composition.

The following is a brief account of fires on the Tiwi Islands from the authors observations. Present day early dry season fires are generally relatively cool with flame heights below 2 metres. They cause little crown scorch and often go out over night. Late season fires can be relatively hot causing considerable crown scorch and may burn for several days. The Tiwi people still light fires, usually for hunting and access purposes, beginning in late May or as soon as vegetation will burn. Fire lighting continues until the following wet season, although frequency and extent decreases with progress of the dry season due to a diminishing supply of unburnt, accessible vegetation. Since about 1965 the Forestry operations have initiated an early season burning programme concentrating on plantation boundaries, but also in a systematic grid over the entire islands. The parts of the treeless plains where this study took place are normally burnt in the early dry season (May-June), although

extensive areas of plains get burnt in the late dry season (September-October).

1.1.6 Forestry

A small native Cypress (*Callitris intratropica*)[2] plantation programme was established on Melville Island in 1960. Early planting was concentrated near Milikapiti and Pickertaramore (Figure 1.1). By the mid 1970's it was apparent that the Cypress Pine could not maintain an 'economic' growth rate (Haines 1986) and this species was replaced by the exotic Caribbean Pine (*Pinus caribaea* Mor.). Since 1980 most of the plantations have been established on the treeless plains at Yapilika (Figure 1.1) where it was found that clearing costs are low and, with the addition of fertiliser, tree growth rates are equivalent to most open-forest sites. The work undertaken in the course of this thesis is concentrated in the Yapilika area.

1.2 Background to the problem of tree versus grass growth

This section gives a brief overview of the problem of the relationship between tree and grass growth to provide a broader context for the thesis.

Sarmiento (1984) has identified a general view in the biogeographic literature that, once established, trees are capable of dominating shrubby and herbaceous vegetation because of the advantages they possess in extracting resources from a site. Thus, a lack of trees in temperate and tropical regions is often associated with environmental constraints which preclude tree growth by affecting the ability of tree species to

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[2]Taxonomic nomenclature follows Dunlop (1989) throughout, unless indicated otherwise.

successfully establish on a site or, for established juveniles to grow onto trees. For example impeded drainage and high salinity levels have been implicated as precluding tree growth from a site (Cole 1982), while high grazing pressure (e.g. Tothill 1971) and fire (e.g. Ellis 1985) may retard the recruitment of saplings into the tree layer.

In a consideration of tree versus grass growth, Walter (1971) has put forward a model in which grasses are superior competitors for water in the top soil and woody plants have exclusive access to lower (subsoil) water supply. This model can be used to help explain why some areas support woody dominated vegetation while other areas support grasslands. For example Walter (1971) explained the existence a shrubland grassland mosaic by concluding that the shrubs could utilise water in deep cracks within a rocky substrate, but were excluded from adjacent areas with deep soils, where the grasses used up all the moisture and prevented it reaching the subsoil. Similarly the anaerobic conditions produced by high water tables in soils may preclude the development of deep root systems by trees, but allow shallow rooted grasses to grow.

A range of vegetation types, characterised by the co-occurrence of woody and grass components and found throughout the tropical regions of the world, are known by the widely used term 'savanna' (Bourliere & Hadley 1983). A central focus of ecological research into savannas has been the relationship between the tree and herbaceous lifeforms (Sarmiento 1984), particularly factors affecting the relative abundance of these elements in space and time.

Savannas have been classified into different 'types' by variations in tree:grass ratios (e.g. Cole 1963; Gillison 1983). On a broad scale the distribution of savanna and the distribution of different savanna types, has been associated with climatic factors, particularly rainfall and

temperature regimes (Whittaker 1975). On more regional and local scales, variations in grass:woody ratios have been related to, changes in edaphic factors such as moisture and nutrient status (Walker *et al.* 1981, Walker & Noy-Meir 1982, Sarmiento *et al.* 1985, Knoop & Walker 1985), disturbance factors, most commonly man induced fire (Harrington *et al.* 1984) and grazing (Blackburn & Tueller 1970) regimes, or an interaction between all these factors (Walker 1987). Due to the strongly seasonal nature of the climate that most savannas experience, many studies also emphasise the temporal dimension of these environmental factors (Medina 1982).

In an adaptation of the Walter (1971) model, it has been suggested that a partitioning of surface and sub-surface resources by grass and trees, where each component is the superior competitor in a different layer, may help explain how these lifeforms can coexist in apparently stable savanna formations (Knoop & Walker 1985). A quantification of surface:sub surface resources can thus be used to help explain observed tree:grass ratio's (Goldstein & Sarmiento 1987) and be used as a basis for predicting variations in composition that may accompany changes in factors such as grazing pressure or fire regime (Walker & Noy-Meir 1982).

A review of the knowledge of the vegetation of northern Australia reveals similarities and differences to the foregoing discussion. The vegetation of the region is dominated by *Eucalyptus* or *Melaleuca* open-forests and woodlands with a grassy ground layer (Wilson *et al.* 1990). These formations have been labelled as forest or woodland savannas (Gillison 1983, Johnson & Tothill 1985). At the community level the distribution of major vegetation types has generally been associated with patterns in landform and edaphic factors (Bowman 1988). Treeless vegetation is generally confined to 'extreme' habitats, such as the grasslands occupying seasonally flooded areas or bare mudflats and samphire in tidally flooded areas (e.g. Wilson & Bowman 1987).

Changes in structure and floristic composition within northern eucalypt forest and woodland communities have been related to subtle variations in edaphic factors, particularly soil moisture conditions (Lacey & Whelan 1976, Andrew 1986, Bowman 1986, Bowman & Dunlop 1986, Bowman & Minchin 1987). The independence between overstorey and understorey composition has been noted (Storey 1976, Rice & Westoby 1985) and it has often been hypothesised that the different vegetation layers and lifeforms tap resources from different soil depths (Storey 1976, Specht *et al.* 1977, Bowman 1986). However, most vegetation surveys in the region have confined measurements of environmental parameters to superficial surface assessments, allowing little verification of this hypothesis.

Fire, which is virtually an annual event in much of the vegetation of the region is thought to interact with site conditions to effect structure, particularly understorey shrub density (Bowman 1986, Bowman *et al.* 1988b). It has been suggested that the absence of saplings in some Northern Territory open-forests may be caused by the high fire frequencies (Bell 1981, Braithwaite & Estburgs 1985, Werner 1986). These latter authors imply that fire may exert an over-riding influence on other environmental factors and that a continuation of current fire regimes may lead to further declines in tree density.

However, compared to the tropical savannas of Asia and Africa, nothern Australan savannas are depauperate in native species of large herbivourous mammals. In some situations grazing pressure from feral and domestic animals is intense (e.g. Werner 1986). However, this is not the case for the plains area on Melville Island (Bayliss & Yeomans 1989). Herbivorous insects probably exert the major grazing pressure on northern Australian savannas, although their effects have been largely ignored by ecologists (Anderson & Lonsdale 1991).

An understanding of the vegetation of the Melville Island treeless plains and its relationship to the adjacent open-forests should provide additional useful knowledge relevant to the ecology of northern Australia forests and tropical savannas in general.

1.3 Thesis Outline

The vegetation of the treeless plains has been broadly classified by structural formation and dominant species (Wells *et al.* 1978). The vegetation appears to be somewhat different to much of the vegetation found throughout the Northern Territory (Wells 1976). Thus, Chapter 2 of this thesis reports on a detailed study of the nature of the vegetation of the plains and a comparison with vegetation described from elsewhere in northern Australia. This chapter also describes the major environmental correlates of the vegetation patterning.

Chapters 3 and 4 focus on the boundary between the plains and the open-forest. Chapter 3 quantifies changes in vegetation structure and floristic composition across the forest plains boundary. Chapter 4 gives a detailed description and analysis of the soils and other environmental factors across the forest plains boundary and relates these to other studies in northern Australia and the vegetation patterns described in Chapter 3.

Chapters 5 presents results from experiments designed to measure the response of seedling and root sucker growth to changes in environmental factors identified in the previous chapters. The conclusion of the thesis (Chapter 6) compares the biotic and abiotic environments of the treeless plains with other savannas before discussing the relevance of the work to some of the general models of savanna systems.

CHAPTER 2 <u>THE NATURE OF THE MELVILLE ISLAND PLAINS: A
FLORISTIC SURVEY</u>

2.1 Introduction

Land resource surveys of the Melville Island plains and surrounding areas
have mapped the environment into 'units' which delineate recurring
patterns of vegetation, landform and soil types (van-Cuylenburg & Dunlop
1973, Wells & van-Cuylenburg 1978). These studies have noted that the
'treeless' plains support a variety of vegetation communities ranging from
low shrubland to woodlands. Furthermore, these plant communities 'may
be different' (Wells 1976) from other plant communities found in the
Northern Territory. However, the vegetation surveys of the area to date
have not been detailed enough to allow precise definitions of vegetation
types and their environmental relationships or comparisons with other
reported vegetation descriptions.

Therefore the purpose of this chapter is to define and describe the plant
communities of the plains and adjacent open-forest and determine
patterns in distribution of plants and associated environmental correlates.
This allows the plains and adjacent vegetation to be placed into a regional
context and a determination of which, if any, environmental factors are
associated with floristic patterns and worthy of more detailed
investigation in subsequent chapters.

The survey was conducted using standard phytosociological methodology
(e.g. Gauch 1982). Classification and ordination analysis techniques are
used as complementary tools to gain maximum insight into the floristic
compositional variation of the survey data. Classification is used to group
the vegetation samples into distinguishable plant communities, which
facilitates vegetation description and mapping and comparison with other
published reports. Ordination is also used to arrange vegetation samples

along gradients and explore the relationships between plants and measured environmental factors.

2.2 Methods

2.2.1 The survey area

A preliminary map (scale 1:500 000) of the treeless communities on Melville and Bathurst Islands, prepared from topographic maps (1: 100 000) and aerial photographs (1:50 000, 1978, colour), shows that the plains extend across the central portion of both islands (Figure 2.1). The area surveyed centres on two main areas in the west of Melville Island; Yapilika (which has been mostly cleared for plantations) and Rola Plains (Figure 1.1 and 2.1). The areas on Bathurst and the eastern part of Melville Island were not included in the floristic survey because they were inaccessible by vehicle from Melville Island.

2.2.2 Field survey

Sampling procedure

Sampling was stratified using the existing Land Unit maps (van-Cuylenburg & Dunlop 1973; Wells & van-Cuylenburg 1978) and, for areas not covered by these surveys, extrapolating patterns on the aerial photographs. Sampling was most intense in the low-woodland, shrubland and open-shrublands which occurred on the red and yellow earth soils. Shrublands and woodlands which occurred on the grey and black, poorly drained soils were sampled at a lower intensity. Areas of open-forest adjacent to the plains were sampled to show the floristic relationship between the plains and the surrounding forest communities. Uncleared areas adjacent to the existing plantations were intensively sampled to accurately show the range of communities which have been cleared.
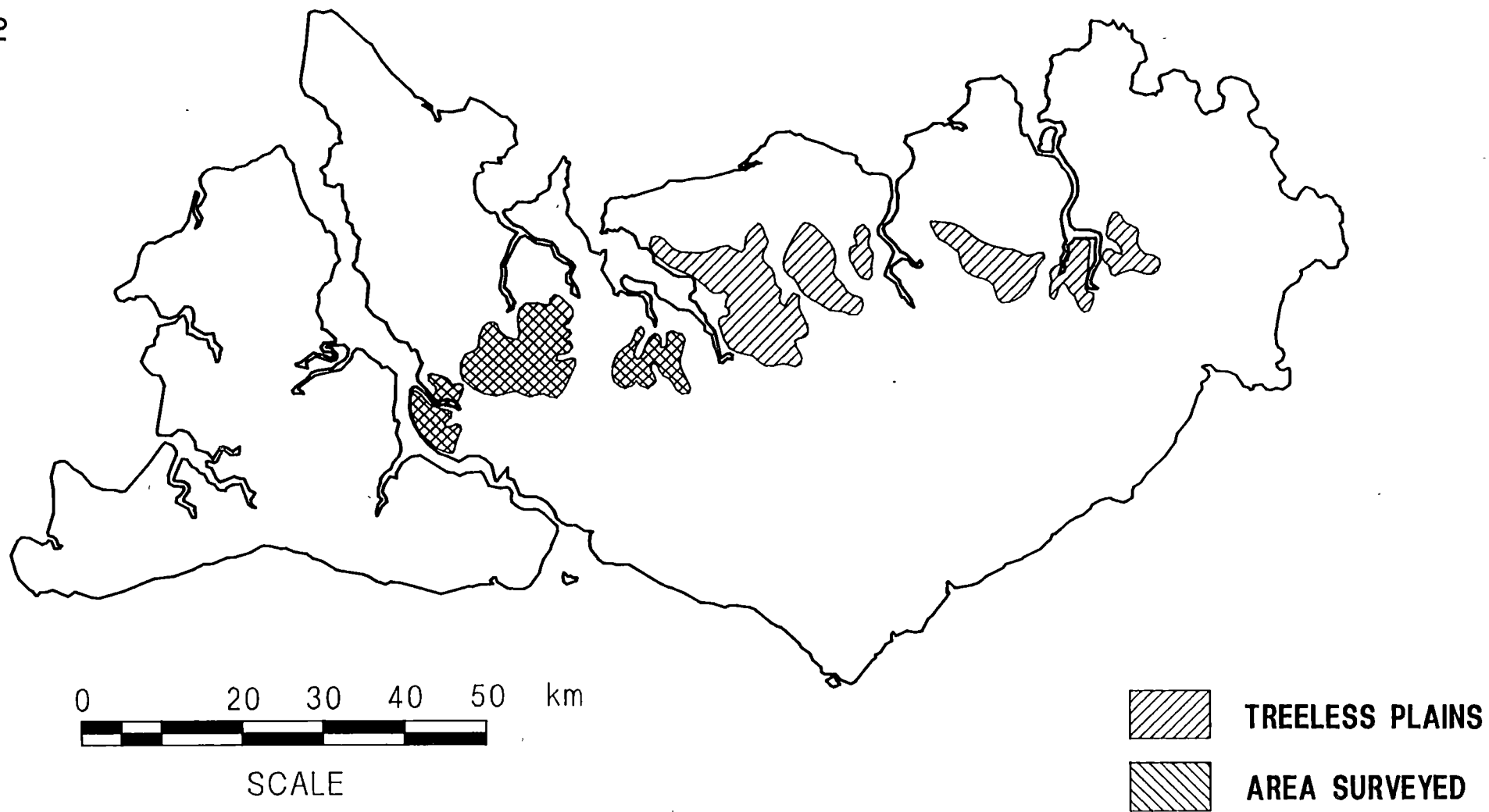
Figure 2.1 Map of Melville and Bathurst Islands showing location of treeless plains and area surveyed in this study.

Prior to field work proposed sampling sites, arranged along road or specific magnetic compass bearings, were marked on maps. Extra plots were located at sites with floristic assemblages that, in the authors opinion, had not been adequately sampled.

Vegetation

The floristic survey was carried out in April 1987, at which time most of the tall annual grasses e.g. *Sorghum intrans* had reached full height, flowered and begun to cure. Plots were located at sites which appeared to be relatively homogeneous in floristic composition and structure. At each plot location, a list was made of all species present in a 10 by 10 metre area. Previous experience in the area had shown that plots larger than this size did not contain significantly greater number of species. Abundance of each species was assessed following the procedures used by Bowman & Minchin (1987), by subjectively estimated into modified Braun-Blanquet (Mueller-Dombois & Ellenburg 1979) percent projected foliage cover (*sensu* Specht 1981) classes of 1 = 1%, 2 = 1-5%, 3 = 6-25%, 4 = 26-50%, 5 = 51-75% and 6 = 76-100%.

Vegetation structure of the dominant stratum following Specht (1981) was noted. Variation in stand structure on open-forest sites was investigated by measuring the diameter at breast height (DBH) of all woody stems greater than 2 metres high in a 30 by 20 m plot.

Environmental variables

The colour of the A2 horizon was noted in the field as red, yellow or grey. (Coventry *et al.* (1983) suggest that soil colour in the red-yellow-grey earths of northern Australia reflects the duration of wet season saturation of the profile, with grey soils being the most waterlogged). Field texture of the surface soil was determined by manipulation of a soil bolus following the procedure described by McDonald & Isbell (1984). A

surface soil sample was collected by hammering a 4 cm diameter steel pipe, 15 cm into the ground and placing the extracted core (about 250 grams of dried soil) into a glass jar. From this sample gravel content (using a 2 mm sieve) and 'wet season' gravimetric moisture content was measured. Surface soil samples were also collected from 72 sites in August 1987 to allow estimation of 'dry season' moisture content.

Following numerical classification of the sites by their floristic composition (see below) soil profiles of sites sampling the range of communities were described, following the methods of Wells *et al.* (1978). Soil from 70 sites, selected to cover the range of variation in environments, were analysed for particle size distribution using the Pipettes and Sieve Method (Coventry & Fett 1979).

2.2.3 Data analysis

Data were stored and analysed using the ecological data storage and analysis package DECODA (Minchin 1990) and the pattern analysis package PATN (Belbin 1987).

Before analysing floristic data, consideration must be given to the array of classification and ordination techniques that have been developed and used and reviewed by many authors (e.g. Gauch 1982; Kershaw & Looney 1985). Detrended Correspondence Analysis (DCA) has become a widely used ordination technique since it was introduced to plant ecology (Hill & Gauch 1980). Kershaw & Looney (1985) have concluded that DCA and the related classification technique Two Way INdicator SPecies ANalysis (TWINSPAN), are the best available techniques of ordination and classification as they have achieved a level of numerical sufficiency which provides extremely powerful and effective methods for organising large data sets.

However, a recent study comparing the reliability and robustness of similarity indices commonly used in ecological numerical analysis (Faith *et al.* 1987) has shown that the 'Kulczynski', 'Bray-Curtis' and 'Relativised Manhattan' measures provide the most robust relationships with ecological distance. The similarity measure used in DCA and TWINSPAN, Chi-square distance, was one of the least successful measures. Furthermore, extensive comparitive tests on simulated vegetation data by Minchin (1987) have shown that a combination of Bray-Curtis similarity and non-metric multidimensional scaling (NMDS) gave one of the most robust and effective measures of compositional variation, when compared to other commonly used ordination procedures.

Thus, in this study the floristic classification was derived by using the raw Braun-Blanquet species cover scores to generate a sample dissimilarity matrix, based on the Bray-Curtis coefficient. From this association matrix a dendrogram was generated by fusing samples using various fusion strategies. The dendrograms were examined in conjunction with species lists, environmental parameters and maps, to determine which, in the authors opinion, gave the most meaningful groups. Environmental parameters were related to final groups by contingency tables or by comparing means using oneway analysis of variance. Preliminary ordination was carried out using DCA to check for the presence of outliers before ordinating using the Global Non-Metric Dimensional Scaling (NMDS) ordination technique based on the above Bray-Curtis compositional dissimilarity matrix. The Global NMDS ordinates samples such that the distances between each pair of samples are in the best possible rank order agreement with their compositional dissimilarities (Minchin 1990).

The procedure used to relate the floristic ordination and environmental variables is that of Bowman & Minchin (1987). This approach recognises that the orientation of the ordination axis is arbitrary and the correlation

between the ordination and environmental variables may be complex. Thus the environmental variables were plotted within the ordination space and inspected for relationships. Distributions were also related to the ordination by the use of rotational correlation (Dargie 1984), which selects the vector in the ordination space which has a maximal linear correlation with the given variable.

2.2.4 Vegetation map

A 1:50 000 scale vegetation map was compiled for the area surveyed. The deductive approach (Kirkpatrick & Dickinson 1985) was taken, whereby mapping units were drawn to best fit the plant communities defined from the floristic survey and analysis. The map was compiled by delineating vegetation patterns on existing land-unit maps and aerial photographs. The final linework was transferred to a base map (derived by photocopy enlargement of a 1:100 000 scale topographic map) using a zoom transfer-scope.

2.2.5 Comparison of classification systems

Land unit and structural classification systems were compared with the floristic classification by constructing 2-way contingency tables and determining significant associations using two sample Chi-square tests.

2.3 Results

2.3.1 Classification

After examining the dendrograms derived from various fusion techniques, that generated by the flexible Unweighted Paired Group Mean Average (UPGMA) with Beta = 0 was chosen. This gave, in the author's opinion, the most meaningful and coherent groups in terms of species composition

and environmental relationships. This fusion procedure is an agglomerative hierarchical strategy which weights objects (in this case species) equally (Gauch 1982) and minimises the stress (the difference in relative order) between the fused association measure and the original association matrix (Belbin 1987).

The upper portion of the dendrogram is shown in Figure 2.2. Seven groups were chosen from the dendrogram to define the final floristic groups. A summary incorporating dominant species and mode structural formation class, for each group (or community) is presented in Table 2.1. The community labels from this table, which incorporates the dominant species and the mode structural formation class of the upper layer, are used for convenience throughout this thesis even though some communities show variation in structure and dominant species.

A full list of groups by species membership is given in Appendix 1. The environmental and structural parameters of each floristic group are presented as a contingency table for nominal variables (Table 2.2; structure, Table 2.3; soil colour) or a mean value for the continuous variables (Table 2.4; wet and dry season moisture, and gravel content, minimum depth to water table, Table 2.5; particle size analysis). Total sand content (fine + coarse) is used in Table 2.5 as a measure of soil texture because the ratio of fine:coarse sand and the clay and silt contents showed substantial variation between samples.

Community descriptions

Following is a summary of the floristic groups (which will be considered equivalent to plant communities) in terms of floristic composition (Appendix A), modal structural formation class (Table 2.2) and characteristic environmental factors (Tables 2.3 - 2.5).

1. *E. miniata* open-forest

2a. *Acacia* spp. shrubland
3. *E. tetrodonta* open-forest

2b. *Acacia* spp. shrubland

4. *G. pteridifolia* low-woodland

5. *L lactifluus* open-shrub

6. *Acacia* spp. open-shrubland

7. *Banksia* low-woodland

0.6   0.7   0.8

DISSIMILARITY
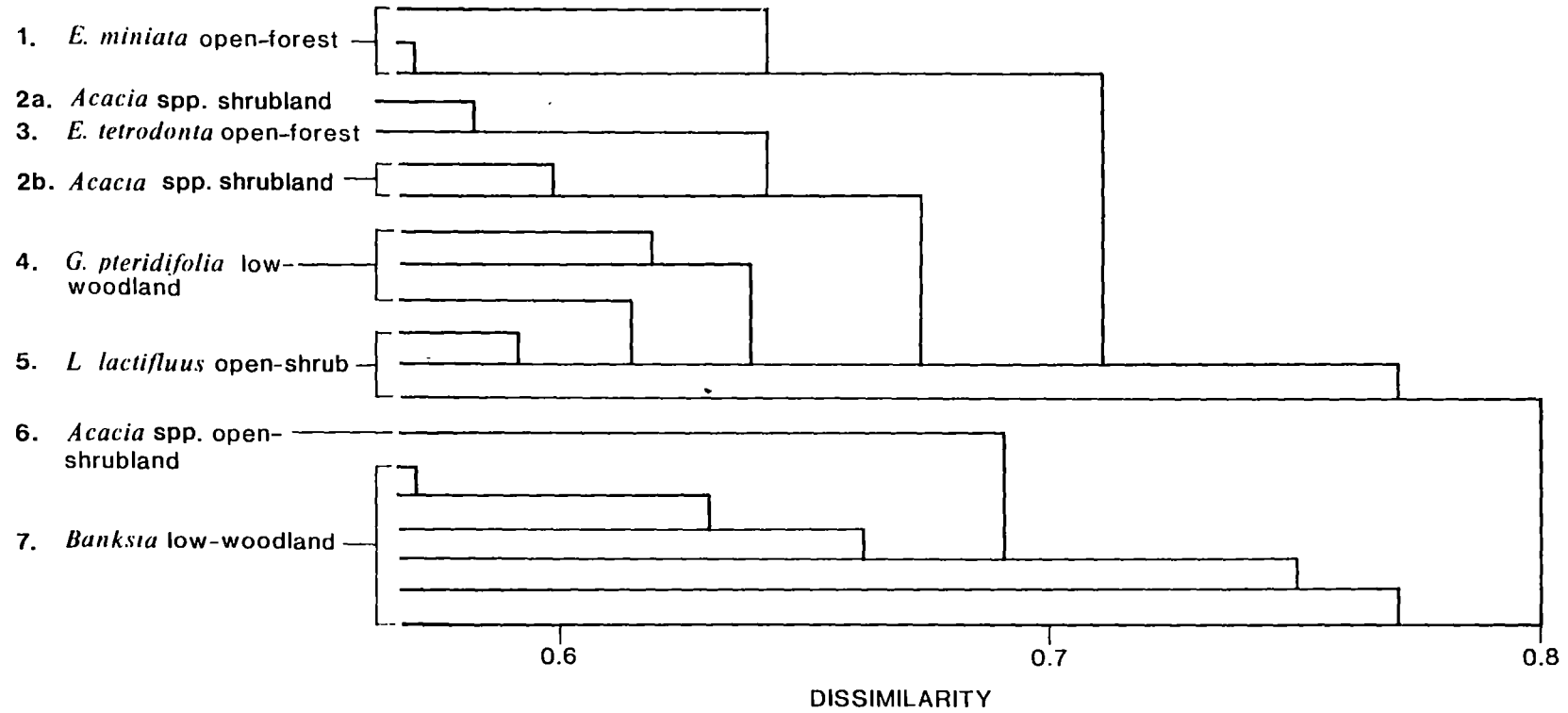
Figure 2.2   Upper portion of UPGMA dendrogram of site classification showing final group names and labels.

Table 2.1 Label and summary of the dominant species and modal structural formation class of plant communities defined by numerical classification of floristic data.

UPGMA Number	Label	Structure and dominant species by layer	
		Upper	Ground
1	*E. miniata* open-forest	Open-forest *E. miniata\nesophila.*	Grass\forbland *Sorghum intrans*\Fabaceae spp..
2a + 2b	*Acacia* open-shrubland	Shrubland of *A. gonocarpa\difficilis*	Open grassland of *Sorghum intrans*
3	*E. tetrodonta* open-forest	Open-forest *E. tetrodonta\nesophila.*	Grass\forbland *Sorghum plumosum.*
4	*G. pteridifolia* low-woodland	Low-woodland *Grevillea pteridifolia.*	Open-grassland *Sorghum intrans.*
5	*L. lactifluus* open-scrub	Open-scrub *Lophostemon lactifluus, Syzygium eucalyptoides.*	Open-grass\sedgeland.
6	*Acacia* shrubland	Shrubland of *A. oncinocarpa\latescens.*	Open-grassland of *Eriachne obtusa*
7	*Banksia* low-woodland	Low-woodland\open-forest of *B. dentata\Melaleuca viridiflora.*	Closed-sedgeland\grassland

Table 2.2 Frequency of sample occurrence by community and structural formation (Specht 1981).Significant positive association, as determined by Chi-square test, indicated by * = P<0.05, ** = P<0.01, *** = P>0.001.

pfc (%)	height (m)	Structural formation	Community 1	2	3	4	5	6	7
30-50	10-30	open-forest	9 ***	-	9 ***	-	1	-	-
3-50	<10	low open-forest	-	2	3	3	4	-	4
10-30	<10	low woodland	1	12	3	10 *	6	3	10 *
30-50	>2	open-scrub	-	2	-	1	3	1	-
10-3	0.25-2	shrubland	-	-	-	2	2	5	1
<1	0.25-2	open-shrubland	-	20 ***	-	1	-	2	1
30-70	<2	grassland	-	-	-	-	-	-	2

Table 2.3 Frequency of sample occurrence by communities and colour of soil A2 horizon. Significant positive associations, determined by Chi-square test, indicated by *=P<0.05, **=P<0.01, *** =P>0.001.

Community	1	2	3	4	5	6	7
Colour							
Red	10 *	35 *	14 *	11	2	12 *	-
Yellow	-	-	1	6	9 **	-	6
Black/ grey	-	-	-	-	4	-	12 ***

Table 2.4 Means of gravel, wet season moisture and dry season moisture content of surface soil, depth to water table and species richness by plant community. The same letters denote row means not significantly different at P<0.05, level as determined by Tukey's range test. No letters are given where F values were not significant (P < 0.05) for row means, as determined by analysis of variance. N is given in brackets where it is less than the total n.

Community	1	2	3	4	5	6	7
Total n	10	36	15	17	15	11	18
Gravel (%)	1.3 A	0.1 A	0.0 A	14.6 AB	7.6 A	0 A	25.2 B
Moisture wet (%)	24.5 (9) A	14.5 (18) AB	18.0 (10) AB	20.7 (4) AB	26.7 (5) A	4.0 (5) B	46.5 (10) C
Moisture dry (%)	8.4 (10) AB	4.7 (19) CD	6.4 (10) AC	8.7 (13) AB	10.0 (7) B	2.8 (10) D	10.9 (9) B
Water table (m)	4.5 (10)	4.1 (19)	2.5 (10)	1.9 (13)	0.3 (7)	- (10)	0.3 (9)
Species richness (nos/40m2)	28 A	25 A	26 A	25 AB	26 A	18 C	20 BC

Table 2.5 Particle size analysis of fine earth (<2mm) fraction by community. The same letters denote column means not significantly different at p<0.05 level, as determined by Tukey's range test. Columns with no letters indicate that analysis of variance showed that F values were not significant.

Community	n	Clay	Silt	Faction Fine sand	Coarse sand	Sands (Coarse + Fine)
1	6	8.1	10.1	64.5 AB	18.4 B	82.9 AB
2	21	5.8	9.3	65.9 AB	20.9 B	86.8 A
3	8	7.5	9.8	70.7 A	15.8 B	86.5 AB
4	17	6.8	4.3	67.1 A	15.1 B	82.2 AB
5	6	7.8	8.5	63.2 AB	20.0 B	83.2 AB
6	9	10.5	3.8	55.9 B	33.4 A	89.2 A
7	12	10.3	8.6	61.1 AB	18.8 B	79.8 B

The divisions at the higher levels of dissimilarity on the dendrogram, separate the *Banksia* low woodland (group 7), the *Acacia* spp. open-shrubland (group 6) and the *Eucalyptus miniata* open-forest (group 1) from the other groups.

Sites in the *Banksia* low woodland (group 7) were not a central focus of the study. Therefore truncation was at a relatively high level of

dissimilarity resulting in a relatively heterogeneous group in terms of floristic composition and structure. The upper stratum in this group is generally a 3-6 m high *Banksia dentata/Melaleuca viridiflora* dominated low woodland/low open-forest, but also included sites dominated by a range of other small tree species or occasionally a *Sorghum intrans* grassland. Ground cover is generally a closed sedgeland or grassland dominated by sedges such as *Fimbristylis* spp., grasses such as *Sorghum intrans*, *Eriachne* spp. and *Germannia grandiflora*, or the rush *Leptocarpus spathaceus*. A layer of root suckering shrubs, such as *Lophostemon lactifluus* or *Syzygium eucalyptoides* is common. This community occurs on duplex or podsolic soils which have a grey, sometimes gravelly A horizon, which were often wet and boggy with water tables at or near the surface at the surface at the time of the floristic survey.

The upper stratum of the *Acacia* spp. shrubland (group 6) is dominated by 1-2 m high *A. oncinocarpa* and *A. difficilis* and other species such as *Calytrix exstipulata* and *Jacksonia dilatata*. Emergent *Grevillea pteridifolia* or *Acacia latescens* occur scattered through this community occasionally forming low woodlands. There is a sparse layer of medium high grasses dominated by *Eriachne obtusa*, *E. triseta* and *Setaria apiculata*. Mean species richness of sites from this group is significantly lower than for all other communities. This community generally occurs on deep, red soils with high coarse sand content, which were significantly drier than most other communities all year.

E. miniata and *E. nesophila* dominate the 20-28m canopy of *E. miniata* open-forest (group 1). Sites generally have an open-shrub layer dominated by *Acacia aulacocarpa*, *Grevillea* spp. and *Livistona humilis*. The open-grass/forbland ground storey is dominated by species such as the grasses *Chrysopogon fallax*, *Sorghum* spp. and *Thaumastochloa major* and forbs *Borreria breviflora*, *Desmodium clavitricha* and other Fabaceae species. Surface soils are sandy-loam red earths with

intermediate wet and dry season moisture contents and occasional lateritic gravels.

The remaining four groups show greater floristic similarity and more subtle differentiation between environmental factors. The *Acacia* open-shrubland (group 2) is made up of two disparate groups. The only difference evident between group 2a and group 2b was a higher abundance of *Sorghum intrans* in the latter. However, both groups have identical structures in the dry season and occur on the Rola plains on deep, sandy, red soils which appeared to be free draining all year round. Thus groups 2a and 2b were combined into one community (group 2). Sites in community 2 generally had a low, <1 metre, layer of shrub species such as *Hibbertia cistifolia*, *Pachynema complanata* and *Distichostemon hispidulus* with occasional emergents to 2 metres of *Grevillea pteridifolia* and *Acacia* spp. forming a low woodland. Species such as *E. tetrodonta*, *E. porrecta* and *E. ptychocarpa*, are occasionally present as low (< 1 metre) shrubs with numerous stems sprouting from underground root stocks (lignotubers or rhizomes). Dominant grasses were either tall *Sorghum* spp. or shorter *Eriachne* spp.

The *E. tetrodonta* open-forest (group 3) is floristically similar to the *Acacia* open-shrubland despite obvious structural differences. Some sites from this group supported a low woodland dominated by *Grevillea pteridifolia*. The *E. tetrodonta* open-forest has a lower proportion of *E. miniata* in the canopy relative to *E. miniata* open-forest (group 1) in addition to differences in the understorey including a higher grass cover and a lower occurrence of species such as *Desmodium clavitricha*, *Bonamia brevifolia* and *Planchonia careya*. Sites from this group generally had wetter, less sandy soils than those from the *Acacia* open-shrubland (group 2) and drier, more sandy soils than those from the *E. miniata* open-forest.

Group 4 consists of a 4-6 metre *Grevillea pteridifolia* low woodland layer over a grassland characterised by *Eriachne burkittii* and *Eulalia mackinlayi*. Species such as *Buchanania obovata*, *Lophostemon lactifluus* and *Petalostigma quadriloculare* are often present as root suckers or shrubs to 2 metres high. Sites from this group generally occur on soils with red or yellow A horizons, which are significantly wetter, with higher water tables than the *E. tetrodonta* open-forest (group 3) and *Acacia* open-shrubland (group 2) sites.

Group 5 is dominated by mixed species, 2-3 metre high open-scrub with *Lophostemon lactifluus* the most common component. Many of the shrubs such as *Lophostemon lactifluus*, *Syzygium suborbiculare* and *Eucalyptus grandifolia*, are present as small multistemmed plants attached to underground lignotubers. Such species normally develop into trees in the Northern Territory. In one area this community was dominated by a low open-woodland of *E. porrecta*. The ground layer is characterised by grasses such as *Eulalia mackinlayi* and *Eriachne burkittii*, the sedge *Rhynchospora heterochaeta* and numerous forbs. Samples from this group generally occurred on sites with yellow gravelly A horizons and relatively high wet season moisture contents and water tables.

2.3.2 Vegetation map

The vegetation map of the survey area is attached as Appendix 2. Table 2.6 shows the composition of each mapping unit with respect to floristic communities, from which the appropriate labels for mapping units were derived. It is apparent from the sample site locations and the vegetation and topographic maps of the area, that there are associations between the communities and their geographic and/or topographic locations. The open-forest plains boundary roughly follows the 50 - 60 metre contour.

Table 2.6 Frequency of sample occurrence by community and mapping unit[1]. Significant positive association, as determined by Chi-square test, indicated by * = P<0.05, ** = P<0.01, *** = P>0.001.

Community	1	2	3	4	5	6	7
Mapping Unit							
Open-forest	10 **	-	9 **	-	-	-	-
Acacia open -shrubland	-	36 ***	6	-	-	-	-
Grevillea low woodland	1	-	-	19 ***	-	-	-
Lophostemon open-scrub	-	-	-	-	15 ***	-	-
Acacia -shrubland	-	-	-	-	-	12 ***	-
Banksia low woodland	-	-	-	-	-	-	18 ***

[1] Mapping units taken from vegetation map in Appendix 1.

The *E. tetrodonta* open-forest occurs adjacent to the Yapilika plains. The *E. miniata* open-forest occurs adjacent to the Rola plains and on higher ground than the *E. tetrodonta* open-forests at Yapilika. The *Acacia* open-shrubland occupies much of the Rola plains area and uncleared areas adjacent to plantations at Yapilika.

The *Grevillea* low woodland community was the major plant formation cleared in the plantations at Yapilika and its current extent within the survey area is limited to remnants on plantation edges and other isolated small patches. The *Acacia* shrubland is restricted to the Taracumbi area and isolated enclaves adjacent to areas of *Acacia* open-shrubland in the Yapilika area. The *Banksia* low woodland and *Lophostemon* scrub occur

in lower lying areas. To the south of the surveyed area these communities are restricted to drainage lines. They increase in extent to the north, where they make up the bulk of the vegetation on the plains.

2.3.3 Comparison of classification systems

Floristic versus structural

Table 2.2 shows the association between the structural and floristic classifications. Minor changes in cover or height of the upper stratum result in one floristic group spanning 'adjacent' structural classes. Thus, each floristic group generally has a distinct modal structural formation class with varying proportions of less common classes. For example the *Grevillea* low woodland (group 4) has minor variants in the low open-forest and open-scrub classes.

However, as pointed out in the descriptions of the communities, some floristic groups span disparate structural classes with different lifeform and dominant species in the upper stratum. For example the *E. tetrodonta* open-forest, *Acacia* shrubland and the *Grevillea pteridifolia* low woodland communities include sites which are dominated by a *Grevillea pteridifolia* low woodland. These communities have similar floristic compositions with slight variations in dominance determining the final grouping. Sites with a *Grevillea* overstorey but with a mat of *E. tetrodonta* root suckers in the ground layer are classified with the *E. tetrodonta* open-forest communities. The *Grevillea* low woodland sites in these groups are discussed in more detail in Chapter 3.

Table 2.7 shows the comparison of stand structure between the *E. miniata* (group 1) and the *E. tetrodonta* (group 3) open-forest. The *E. miniata* forest has significantly higher stocking and basal area figures in the 3-4, 5-6, 21-25, 31-40 centimetre and total diameter classes, than the *E. tetrodonta* open-forest.

Table 2.7 Means for stand structure of *E. tetrodonta* open-forest (n=30) and *E. miniata* open-forest (n=14). Significant between community differences as determined by One-Way Analysis of Variance indicated by * = P<0.05, ** = P<0.01, *** = P<0.001, NS = P>0.05.

Diam class	0-2	3-4	5-6	7-8	9-10	11-15	16-20	21-25	26-30	31-40	41-50	51-60	total
Basal Area (m2/600 m2)													
E. miniata open-forest	0.04	0.16	0.26	0.24	0.15	0.63	0.91	1.58	1.76	4.00	0.77	1.15	11.65
E. tetrodonta open-forest	0.03	0.08	0.14	0.20	0.14	0.50	0.55	0.78	1.20	1.59	0.90	0.27	6.38
Significance	NS	*	*	NS	NS	NS	NS[1]	*	NS	NS[1]	NS	NS	**[1]
Frequency (nos/600 m2)													
E. miniata open-forest	12.8	9.9	6.5	3.2	1.3	2.9	2.1	2.3	1.7	2.4	0.3	0.3	45.7
E. tetrodonta open-forest	8.5	5.2	3.5	2.7	1.2	2.3	1.3	1.1	1.2	1.0	0.3	0.1	28.2
Significance	NS	**	NS[1]	NS	NS	NS	NS[1]	**	NS	**[1]	NS	NS	***[1]

[1] Transformed by log10 (x+1) to equalise the variances

Table 2.8 Frequency of sample occurrence by community and land unit[1]. Significant positive association, as determined by Chi-square test, indicated by * = P<0.05, ** = P<0.01, *** = P>0.001.

Community	1	2	3	4	5	6	7
Land unit							
3a (open-forest)	3 **	-	8 ***	-	-	-	-
3c (open-forest)	1	-	1	-	-	-	-
4a (tall shrubland)	-	-	-	1	1	-	1
4b (low shrubland)	-	-	-	2	-	-	1
5a (low open-woodland)	-	7	4	10 ***	1	-	-
5b (tall shrubland)	3	28 ***	-	2	10 *	3	5
6c (tall open-shrubland)	-	-	1	1	1	-	1
7a (grassland)	-	-	-	1	2 ***	-	6
Unmapped	3	1	1	1	-	8	5

[1] Land units taken from van-Cuylenburg & Dunlop (1973) and Wells & van-Cuylenburg (1978)

Floristic versus land unit

Table 2.8 shows the relationship between floristic communities defined in this survey to those defined in the land unit maps of van-Cuylenburg & Dunlop (1973) and Wells & van-Cuylenburg (1978). Discrepancies

between the two approaches fall into three categories:

1. Scale. Some of the small patches of open-forest (< 2 ha) have been mapped as tall-shrubland on the land unit map. This is due to the small scale of the land-unit map compared to Appendix 2.

2. Inadequate ground-truthing. The description of the vegetation types associated with land unit 5b most closely resembles that of community 2 (*Acacia* shrubland). However, this land unit is associated to a significant extent with floristic groups 2 (*Acacia* open-shrubland) and 5 (*L. lactifluus* open-scrub) and to a non-significant extent, with groups 1 (*E. miniata* open-forest), 4 (*G. pteridifolia* low woodland), 6 (*Acacia* shrubland) and 7 (*Banksia* low woodland). The monochromatic photos used in the land unit survey do not readily distinguish community 5 from community 2 and thus may have caused confusion on the land unit map. The discrepancies mainly occur in the extensive areas of community 5 in the north of the study area, where access was limited at the time of the land unit survey. In this thesis this area was surveyed using a road constructed in 1983 and by foot.

3. Lack of correspondence between structure of dominant layer and floristic composition. The land unit map placed all *Grevillea* low woodland sites into one unit (5a). The floristic classification divided these sites into two distinct communities (2 and 4) which occupy distinguishable edaphic environments. Similarly the floristically distinct *Acacia* open-shrubland (community 2) and *Acacia* shrubland (community 6) were defined by the land unit mappers under one unit (5b).

2.3.4 Ordination

Number of dimensions
Unlike other ordination techniques, where the trend shown on any axis is

unaffected by how many axes are used in the final presentation of results, the total number of dimensions chosen for NMDS ordination affects the patterns shown on each axis. Thus the number of dimensions used in the final presentation was first determined, by considering the following factors.

Firstly, a plot of number of dimensions versus stress (Figure 2.3) was examined. In general terms stress is used to indicate how closely the relative position of the sites in the ordination space resemble the dissimilarity matrix from which the ordination was derived (Minchin 1990). In other words the lower the stress the better the ordination. An abrupt flattening of the curve means that additional dimensions do not greatly improve the ordination and thus indicates the appropriate dimensionality (Bowman & Minchin 1987). Figure 2.3 shows that there is no clear-cut asymptote, the levelling occurs gradually over the second and third dimensions.

Secondly the relative positioning of individual sites resulting from the 10 random starting points was compared. This was carried out using Procrustes rotation which eliminates differences due to the random orientation of axis. The two dimensional (2D) solutions gave 7 samples with mean stresses of between 0.14 and 0.99 while the three dimensional (3D) solution produced no mean sample stress greater than 0.14. This indicates that the 2D solution tends to place the same samples in different positions relative to the other sites from different random starts. By comparison the 3D solution is more stable as all sites are repeatedly placed in similar relative positions.

Thirdly, the classification results were directly plotted within the 2D and 3D spaces (Figure 2.4 and 2.5). There are only minor differences in the patterns on the first and second axis between the 2D and 3D solutions. Thus, both solutions clearly distinguish communities 1, 2, 3 and 6 from

4, 5 and 7, on the first axis and communities 1 and 3 from 2 and 6 on the second axis. However communities 4, 5 and 7 are somewhat mixed on the second axis of the 2D solution compared to the 3D solution. The sites with the highest mean stresses following Procrustes Rotation in the 2D solution came from groups 4, 5 and 7.

Thus the 3 dimensional ordination was accepted as the most meaningful representation of the floristic variation amongst the sites.

2.3.5 Vegetation environmental relationships within the ordination space

Floristic and structural trends within the ordination space have already been partly illustrated by Figure 2.5. The first axis clearly differentiates the open-forest and *Acacia* open-shrubland communities with low scores from the *Lophostemon* and *Banksia* low woodland with high scores. The second axis separates the *Acacia* open-shrublands from the open-forest (at the low end of the first axis) and the *Banksia* low woodland from the *Grevillea* low woodland (at the high end of the first axis).

The distribution of the values of the environmental variables on the NMDS ordination are shown in Figure 2.6. The direction and strength of the linear correlation of the vectors fitted between ordination scores and environmental values are summarised in Table 2.9, for the two and three dimension solutions.

Soil colour ($r = 0.84$ - 0.85), gravel ($r = 0.52$ - 0.53), sand ($r = 0.59$ - 60) and wet ($r = 0.79$) and dry ($r = 0.76$) moisture show strong highly significant ($P < 0.001$) relationships with floristic composition. Most vector directions trended across the first axis, with the difference in absolute vector/NMDS1 angles generally less than 10 degrees. Thus sites with high first and second axis scores generally had grey, moist, gravelly soils while sites with low first axis scores had red, dry, sandy,

gravel free soils. Only the colour vector showed some variation in the second dimension, with a vector/NMDS2 angle of about 60 degrees.

No correlations were substantially improved by the addition of the third axis. Only the vector for sand content had a substantial third dimension component (69 degrees). The other vector/NMDS3 angles were between 80 and 101 degrees, indicating little relationship between environmental variables measured and the third dimension of floristic composition.

Table 2.9 Direction (degrees) and strength (r) between fitted vectors and NMDS axis

Two Dimensions

Variable	Max r	Significance	Angle NMDS1	NMDS2
Colour	0.84	P<0.001	151	61
Moisture-wet	0.79	P<0.001	170	80
Moisture-dry	0.76	P<0.001	166	104
Gravel	0.52	P<0.001	177	93
Sands	0.59	P<0.001	8	82

Three Dimensions

Variable	Max r	Significance	Angle NMDS1	NMDS2	NMDS3
Colour	0.85	P<0.001	149	62	100
Moisture-wet	0.79	P<0.001	165	79	101
Moisture-dry	0.76	P<0.001	166	104	90
Gravel	0.53	P<0.001	171	93	81
Sands	0.60	P<0.001	22	83	69
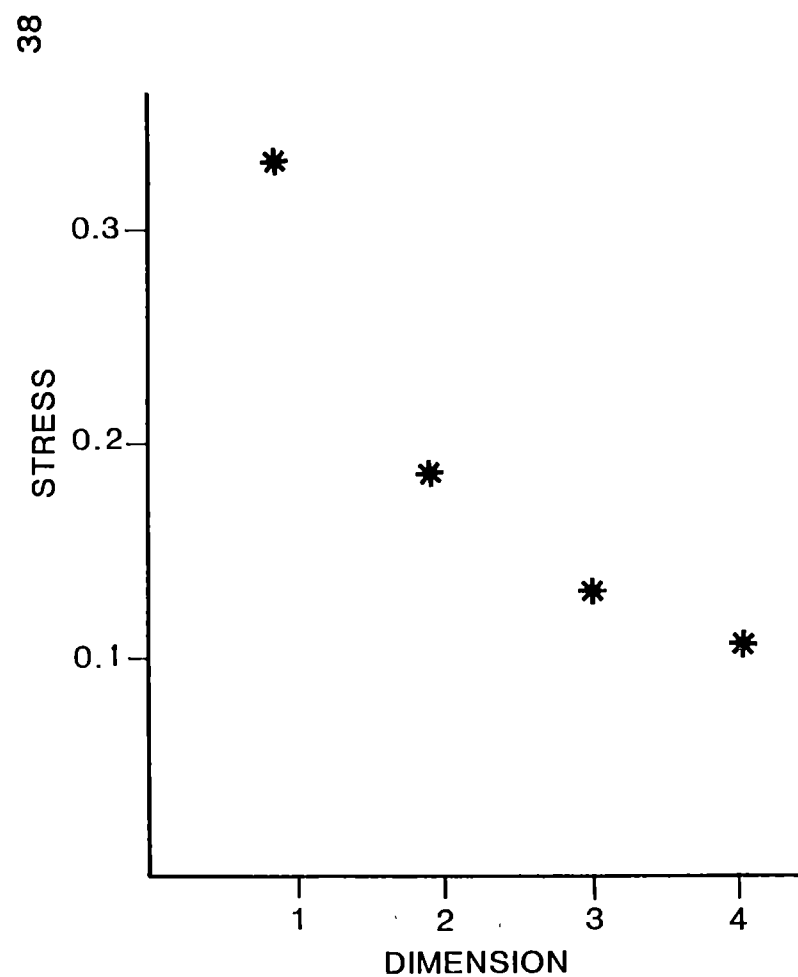
Figure 2.3 Plot of number of dimensions of NMDS sample ordination versus stress.
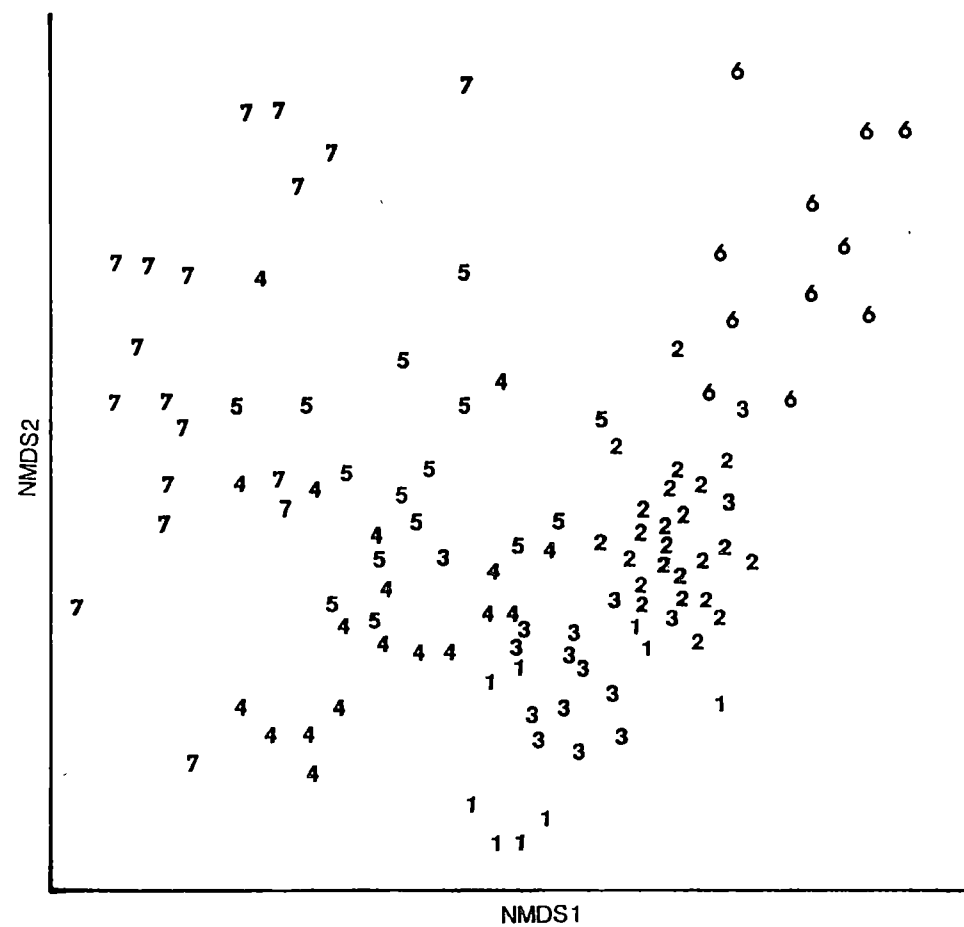
Figure 2.4 UPGMA classifactory group numbers plotted on two dimensional NMDS sample ordination.
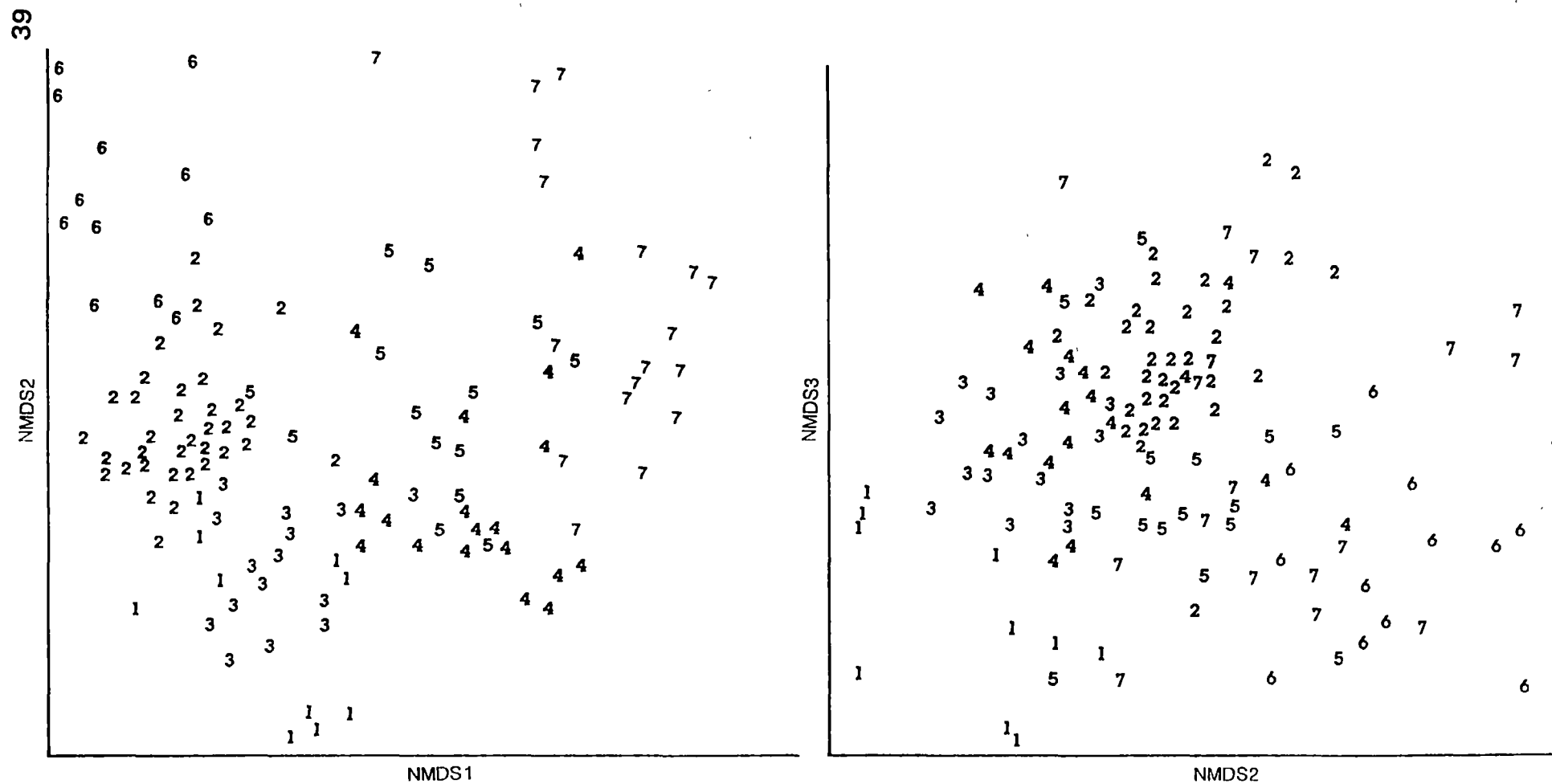
Figure 2.5 UPGMA classifactory group numbers plotted on three dimensional NMDS sample ordination.
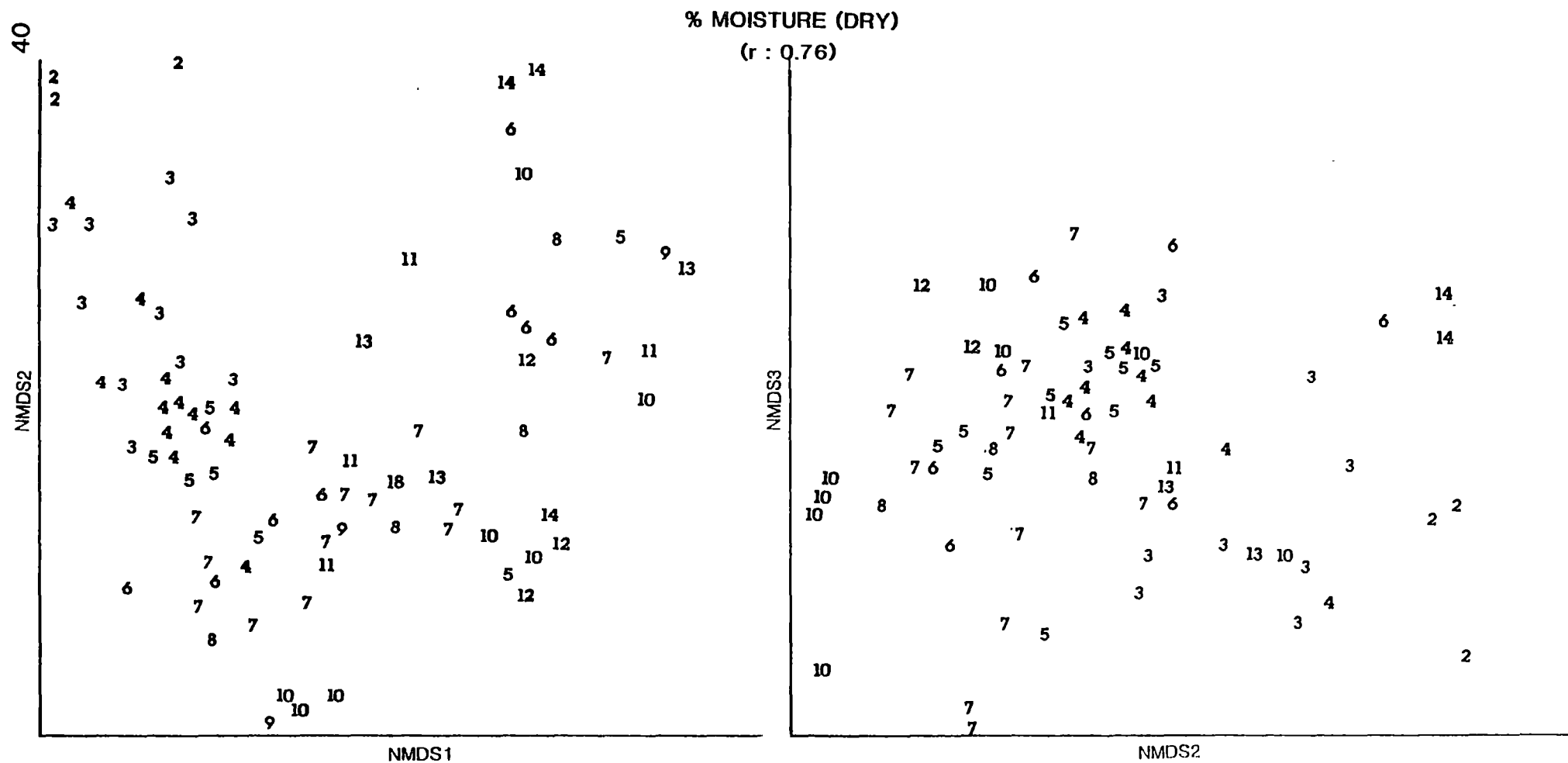
Figure 2.6.1 Distribution of surface (0-10cm) soil variables on the three dimensional NMDS sample ordination of floristic data - Moisture: % August 1987 (dry)
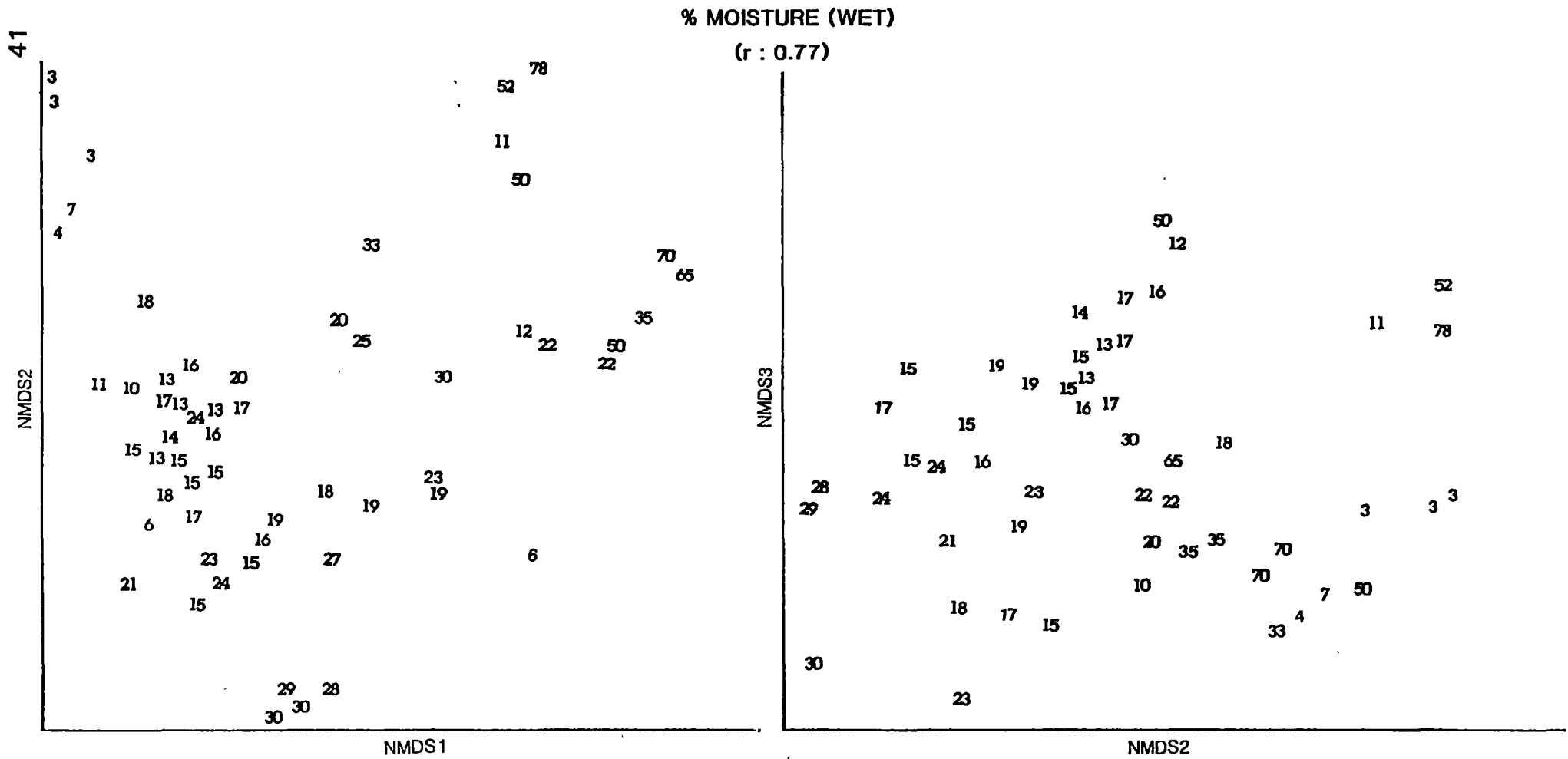
Figure 2.6.2   Distribution of surface (0-10cm) soil variables on the three dimensional NMDS sample ordination of floristic data - Moisture: % March 1987 (wet)
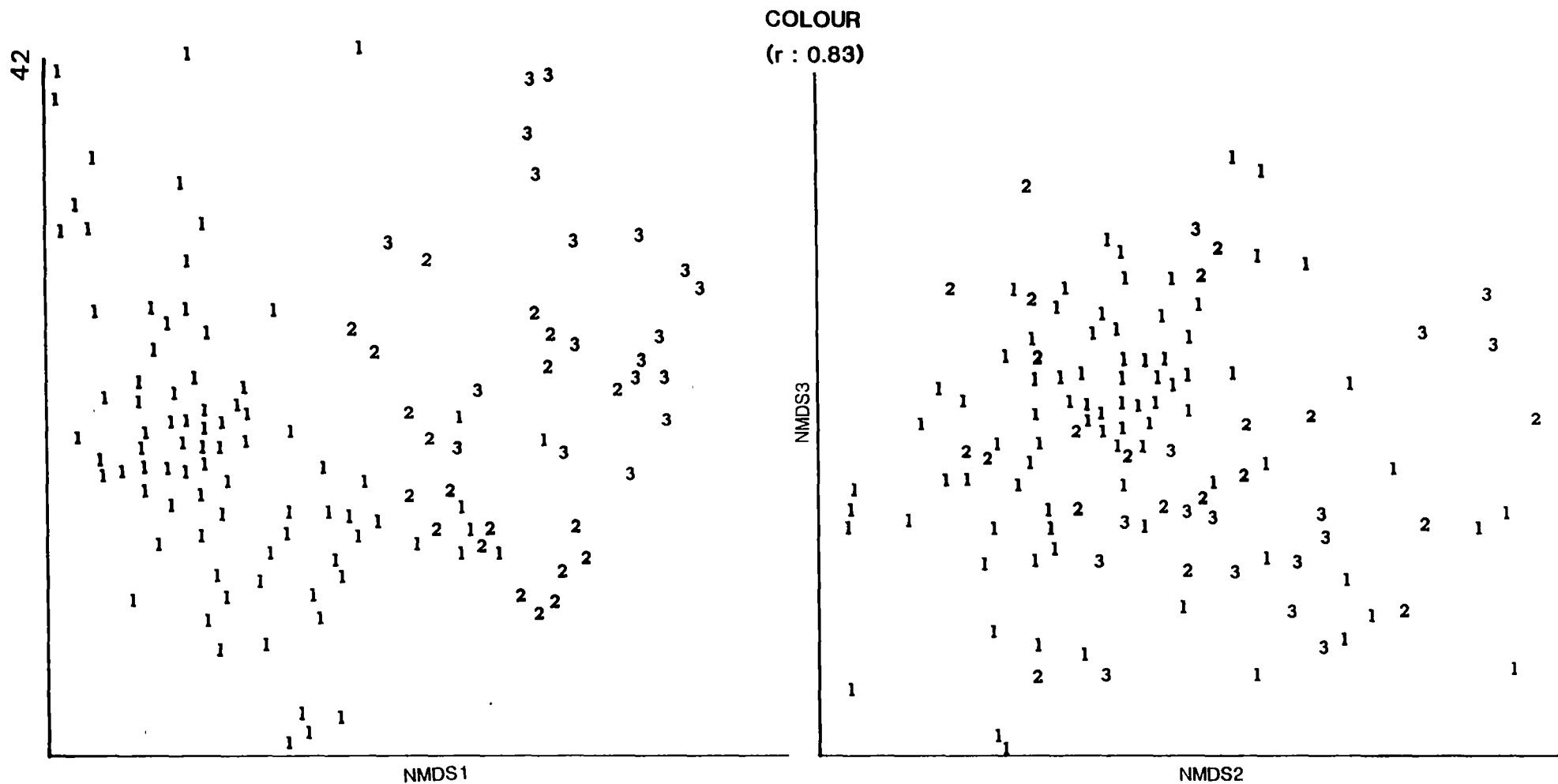
Figure 2.6.3   Distribution of surface (0-10cm) soil variables on the three dimensional
NMDS sample ordination of floristic data - Colour: 1 = red, 2 = yellow,
3= grey or black
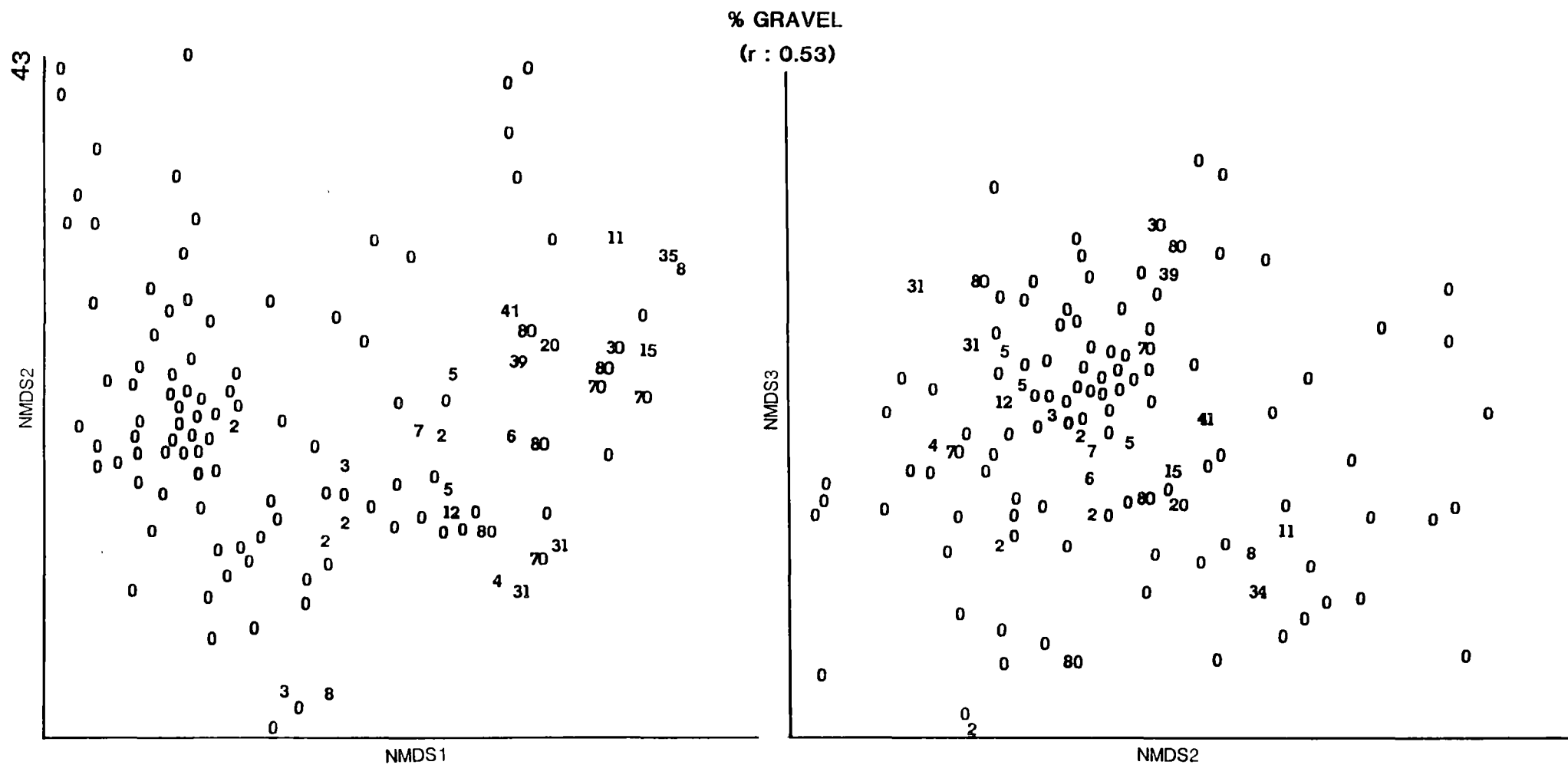
Figure 2.6.4   Distribution of surface (0-10cm) soil variables on the three dimensional NMDS sample ordination of floristic data - Gravel: %
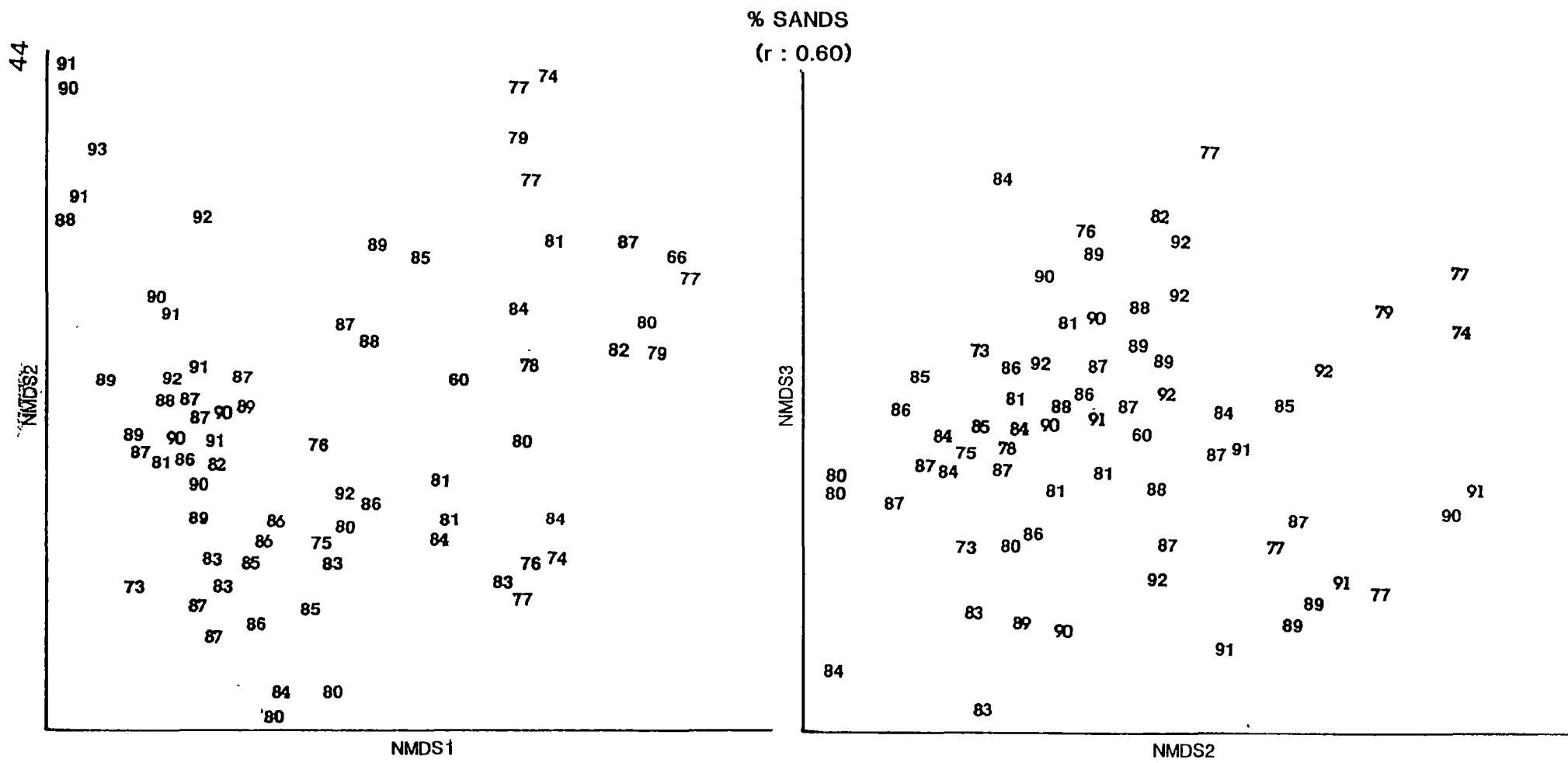
Figure 2.6.5   Distribution of surface (0-10cm) soil variables on the three dimensional
NMDS sample ordination of floristic data - Sands: % of fine earth
faction (% fine sand + % coarse sand)

Inspection of Figure 2.6 also reveals non-linear relationships between environmental variables and ordination scores. At the lower end of the first axis there is a clear gradation across the second axis from dry, sandy sites to more moist, loamier sites, corresponding to the change from open-forest to open-shrubland. Towards the high end of the second axis the trend in dry season moisture breaks down and tends more across the first axis parallel with wet season moisture.

2.4 Discussion

2.4.1 Comparison of classification systems

The Land Unit System has been widely used in resource surveys in the Northern Territory and forms the basis for management in many areas, including the forestry operations on Melville Island. The errors due to scale and inadequate ground truthing are inherent in any survey and determined by individual mappers, their aims and resources available. The differences in classification of the *Grevillea pteridifolia* low woodland highlights the extra information that can be obtained by using full floristic lists to define plant communities. Using only dominant species and structure failed to delineate differences in vegetation types which were related to subtle changes in environmental factors. As the floristic differences are related to soil moisture factors which in turn are related to pine tree growth (Merv Haines pers. comm. 1988), these differences are important to pine plantation management.

Structure is often used for primary classification of Australian vegetation (e.g. Beard 1981) with floristic composition used as secondary classes or for more detailed descriptions. However, both floristic and structural classifications impose arbitrary classes on the continuous variables of floristic composition, height and cover. Thus, "similar" vegetation is

often placed into adjacent structural or floristic groups. Other workers in the Northern Territory show that simultaneous uniformity of structure and floristic classifications is not possible (Rice & Westoby 1985, Kirkpatrick *et al.* 1988) and that both are required to give a complete description of the composition of the vegetation.

2.4.2 Comparison of the Melville plains communities with other plant communities

Savanna or Heaths

The structural terminology used here is consistent with the majority of Australian vegetation descriptions and will be consistently used in this thesis. However, the communities described resemble formations grouped under the headings 'savannas' and 'heaths' by other authors. Both terms were originally defined to describe specific vegetation types, but have been subsequently applied to a wide variety of communities which show some unity in environmental controls such as climate, soils and fire. Thus recent definitions of the terms often include physiognomic, floristic, environmental and functional components. It is useful to discuss the definition of these terms to facilitate comparisons of the vegetation described here with other vegetation from within Australia and around the world.

The term 'heath' was originally applied to plant communities in Europe dominated by species from the family Ericaceae (Beadle 1981). In Australia, heaths are often defined in environmental, structural or floristic terms (Specht 1979). They are generally found over a wide climatic range, on acidic, nutrient poor soils which are subjected to seasonal water-logging or drought and are invariably frequently burnt (Groves & Specht 1981). Typical Australian heath plants possess characteristics that are thought to have developed to cope with dry, nutrient poor conditions (Barlow 1988). They are thus evergreen, with reduced, hard,

sclerophyllous leaves and are generally less than two metres high (Specht & Rayson 1957, Specht 1981). Specht (1979) has listed typical Australian heath taxa.

Plant communities in the Northern Territory described as heaths include *Calytrix* spp. mixed shrublands which occur on sand-stone pavements with skeletal soils (Rice & Westoby 1985; Taylor & Dunlop 1985; Kirkpatrick *et al.* 1988, Bowman *et al.* 1990), *Verticordia, Banksia* shrublands which occur on poorly drained, sandy soils across the Top End (Specht 1958) and *Jacksonia odontocarpa, Acacia* spp. shrublands which occur north of the Barkly Tableland (Beadle 1981).

Bevege (1981) compared the Melville Island plains to parts of Cape York Peninsula, where heath and eucalypt woodlands occur in close proximity (Pedley & Isbell 1971, Lavarack & Stanton 1977). Open-heath on Cape York occurs on low swampy areas on relatively poorly drained podsolic soils, while closed-heaths occur on deep sandy yellow/red earths or deep red sands (Pedley & Isbell 1971). The latter have many species in common with the Melville Island plains such as *E. tetrodonta, Banksia dentata, Schoenus sparteus* and *G. pteridifolia*. Many of the species from the Cape York heaths are also found in the surrounding *E. tetrodonta/ E.* sp. aff. *polycarpa* (synonym *E. nesophila*) open-forest (Pedley & Isbell 1971). Many species found on the Melville Island plains, such as *Jacksonia dilatata, Schoenus sparteus, Grevillea pteridifolia, Acacia difficilis, Patersonia macrantha, Leptocarpus spathaceus* and *Calytrix exstipulata* are listed as heath plants by Specht (1979). These species are common and characteristic understorey components of the open-forest found on sand sheets at Murgenella (Bowman *et al.* 1988a). These and other species such as *Acacia gonocarpa* are also common components of the heathlands found on rugged sandstone plateaux in the Northern Territory (Taylor & Dunlop 1985; Dunlop 1988: Kirkpatrick *et al.* 1988).

However, all species found on the Melville Island plains are also found in open-forests and woodlands in the Top-End. Furthermore tall grasses, particularly *Sorghum* spp, are a major component of the plains communities, whereas graminoids are usually a minor part of heathlands (Specht & Rayson 1957, Specht *et al.* 1977). In the context of the above discussion the plains communities could be described as shrublands which are related to heaths (*sensu* Specht 1979) or grassy heaths.

Savanna is a term which was originally applied to treeless grassy plains (Bourliere & Hadley 1983). However, recent reviews of savannas (e.g. Huntley & Walker 1982, Bourliere & Hadley 1983, Gillison 1983, Johnson and Tothill 1985) have interpreted the term in a very broad sense with central themes of a co-dominance by woody and herbaceous vegetation and an associated climate characterised by a strongly seasonal rainfall. Much of the vegetation on the plains conforms to more strict definitions of savanna, which include only those communities which are dominated by grasses and have a scattered low tree or shrub layer (Eiten 1978). All the plant communities described in this chapter can be considered savanna variants under broader definitions of savanna; the open-forests are very tall tree savanna and the plains are low-woodland or shrubland savanna (Walker & Gillison 1982).

Walker (1987) asserts that discussion about the precise limits of the definition of savanna are sterile and it is more fruitful to compare differences than argue about whether particular communities should or should not be classified together. In a similar vein, it is sufficient to say that the Melville Island plains communities are comparable in structure and composition to many vegetation types which are lumped under the headings of savanna and heath. Detailed comparisons between the Melville Island communities and various savannas or heaths (in the remainder of the thesis) may therefore provide useful insights into

functional attributes and environmental determinants. One caveat to this is that the boundaries discussed here should not be confused with the numerous savanna-forest boundary studies from elsewhere in the tropics (e.g. Clayton 1958, Hill & Randall (1968) quoted by Hopkins 1983) which, from the northern Australia perspective, are equivalent to savanna-rainforest studies (Stocker 1968, Bowman & Dunlop 1986).

Other north Australian plant communities

Bowman & Wilson (1988) have collated presence/absence species lists of published and unpublished floristic surveys from across northern Australia and ordinated them to provide quantitative comparisons of various open-forest/woodland communities. Data from Melville Island surveys (from this study and Fensham 1990) were included in the analysis. The ordination showed that the plains communities on red soils (groups 2, 4 and 6) were compositionally most similar to the *E. miniata*, *E. tetrodonta*, *E. nesophila* open-forests on Melville Island and Cobourg Peninsula. These open-forest and plains communities occurred on the 'wet' end of the first axis of the ordination, which Bowman & Wilson (1988) interpreted as a rainfall gradient. The *Banksia* and *Lophostemon* shrublands from Melville Island (groups 5 and 7) and *Melaleuca*/eucalypt woodlands/shrublands from elsewhere in the Northern Territory, were distinguished from the open-forests and plains on the second axis, which was interpreted as a drainage gradient.

Large areas of *Livistona humilis* shrubland which occur on low lying plains near Channel Point, 100 kilometres south-west of Darwin (Forster 1977, Wood & Sivertsen 1984) are similar in structure and dominant species to the *Lophostemon* shrubland (group 5). In parts the Channel Point shrubland occurs on red soils and has a similar appearance to the *Grevillea* low woodlands at Yapilika (B. Wilson pers. ob.). Structurally the *Grevillea* low woodlands (groups 4 and parts of 2) are similar to the *Grevillea pteridifolia*/mixed species low woodland communities which

occur throughout the coastal regions of the Top End (Stocker 1972; Wilson & Bowman 1987). However the latter communities are generally restricted to drainage lines with sandy soils and have understories more similar in composition to the wetter parts of the Melville Island plains (groups 5 and 7).

Thus, the Melville Island plains support vegetation which is similar to shrublands and heaths in the Northern Territory and Cape York Peninsula but which is structurally and/or floristically distinct from any published descriptions of vegetation from northern Australia.

2.4.3 Vegetation-environment relationships

The major environmental correlates of vegetation patterning described in this chapter are similar to other studies from northern Australia (Pedley & Isbell 1971; Specht *et al.* 1976, Langkamp *et al.* 1976, Burgman & Thompson 1982, Taylor & Dunlop 1985, Bowman 1986, Bowman & Minchin 1987, Bowman *et al.* 1988a). Indirect gradient studies of forests and woodlands in the region, generally produce a trend on the major axis from sites at one end with free draining red or light coloured soils dominated by eucalypts, to *Melaleuca* or mixed species dominated communities on poorly drained yellow and grey/black soils at the other end. Secondary gradients in these studies have generally been interpreted as soil texture and related factors including dry season soil moisture.

Dry season soil moisture content is only an approximate measure of moisture available to the plants. Moisture availability is also affected by factors such as soil texture and soil depth. At the high end of the first axis in this thesis, soil texture and moisture content was relatively constant across the second axis, while effective soil depth varied. The *Banksia* woodland occurred on duplex soils with a clay layer at about 0.5

metre depth, which may present an impenetrable barrier to woody roots, effectively reducing moisture availability on these sites. Thus the relationship between moisture availability and vegetation patterning may be more complex than that indicated by the superficial moisture parameters measured.

Changes in soil dry season moisture are often associated with changes in soil type; from deeper sandy-loam laterite to shallow sands (Bowman *et al.*1988a), or geology; from laterite to sandstone (Kirkpatrick *et al.*1988). In a study on open-forests near Darwin, Bowman & Minchin (1987) assumed that measured changes in fertility and texture would be accompanied by parallel changes in dry season soil moisture. Langkamp *et al.*(1976) suggest that the major compositional gradients on Groote Eylandt were associated with the ability of plants to withstand the dry-season drought, even though parallel to this trend was a gradient from laterite to sandy, manganese rich soil.

Thus, the relationship between floristic and structural variation and dry season moisture supply is often confounded by several inter-correlated factors, particularly soil texture and fertility. Subsequent chapters will investigate these and other environmental factors in more detail.

CHAPTER 3 <u>THE NATURE OF THE FOREST PLAINS BOUNDARY: VEGETATION PATTERNING</u>

<u>3.1 Introduction</u>

Hobbs (1986) has noted that the definition of a vegetation boundary involves locating a discontinuity within a change from one vegetation type to another, although there is no standard way of defining, or even describing such boundaries. Some vegetation boundaries which have been described in the literature involve sudden and obvious changes in structure and floristic composition, such as the transition from eucalypt open-forest to monsoon thickets in northern Australia (Stocker 1969; Russell-Smith 1986; Bowman & Dunlop 1986). Other boundaries are somewhat arbitrary lines drawn across continual floristic and/or structural changes (Werger *et al.* 1983, Wilson & Bowman 1987).

Canny (1981) has described all boundaries as arbitrary, human perceptions, but has also hypothesised that their nature and behaviour should comply to general rules. Classification of boundary types is usually based on some measure of rate and pattern of changes. van der Maarel (1976), Hobbs (1986) and others (see collection of papers edited by Littlejohn & Ladiges 1981) have related different biological boundary types to the environmental controls acting on those boundaries.

Thus, a detailed examination of vegetation changes across the forest plains boundary may provide useful insights into possible environmental controls. This chapter describes changes in vegetation structure and floristic composition across the forest plains boundary. Structure is measured in terms of abundance of woody individuals and floristic composition is measured in terms of changes in dissimilarity of sites with distance. These patterns are then discussed in relation to other boundary studies reported in the literature.

3.2 Methods

3.2.1 Boundary types studied

The boundary between open-forest and treeless plains can be classified according to the communities adjacent to the transition on the vegetation map (Appendix 1) as follows:

1. *E. tetrodonta* open-forest to *Acacia* open-shrubland.

2. *E. miniata* open-forest to *Acacia* open-shrubland.

3. *E. miniata* open-forest to *Grevillea* low woodland.

4. *E. tetrodonta* open-forest to *Lophostemon* scrub or *Banksia* low woodland.

5. *E. tetrodonta* open-forest to *Acacia* shrubland.

Boundary types 1 and 2 were selected as the focus for this study because these are the most widespread, were associated with the least obvious environmental correlates and are in the least disturbed condition. One example of type 3 was chosen for study, as this transition is locally common around the Yapilika plantations, although site choice was limited due to fire-break and road clearing. Boundary types 4 and 5 were not considered for detailed study as these boundaries were associated with abrupt, obvious changes in soil conditions, as outlined in the floristic survey (Chapter 2). In addition a transition from *Acacia* open-shrubland to *Banksia* woodland was described as an example of an abrupt boundary with obvious changes in environmental conditions, to allow comparison with other boundary types. Seven sites were selected for study (see Map Appendix 1) These were;

- *E. miniata* open-forest to *Acacia* open-shrubland (transects 1, 2 and 3)

- *E. tetrodonta* open-forest to *Acacia* open-shrubland (transects 4, 5 and 6),

- *E. miniata* open-forest to *Grevillea* low woodland (transect 7).

Transect 5 was continued across the plains to describe a transition from the *Acacia* open-shrubland to the *Banksia* woodland.

Structural terminology will henceforth be abbreviated to 'forest', 'shrubland' and 'woodland' as appropriate.

3.2.2 Structure

The change in woody vegetation cover from the open-forest to the plains was assessed on each boundary, using five metre wide by varying length transects which were established at right angles to the transition. The location, height (by triangulation using a Suunto clinometer), diameter at breast (1.3 metre above the ground) height (DBH, using a diameter tape) and crown width (by projecting the crown onto the ground and measuring with a tape) and depth (by subjective estimation or clinometer) of the crown, of every woody individual greater than 1.5 metre high were recorded across each transect. This information was portrayed as a vegetation profile diagram.

Change in forest stand structure of the forest with distance from the boundary was assessed by locating 20 by 30 metre contiguous plots across a 300 metre transect within the forest, at transects 3, 4, 5 and 7. These transects were chosen to cover the range of boundary types. The transect dimensions were chosen after trials indicated that smaller sizes contained too few individuals to give consistent measures of structure. At each plot the DBH of trees by species was measured.

The number of juvenile individuals (defined as woody species <2 metre high) was assessed by locating ten contiguous 1 by 10 metre plots across each boundary transect with five plots under the forest canopy

and five on the plains. Eucalypt seedlings which appeared to have germinated in the current wet season (defined as being small (<5 centimetre) and hairy with no substantial (<1 centimetre diameter) lignotuber development) were searched for several times over the period 1986 to 1988 on all transects.

3.2.3 Floristic composition

Floristic changes across the boundaries were firstly assessed by including representative sites from all transects in the floristic survey and analysis reported in Chapter 2. Secondly, on a representative transect of each boundary type, a more intensive description of the floristic change was carried out. On transects 3, 5 and 7, 10 by 10 metre plots were located at 20 metre intervals across the boundaries. A list of the names of all species and their abundance in each plot was made. The sites were ordinated for each transect separately using the methodology described in Chapter 2 with the exception that the rescaling option in DECODA was used (Minchin 1990). This option calculates one unit on the ordination axis to equal, on average, one half change of Beta diversity. This allows direct comparisons of 'total variation' to be made between the ordinations of the different transects. The results were portrayed as a differential (Hobbs 1976) or ecological (McQueen 1981) profile i.e. by plotting distance against ordination score.

3.3 Results

3.3.1 Structure

Figures 3.1.1 to 3.1.6 show the vegetation profiles on 6 transects (Note: the soil profiles included on these Figures will be discussed in Chapter 4). The results from transect 4 are not presented here as it was very similar to transect 5. On all transects the change from forest to the transition

zone to shrubland is abrupt, although there are tree outliers on the plains (e.g. transect 3). On transect 1 - 6 an intermediate *Grevillea* woodland community occurs between the forest and the shrubland. This zone varies in width from 60 metre (transect 5) to 350 metre (transect 1). The floristic classification reported in Chapter 2 placed these *Grevillea* woodlands into floristic group 2 (*Acacia* shrubland) or group 4 (*E. tetrodonta* forest). As discussed previously, these areas are floristically distinct from the *Grevillea* woodland (group 5) which is represented on transect 7. To avoid confusion the intermediate *Grevillea* woodlands on transects 1 - 6 will be referred to as the 'transition' community or zone.

In contrast the change from the *Acacia* shrubland to the *Banksia* woodland on transect 5 is much more abrupt. There is no structural change over the upper sections of the continuation of transect 5, but on the lower section of this transect an abrupt change from *Acacia* shrubland to low woodland occurs in less than 50 metres.

Table 3.1 shows correlation coefficients between stem frequency and distance from the open-forest boundary, for all DBH size classes at transects 3, 4, 5 and 6. Most of the correlation coefficients between frequency and distance from the boundary are negative, indicating that within the forest there tends to be a slight decrease in basal area as the boundary is approached. However, no size classes show significant correlation and all r values were less than 0.4 indicating very weak relationships. This trend is verified by the analysis of variance of the differences in mean basal area of ten plots near (0-150 metre), and ten plots away (151-300 metre) from the boundary (Table 3.2). This table shows that there is no significant decrease in mean basal area with distance within transects, although there are significant differences between transects. Thus although there is a change in the overstorey structure between the *E. miniata* and *E. tetrodonta* forest types (Chapter 2), the change in overstorey structure at the forest - plains boundary is abrupt.

Figure 3.1.1-7   Profiles of woody vegetation and soils across forest - plains boundary transects 1-7

Vegetation Key

Eucalyptus spp.

Grevillea pteridifolia

Acacia spp.
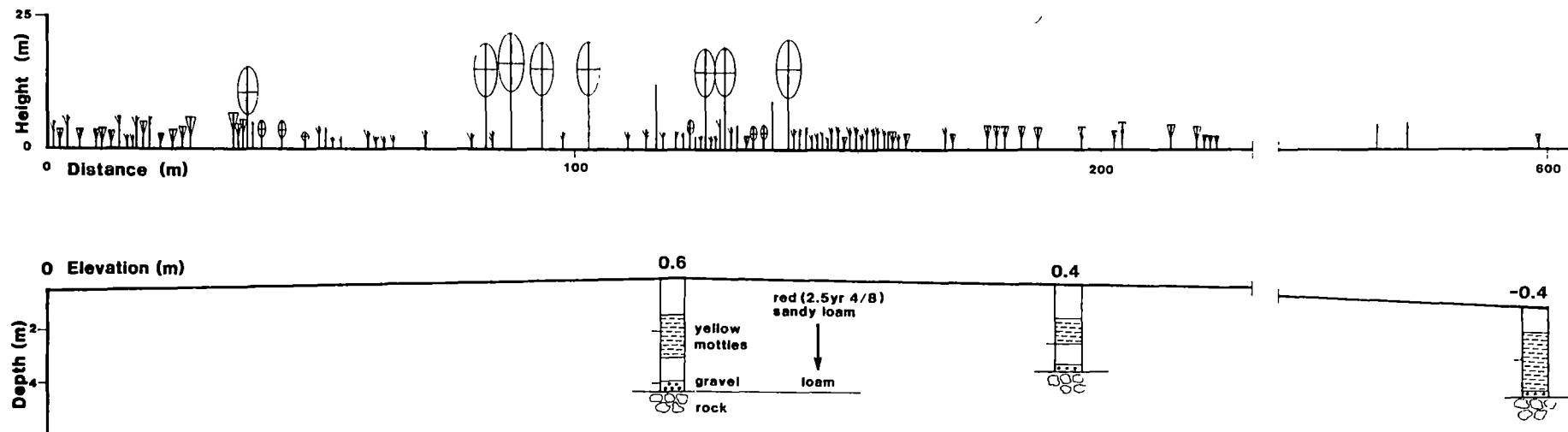
Figure 3.1.1   Profiles of woody vegetation and soils across forest - plains boundaries
- *Acacia* shrubland to *E. miniata* forest to *Acacia* shrubland, Transect 1
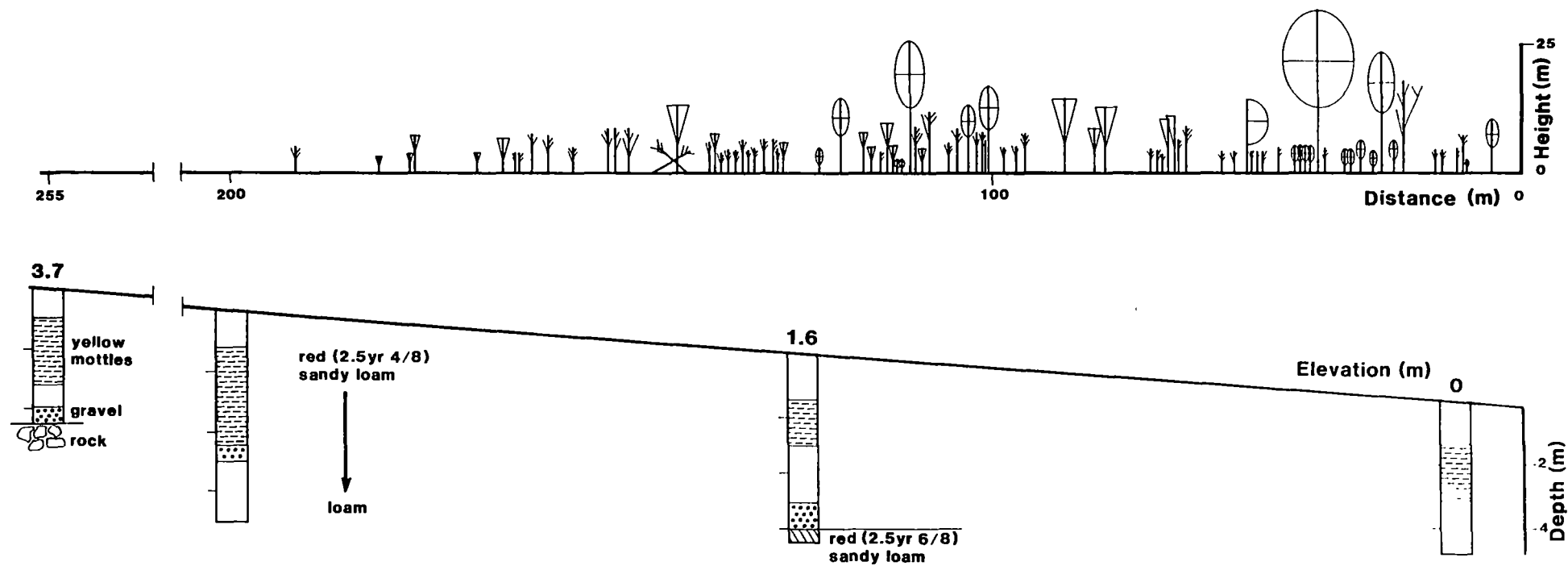
Figure 3.1.2 Profiles of woody vegetation and soils across forest - plains boundaries
- *Acacia* shrubland to *E. miniata* forest - Transect 2
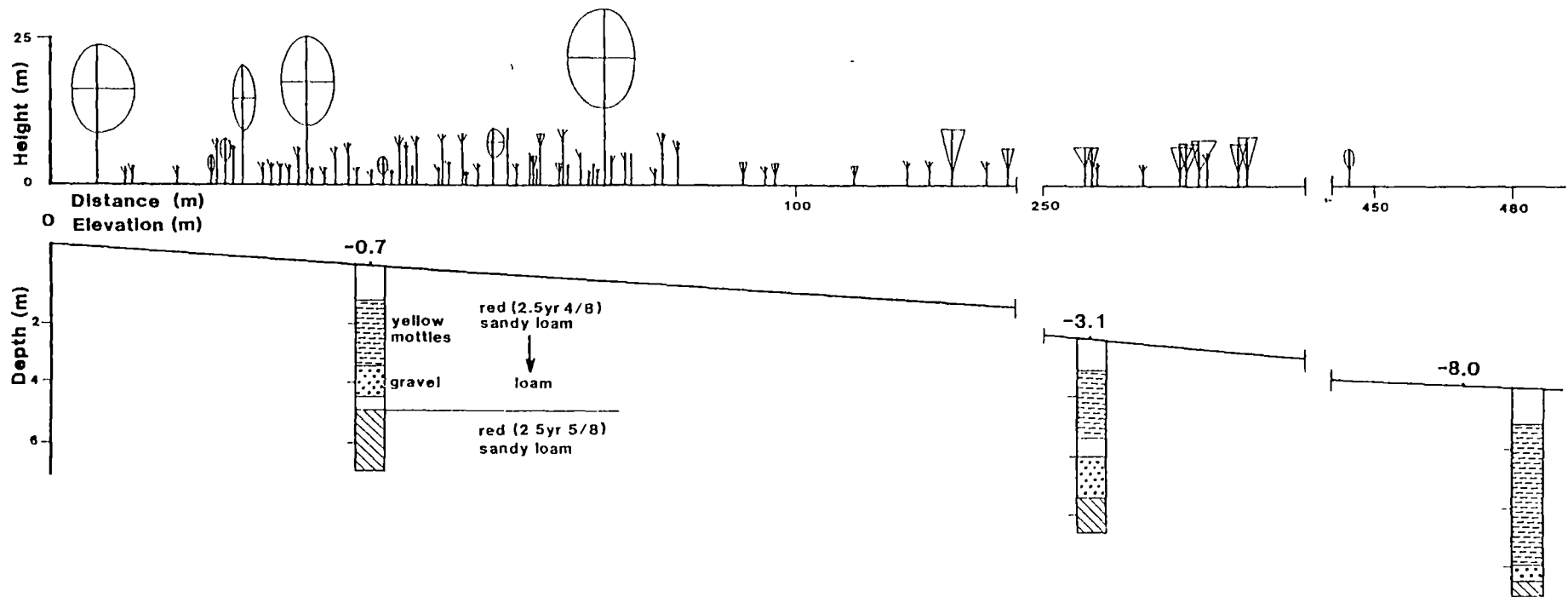
Figure 3.1.3   Profiles of woody vegetation and soils across forest - plains boundaries
- *E. miniata* forest to *Acacia* shrubland, Transect 3
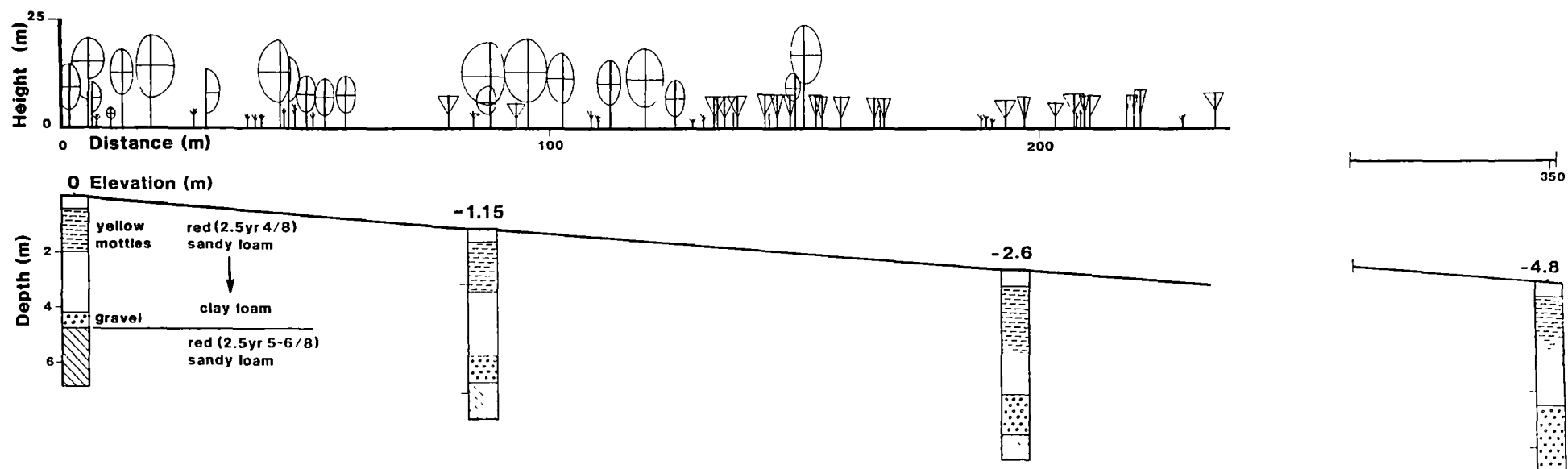
Figure 3.1.4   Profiles of woody vegetation and soils across forest - plains boundaries
                     - *E.tetrodonta* forest to *Acacia* shrubland, Transect 5

Height (m)

20

0

930   Distance (m)   1150

-13.8   Elevation (m)

Depth (m)

2

4

yellow
mottles

red (2.5yr 4/8)
sandy loam

↓

loam

black (10yr 2/1)
loam

brown (10yr 3/3)
clay loam

medium clay with
white / yellow /
grey mottles

-16.7

-17.8

grey (10yr6/2)
clay loam
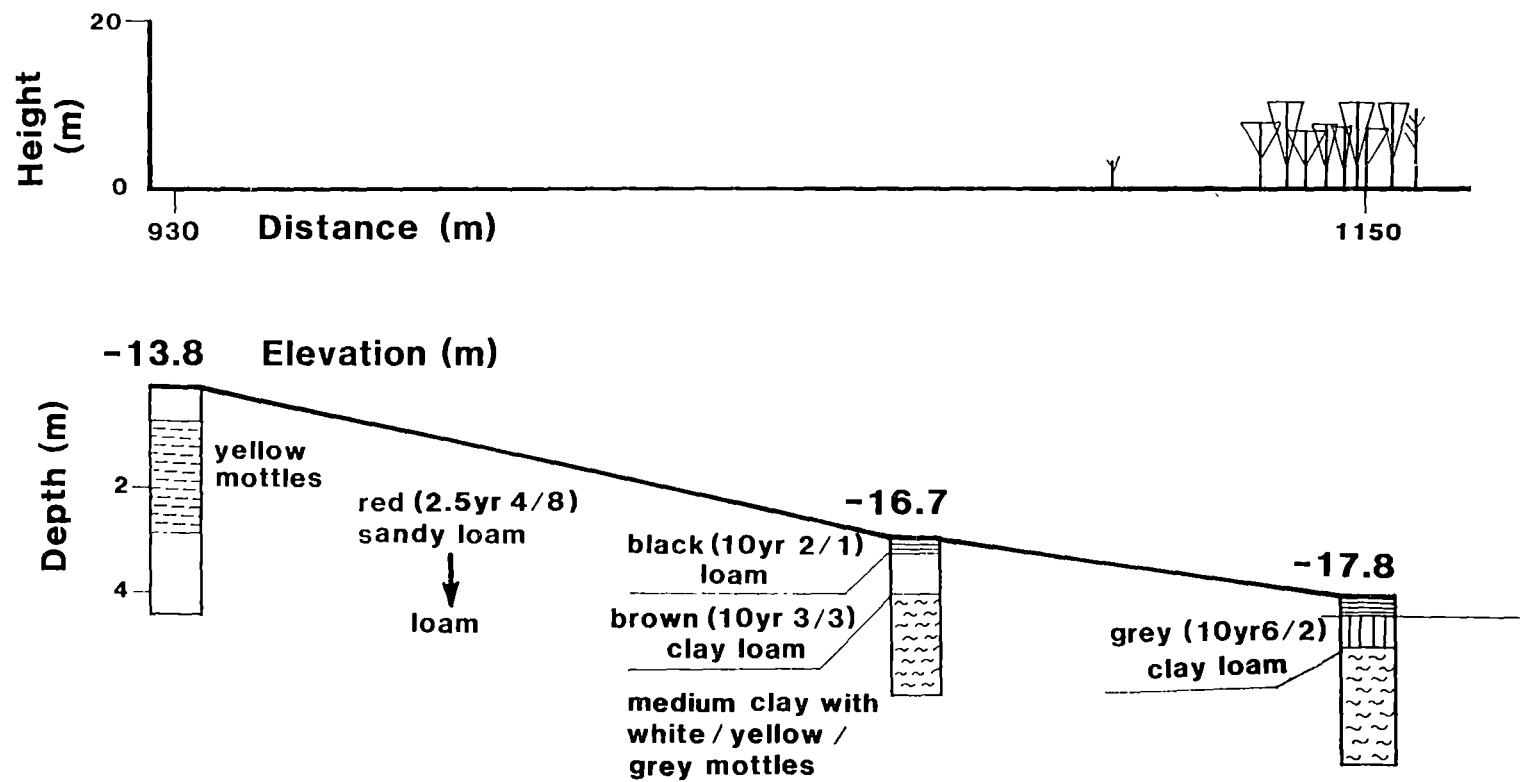
Figure 3.1.5   Profiles of woody vegetation and soils across forest - plains boundaries
- *Acacia* shrubland to *Banksia* woodland, Transect 5

63
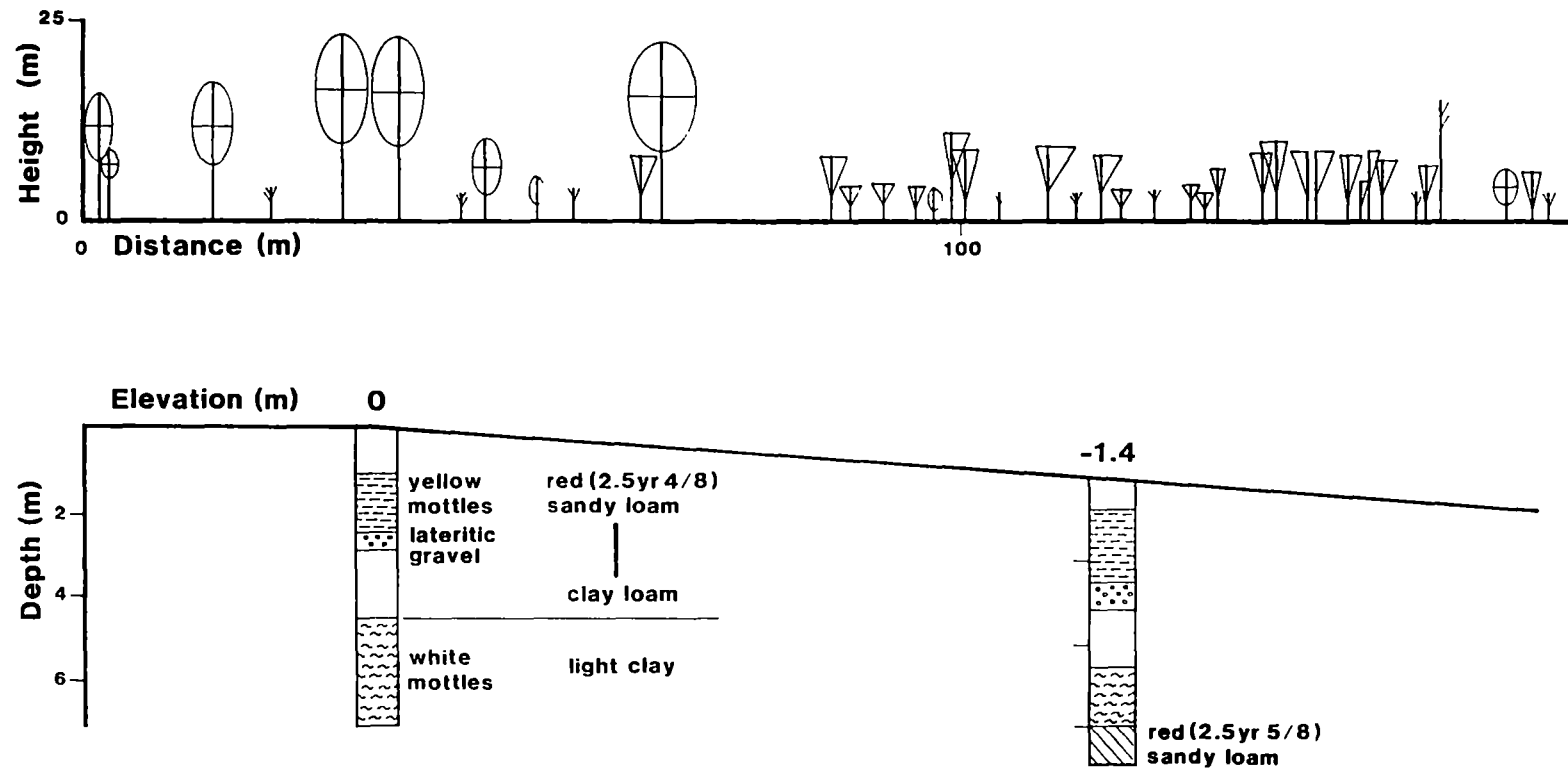
Figure 3.1.6 Profiles of woody vegetation and soils across forest - plains boundaries
- *E. tetrodonta* forest to *Acacia* shrubland, Transect 6
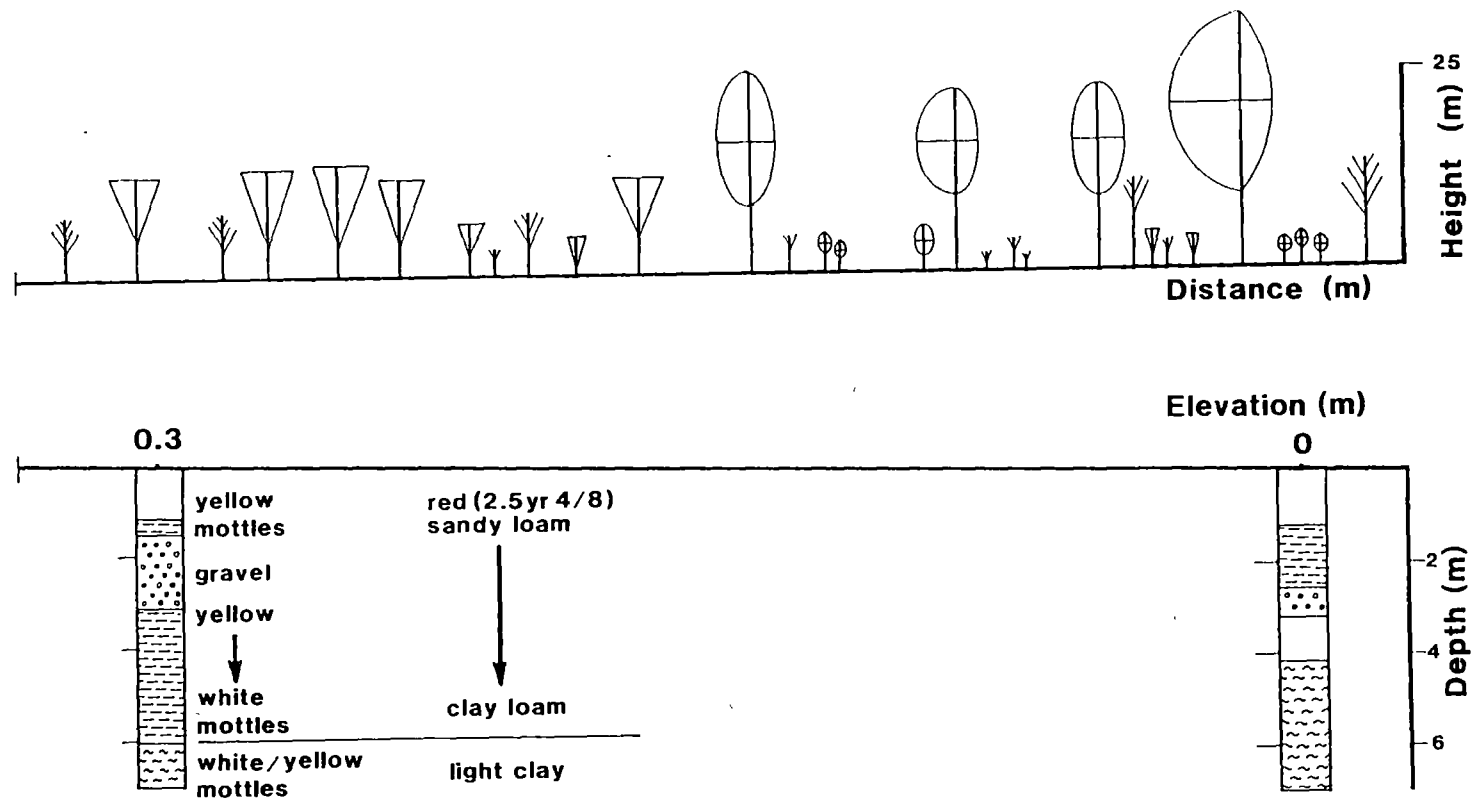
Figure 3.1.7   Profiles of woody vegetation and soils across forest - plains boundaries
- *Grevillea* woodland to *E. miniata* forest, Transect 7

Table 3.1 Correlation (r) between basal area by size class and distance from the boundary (up to 300 meters), at transects 3, 4, 5 and 6.

Size Class Species (cm)	Eucalypts	All
0-1 (<2m ht.)	0.15	0.17
1-2	-0.15	0.02
3-4	0.14	0.21
5-6	-0.24	-0.45
7-8	-0.07	-0.17
9-10	-0.07	-0.28
11-15	0.13	0.04
16-20	0.09	0.02
21-25	-0.36	-0.36
26-30	-0.28	-0.28
31-40	-0.17	-0.18
41-50	0.14	0.14
51-60	-0.16	-0.19
total	-0.16	-0.19

Figure 3.2 shows the change in frequency of eucalypt and other juveniles (<2 metre) across the boundaries. There are significantly more eucalypts juveniles under the forest canopy (Table 3.3) than on the plains. The decrease in numbers occurs abruptly at the edge of the forest canopy, although there are isolated individuals or small clumps of eucalypt juveniles on the plains. There are significant differences between the transects in the number of eucalypt and other juveniles (Table 3.3). Transects 1, 2 and 3 have more juveniles than the other transects. The isolated forest patch at transect 1 was notable for its complete lack of eucalypt juveniles.

Table 3.2 Analysis of variance of mean stand structure (nos/300m2) of ten plots 0-150m from the boundary with 10 plots 151-300m from the boundary, on transects 3, 4, 5 and 7. Significance levels denoted by * = p<0.05, ** = p<0.01, *** = p<0.001.

Dependant		Ht(m) <1.5	Diam(cm) 1-2	3-4	5-6	7-8	9-10	11-15	16-20	21-25	26-30	31-40	41-50	51-60	total
Source	**DF**														
All Species															
Distance	1	-	-	-	-	-	-	-	*	-	-	-	-	-	-
Transect	3	-	***	**	-	**	-	-	-	-	-	-	-	-	-
Dist*Tran	3	-	-	-	-	**	-	-	*	-	-	*	-	-	*
Eucalypts															
Distance	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Transect	3	-	***	*	-	**	-	*	-	-	-	-	-	-	-
Dist*Tran	3	-	-	-	-	**	-	-	*	-	-	*	-	-	*
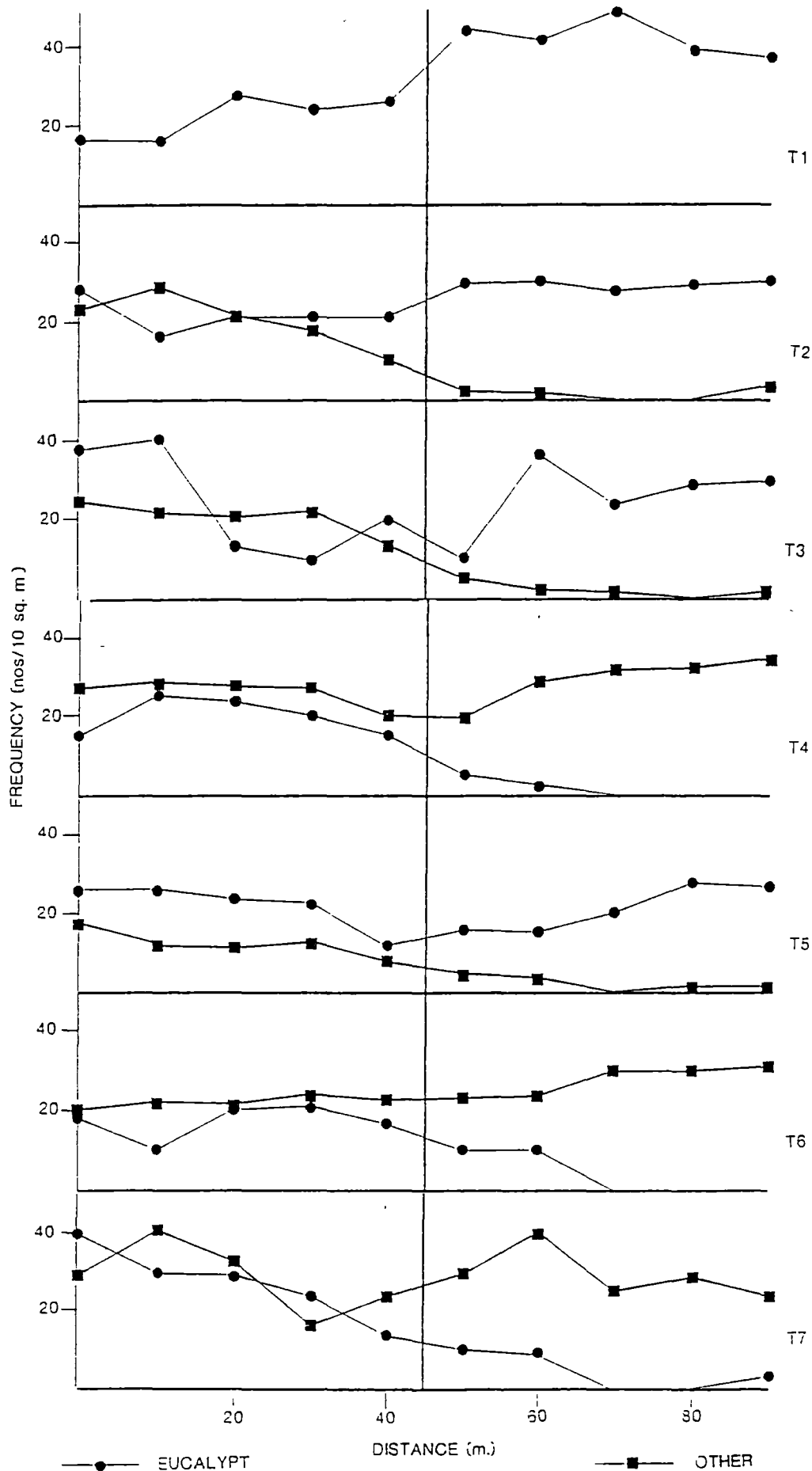
Figure 3.2 Frequency (nos/10m2) of juveniles (<2 m ht.) across the forest plains boundary transects 1-7 (T1-T7). Vertical line at 50 metre distance denotes edge of forest canopy.

Table 3.3 Analysis of variance of number of juveniles across boundary transects (shown in Figure 3.2) Values logarithmically transformed to equalise variances. Level of significance indicated by * = P<0.05, ** = P<0.01 and *** = P<0.001.

	DF	Eucalypts	Other	Total
Effect				
Transect	3	***	*	NS
Community	1	***	**	NS
Transect* Community	2	***	***	***

The number of non-eucalypt juveniles shows a reverse trend to eucalypt juvenile patterns, there being significantly less non-eucalypt juveniles under the forest canopy compared to the plains. There is no significant difference in total number of juveniles on either side of the boundary, although there are slightly more on the plains side. Seven eucalypt seedlings (5 *E. tetrodonta* and 2 *E. nesophila*) were found in the vicinity of the boundary near transects 4 - 6 in the 1987/88 wet season. A search near other boundary transects confirmed this paucity of seedlings. All eucalypt seedlings were within the forest canopy. Very few eucalypts were observed to flower in the vicinity of the plains during the course of this study.

3.3.2 Floristic Composition

Figure 3.3 shows the relationship between neighbouring sites across the boundary transects, within the NMDS ordination space of the floristic survey reported in chapter 2. There is a consistent general trend in floristic composition from forest to *Acacia* shrubland across the second axis, with minor changes across the first and third axes. The change at transect 7, from forest to *Grevillea* woodland, is distinct from the other transects occurring at about 45 degrees to the first and second axis. The

change from the *Acacia* shrubland to the *Banksia* woodland community at the bottom of transect 5, shows an erratic and discontinuous pattern across the first axis.

A preliminary analysis of each transect studied in detail was carried out to determine which axis was best related to distance across the transect and how the relative positions of the sites were affected by deleting tree species (*E. miniata*, *E. tetrodonta* and *E. nesophila*) from the analysis. The results from transect 5 are presented here (Figure 3.4) as an example of the trends that were apparent on all transects.

Figure 3.4 shows that there is little obvious relationship between the second axis and distance while the first axis is strongly related to distance. It also shows that there is little difference in the relative positions of sites whether the tree species are included in the analysis or not. Thus changes in floristic composition occur in the understorey as well as the overstorey. This is also illustrated by Table 3.4, which shows the variation in species abundance across transect 5. Although many of the species in the understorey are widespread, some such as *Planchonia careya*, *Eriachne triseta* and *Mitrasacme* sp. are largely restricted to the open-forest while others, such as *A. gonocarpa*, *Calytrix exstipulata* and *Eragrostis cummingii*, are found predominantly on the plains.

Thus, the other three profiles studied are presented in Figure 3.5 using first axis scores versus distance derived from an ordination using all species in the analysis. The changes in floristic composition across the boundaries are subject to 'noise', however some general trends are apparent. The floristic changes that accompany the change from open-forest to shrubland/low woodland occur gradually over intervals of 100 metre or more. On transects 3 and 5 ordination score changes uniformally with distance through the forest and transition zone but shows little relationship with distance within the *Acacia* shrubland.
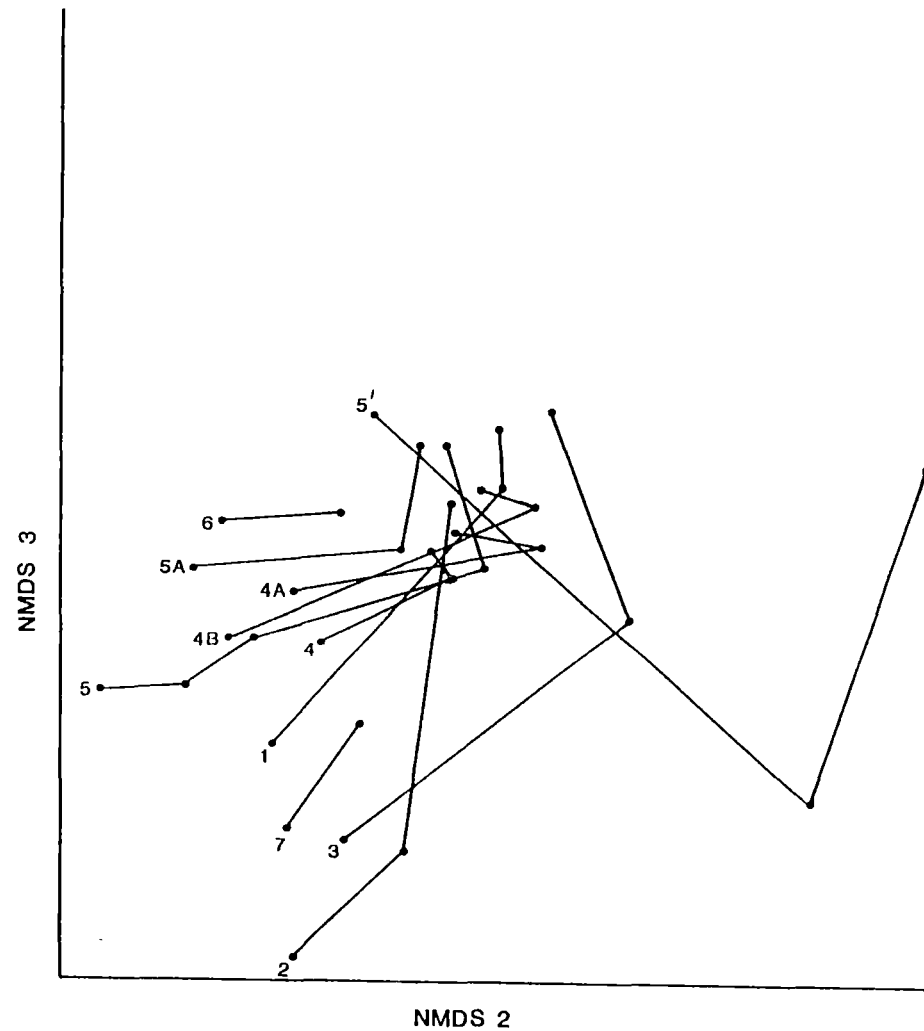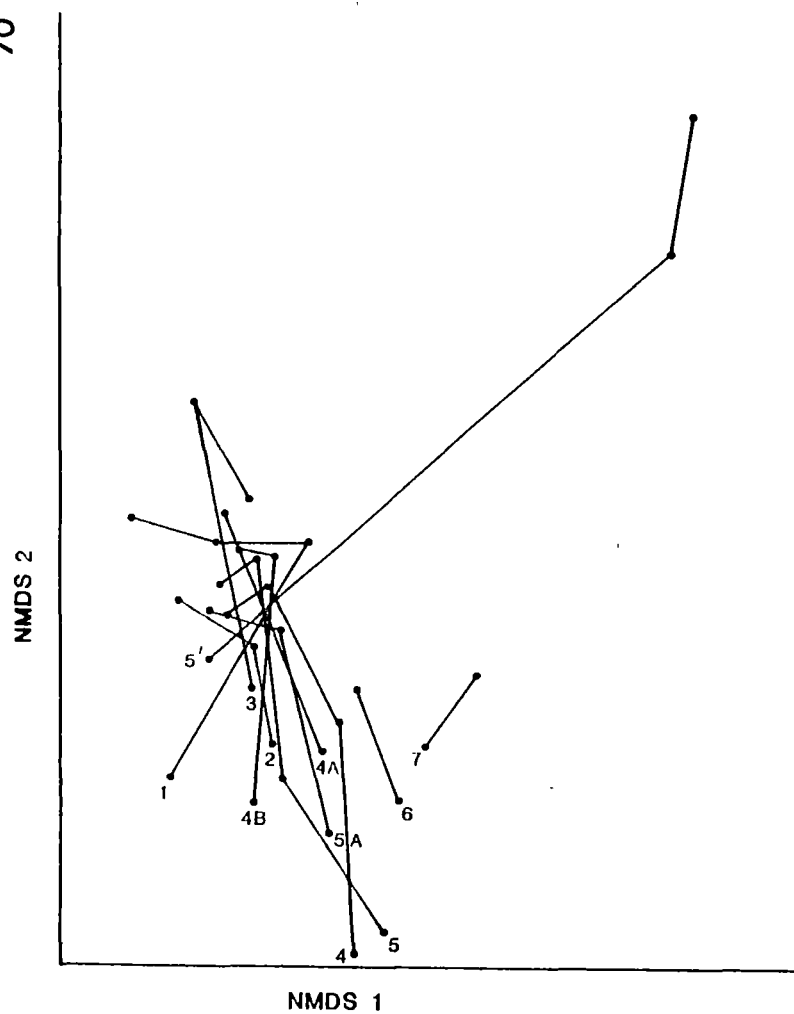
Figure 3.3   Boundary transects plotted on the 3D NMDS ordination (from Chapter 2). Forest end of transects denoted by labels 1 - 7. Sub-transects adjacent to transects 4 and 5 are denoted by the letters A, B and C. Transect 5 is divided into the upper (5) 'dry' and lower (5') 'wet' sections.

ALL SPECIES

EXCLUDING TREES

NMDS2

NMDS2

NMDS1

NMDS1
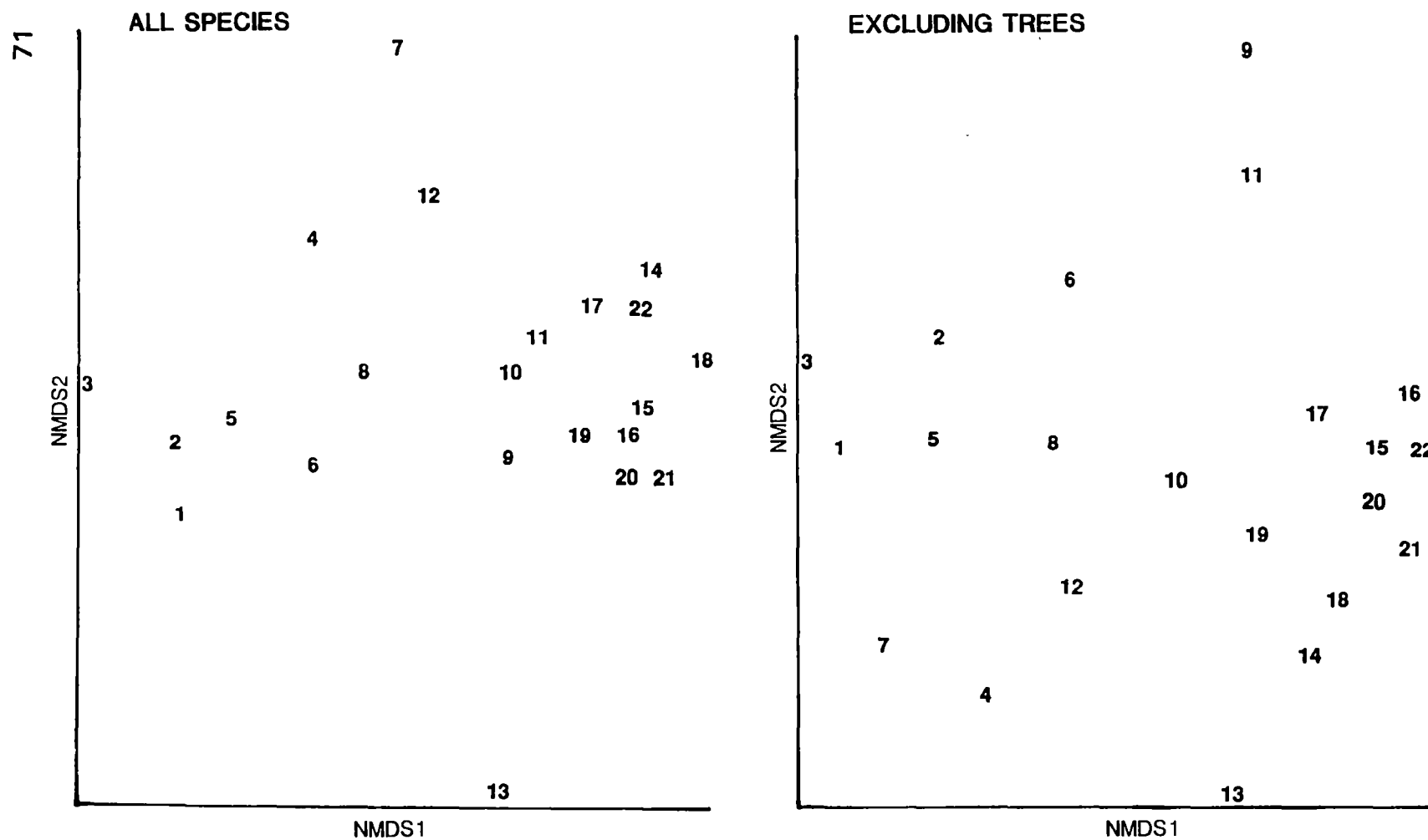
Figure 3.4 Two dimensional sample NMDS ordination of detailed study across transect 5, using all species and excluding trees (*E. miniata* , *E. tetrodonta* and *E. nesophila*). Numbers indicate order of samples along transect from the forest end (number 1) to the plains end (number 22).

TRANSECT 3

TRANSECT 7

DISTANCE (m)
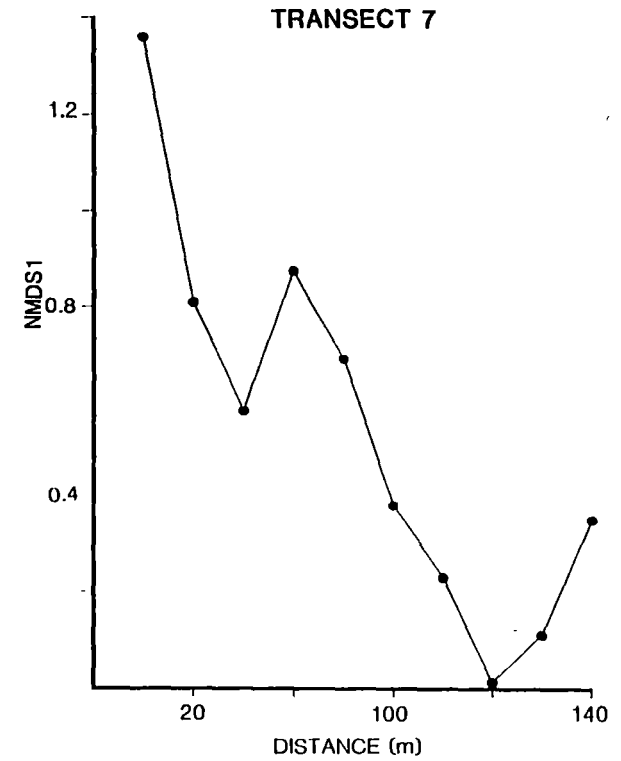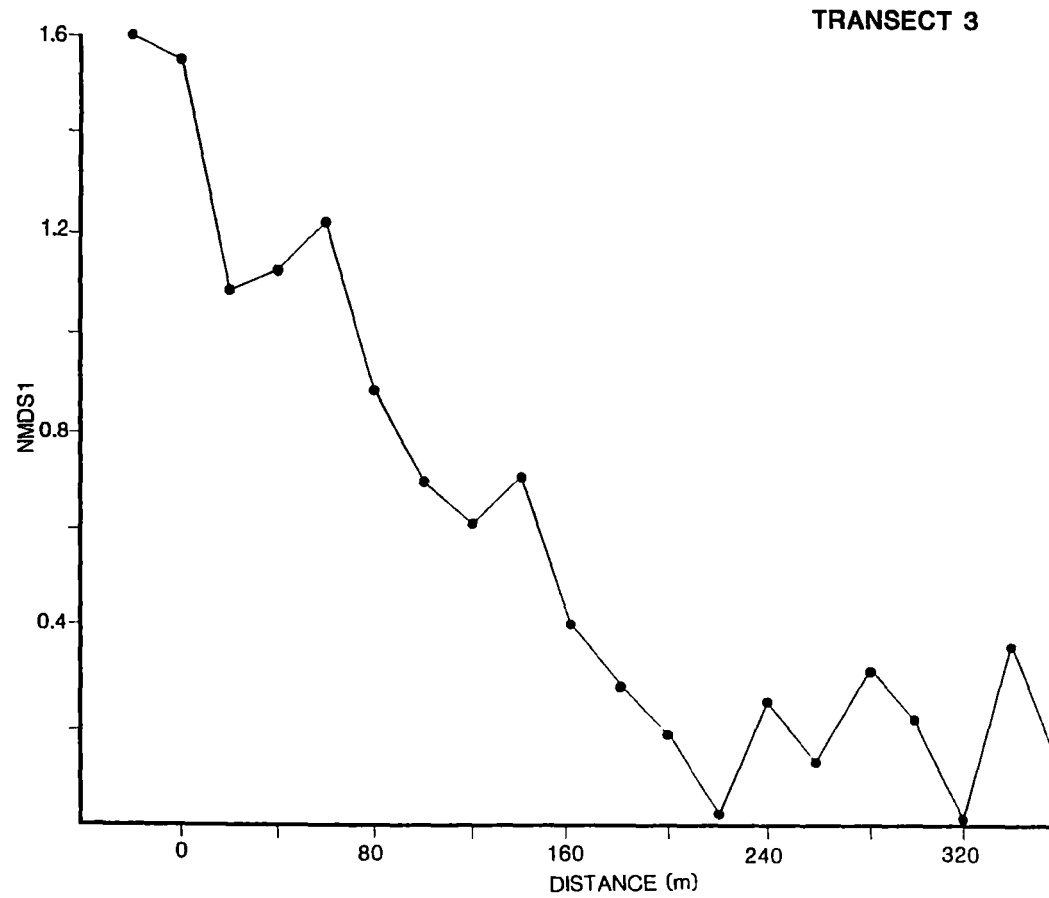
DISTANCE (m)

Figure 3.5.1 Distance versus site NMDS ordination score for sites from detailed studies across - *E. miniata* forest to *Acacia* shrubland (transect 3) and *E. miniata* forest to *Grevillea* woodland (transect 7)
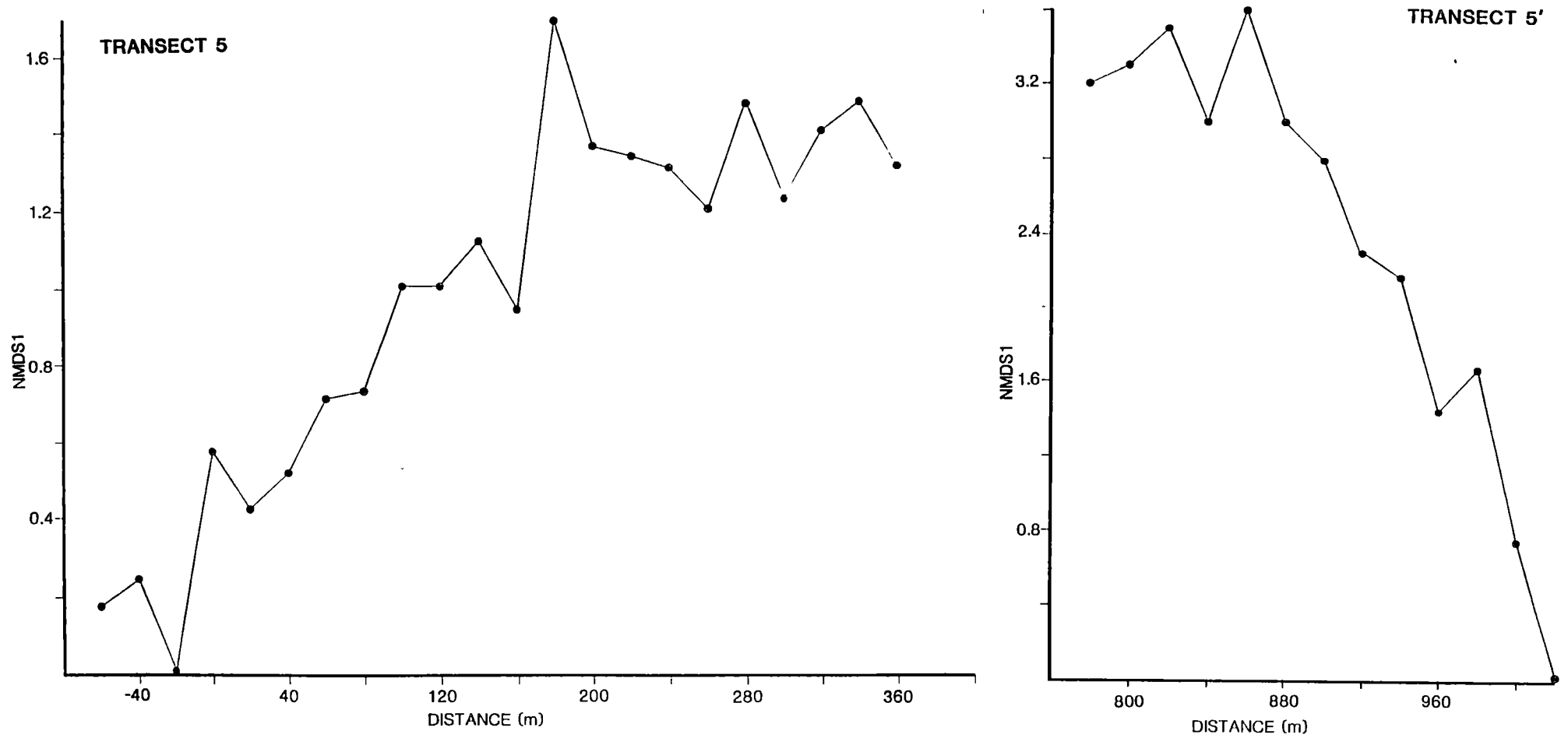
Figure 3.5.2   Distance versus site NMDS ordination score for sites from detailed studies across - *E. tetrodonta* forest to *Acacia* shrubland (transects 5) and *Acacia* shrubland to *Banksia* woodland (transect 5')

Table 3.4 Sorted table of species abundance across *E. tetrodonta* open-forest to *Acacia* shrubland, at transect number 5. Distance refers to distances on Figure 3.1.4.

plot position [1]	-40	0	20	40	60	80	100	120	140	160	180	200	220	240	260	320	340
Species																	
E.miniata	4																
Pseudopogonatherum contortum		2	3														
Eriachne triseta	3	1	1														
Planchonia careya		2	2	1	1	1											
E. tetrodonta	1	2	3	2	2	1	2										
Mitrasacme sp.		1	1	1	1	1		1									
E. nesophila	2		2	3		3		1									
Polygala orbicularis		2		1	1	1	1										
Desmodium brownii				1													
Gardenia suffruticosa					1							1					
Hibbertia cistifolia	3	2	2	1	1	2	2		1		1	1	2	1	1		
Polygala eriocephala			1	1		1	1		1	1	1	1	1	1	1	1	1
Sauropus glauca	2	1	1	1	1			1							1		
Acacia oncinocarpa		4	1	2	3	2	3	3	2	2	1	2		2			3
Livistona humilis			1	1	1	1		1	1			2		3			
Acacia latescens	2	1						1		1		1					
Grevillea sp.nov.	3	2	2	2	2	1	1	1	1	1	1	2	2	3	2	1	1
Buchanania obovata			1	1	1	1			1	1							
Thaumastochloa major		2		1	2	1	2	1	1	1	1						1
Sorghum spp.	3	3	2	2	3	2	3	2	3	3	3	2	2	2	2	2	3
Eriachne avenacea	2	2	3		3		3	2	3	3	3		3	3	3	1	2
Heliotropium tenella		1	1	1	1			1							1		
Persoonia falcata	1	1	1		1	1	1		1	1	2	1			1		1

cont....

Table 3.4 cont...

plot position [1]	-40	0	20	40	60	80	100	120	140	160	180	200	220	240	260	320	340

<u>Species</u>

	-40	0	20	40	60	80	100	120	140	160	180	200	220	240	260	320	340
Borreria brevifolia		1	1	1	1	1	1	1	1	1	1		1	1	1	1	1
Pachynema complanata	1	2	1	1	1	1	1	1	1	1	1	1	2	1	3	1	1
Wrightia saligna				1	1	1	1		1	1	1						1
Distichystemon hispidulus	1	1		1	1	1	1	1	2	1	2	1	2	1	2	1	1
Grevillea pteridifolia				1	1	2	2	2	2	1	1	2					
Drosera petiolaris		1			1		1	1	1	1	1	1	1	1	1	1	1
Stackhousia intermedia			1			1		1	1	1			1		1		
Acacia difficilus				1	2	1	2	1		1	1	2	2	2	2	2	2
Buchnera linearis			1						1		1				1		1
Eriachne obtusa						2	2	1	1	3	3	2		2	2	1	1
Goodenia leosperma										1	1	1			1		1
Mitrasacme elata						1		1	1	1	1	1	1	1	1	1	1
Eragrostis cummingii						1		2		1			1	1	1	1	1
Acacia gonocarpa							1	1	1		2	2	2	2	2	2	1
Calytrix exstipulata						1	1		1	1	1	1	1	1	1		1
Trachymene didiscoides									1		1	1	1				
Setaria apiculata									1	1	1	1		1			1
Aristida hydrometrica												1	1	1	1	1	1
Panicum mindanaense									1	1	2	3	1	1	1	1	

[1] Metres from origin as per Figure 4.1

Transect 7, which represents a change from *E. miniata* forest to *Grevillea* woodland, exhibits greater total variation, as indicated by the larger range of the scaled axis, and more abrupt transition, than transects 3 and 5.

The floristic change across the shrubland *Banksia* woodland boundary (lower end of transect 5) is abrupt and erratic, with a greater changes in ordination scores over shorter distances, compared to all other transects. This change shows relatively rapid (steep) changes between communities over of 20 - 40 metre intervals.

3.4 Discussion

3.4.1 Tree regeneration in the vicinity of the plains.

Bowman (1986) has reported *E. tetrodonta* seedlings germinating in eucalypt litter in the absence of fire stimulation. Fensham (1990) found areas of eucalypt forest on Melville Island with abundant (100/square metre) seedling establishment, but also noted a paucity of mature trees flowering and fruiting. Thus it appears that flowering, seeding and germination in these forests may be patchy and sporadic. Mott *et al.* (1985) raise the possibility of episodic germination events being an important mechanism in seedling establishment in northern Australian forests and woodlands. However, in the absence of further information on eucalypt flowering, seed production, germination and periodicity of these factors, it is difficult to conclude whether the flowering and seedling densities observed on Melville Island are atypical of the northern eucalypt forests and woodlands in general.

Clumps of juvenile eucalypts (<2 metre height), which are connected to underground lignotubers are a common component of northern eucalypt forests (Lacey & Whelan 1976). *E. miniata* and *E. nesophila* reproduce their aerial parts asexually from lignotubers (Lacey & Whelan 1976),

while *E. tetrodonta* shoots originate from adventitious buds, rhizomes or suckers on the roots (Lacey 1974). For the sake of simplicity all such shoots will be referred to as suckers in the remainder of this thesis.

The *E. tetrodonta* root suckers found on the plains were generally limited to small (<1 ha) patches and at lower densities than under the forest canopies. Thus it would appear that these suckers have only limited ability to spread out from the forest onto the plains. The lack of juvenile growth on the forest floor on transect 1 and the scattered nature of surrounding clumps of eucalypt trees (Appendix 1) may indicate that the forests may be decreasing in extent and that the clumps in this area are relicts of a larger forest. Comparison of 1963 and 1979 aerial photographs revealed no boundary changes, although such changes may take place over a longer time frame. Further work on the establishment and growth of eucalypt regeneration on and adjacent to the plains is reported in Chapter 5 of this thesis.

3.4.2 Vegetation patterning across the boundary

Attempts have been made to classify boundary types based on rates and patterns of changes across the transitions. In a consideration of how vegetation is arranged across boundaries, van der Maarel (1976 after van Leeuwen 1966) has differentiated five theoretical types, which represent a continuum between the two extremes cases of a 'sharp' boundary and a 'gradual' boundary. Intermediate types vary in the rate and pattern of change. Figure 3.6 presents three such theoretical boundary arrangements on axis of 'vegetation similarity' versus distance.

The terms 'ecotone' and 'ecocline' are also often used to classify biological boundary types. An ecotone is defined as a 'habitat created by the juxtaposition of distinctly different habitats' (Brandt & Wadsley 1981). Usually ecotone communities possess characteristics of the

ABRUPT INTERMEDIATE GRADUAL
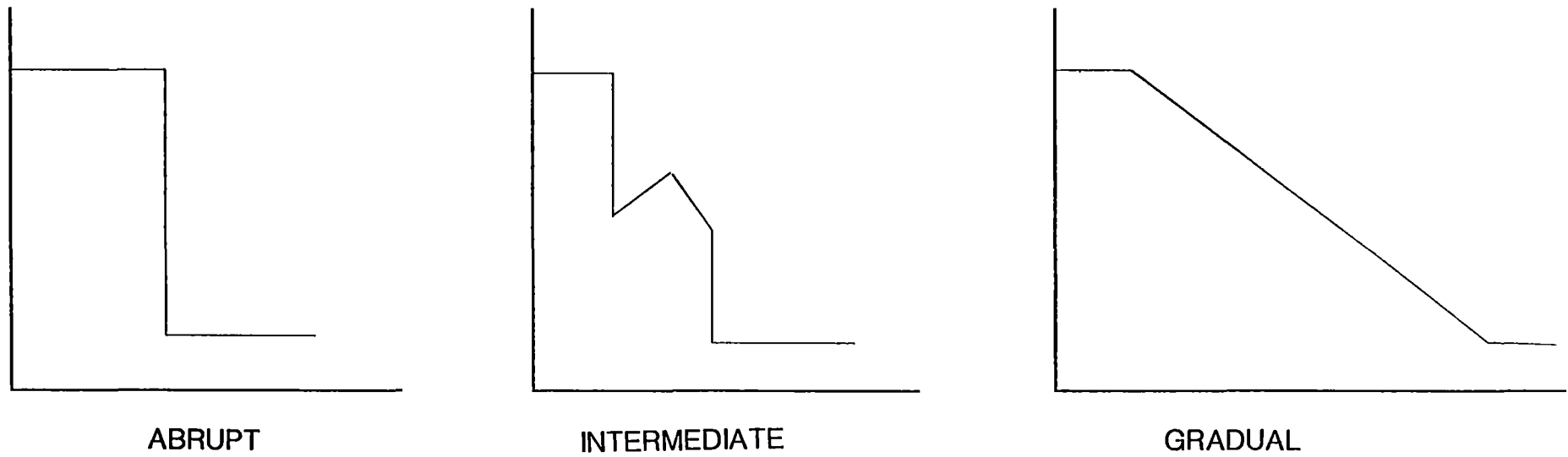
Figure 3.6 Examples of theoretical boundary types (after van der Maarl 1976) showing a gradual abrupt and intermediate type. Horizontal axis is distance and vertical axis is measure of vegetation similarity.

adjoining communities but are distinct from both. An ecocline is a zone resulting from a blending of two distinct vegetation types in a gradual manner (van der Maarel 1976).

However, these theoretical terminologies cannot be applied to the Melville plains boundaries unambiguously because the structural and floristic changes occurred independently of each other. For example the *Grevillea pteridifolia* transition zones on transects 1, 2, 3, 4 and 5 had distinct, intermediate structural characteristics to the neighbouring shrubland and forest communities. This structural transition is an abrupt boundary with a distinct ecotone. The structural change was not, however, accompanied by an analogous change in floristic composition, which showed broad clinal variation across the transition zone. An extension of the floristic study into the forests at transect 4 and 5 may have revealed that the *E. tetrodonta* forests are part of a broad floristic ecotone between the plains and the *E. miniata* (group 1, Chapter 2) forests.

In a study across shrubland - grassland boundaries in California, Hobbs (1986) noted that abrupt physiognomic boundaries were accompanied by either abrupt or gradual changes in species composition which made it difficult to apply the above boundary classifications unambiguously. In the same study, Hobbs (1986) described gradual transitions occurring over 30 - 40 metre and abrupt boundaries over less than 30 metre. Clayton (1958) described 'abrupt' transitions between forests and savanna in Nigeria occurring over 50 metre. However, comparisons with the Melville Island transects are distorted by differences in scale of measurement including total transect length and size of plots. Thus the boundary classifications and terms such as 'abrupt' and 'gradual' can only be applied in a relative sense.

There was no evidence of a gradational decrease in tree cover within the forest and the change from forest to transition and transition to shrubland

occurs over intervals of 20 - 30 metre. Thus the structural boundary is considered abrupt. Similarly the change in structure and floristic composition as measured by ordination score, across the shrubland to wet woodland, occurs abruptly over less than 20 metre and shows distinct floristic ecotones. By comparison the change in floristic composition across the forest plains boundary occurred gradually through the forest and the transition zone, over intervals of at least 100 metre and is thus considered a gradual ecocline type.

The relationship between boundary patterns and environmental factors will be discussed further in Chapter 4.

CHAPTER 4 <u>THE NATURE OF THE FOREST PLAINS BOUNDARY:</u>
<u>ENVIRONMENTAL PATTERNING</u>

<u>4.1 Introduction</u>

Early vegetation descriptions within the Northern Territory were carried out as a component of Land Systems mapping (Christian & Stewart 1953) which is based on the assumption that vegetation, landform and soils are related. Such broad scale vegetation surveys associated changes in vegetation communities with various environmental factors which are readily visible without recourse to quantitative measurements (Christian & Stewart 1953, Specht 1958, Storey 1969, 1976). More recent studies using quantitative numerical analysis techniques, have related changes in structure and floristic dominance within eucalypt open-forests and woodlands to more subtle changes in environmental factors (Bowman 1986, Bowman & Minchin 1987, Bowman *et al.* 1988a).

Many of the above studies however, have used superficial, indirect measures of the environment with no temporal component, which allow only relative comparisons. This has made it difficult to determine the relative importance of inter-correlated environmental factors, such as soil texture, moisture and fertility, or determine which factors may be reaching levels critical to tree growth.

Thus in this chapter, a detailed study is undertaken to determine which environmental factors vary significantly across the forest plains boundary and which are at levels that may be limiting tree growth on the plains. Measurements focus on the edaphic factors suggested by the floristic study in Chapter 2: soil fertility, texture and moisture (percent and potential) and water table flux. Variations in environmental factors are related to the structural and floristic patterns described in Chapter 3.

4.2   Methods

4.2.1 Study sites

The boundary transects used for the description of changes in vegetation (chapter 3) were used to study changes in environmental variables. Three study sites were established on each of transects 1 - 5, one fifty metres from the boundary in the forest, one in the middle of the transition zone and one in the *Acacia* shrubland.   On transects 6 & 7, two sites were established 50 metres either side of the forest-plains boundary. Three sites were also established on the transition from the *Acacia* shrubland into the *Banksia* woodland on the lower end of transect 5.

4.2.2 Soil profiles

At each site a hole was augured to a depth of seven metres or to the bed-rock.   The soil profile was described in terms of soil texture, colour, mottling and gravel content following the procedures of McDonald & Isbell (1984).   Changes in surface elevation between soil pits was measured with a theodolite. Soil samples from 0-15, 60-90 and 105-120 cm were collected for subsequent laboratory analysis.   The soil profiles are presented diagramatically.

4.2.3 Soil particle size analysis

At each site, soil samples were taken from 0-15, 25-35 and 80-90 cm. depth.   Extra samples were taken from two additional auger holes at transect 7.   Particle size distribution was determined for each sample using the pipette and sieve method (Coventry & Fett 1979).

4.2.4 Soil nutrients

Soil samples were taken from transects 4-5 at 6 replicate sites from the forest, transition and shrubland communities. At each site soil was collected from depths of 0-15, 25-35 and 100-120 cm, placed into bags, taken to the laboratory and analysed as follows:

1.   pH (1:5 solution)

2.   Electrical conductivity (1:5 solution)

3.   Nitrogen (Total: CSIRO 1982)

4.   Phosphorus (available, CO_2 extracted: Lindsey & Norvell 1969)

5.   Potassium (available, CO_2 extracted.: Lindsey & Norvell 1969)

6.   Carbon (% of total, Walkley-Black chromic acid digestion method: Heanes 1984)

7.   Calcium (available, ammonium acetate extracted: Juo *et al.* 1976)

8.   Magnesium (available, ammonium acetate extracted: Juo *et al.* 1976

9.   Copper (available, DTPA extracted: Lindsey & Norvell 1969)

10.   Zinc (available, DTPA extracted: Lindsey & Norvell 1969)

11.   Sodium (available, ammonium acetate extracted: Juo *et al.* 1976)

12.   Aluminium (1:5 soil:0.01 $CaCl_2$ extract)

The laboratory facilities available to carry out the above analyses only allowed results to be presented in units which were not compatible with many published studies. Therefore to allow comparisons with other studies, further analysis was carried out on bulked samples from each community by a commercial laboratory (see Bowman *et al.* 1990 for details of methods).

4.2.5 Soil moisture and water table

The holes dug for soil profile description were converted to wells by

casing with 50 mm PVC pipe. The well collars were sealed with clay to prevent rain trickling down the hole. Water-table fluctuations were measured periodically (about once every 6 weeks) from June 1986 - August 1987.

Percentage soil moisture flux was assessed at 6-8 week intervals over the period August 1986 - August 1987. At each sampling time a soil core was taken by hammering a hollow, 30 mm diameter water pipe into the ground, 15 cm at a time. Soil samples from 0-15, 30-45, 60-75 and 105-120 cm were collected, placed into airtight jars and taken back to the laboratory where the gravel and gravimetric water content were determined. One soil moisture sample was taken at each well location on transects 1 ,2, 3, 6 and 7. Transects 4 and 5 were studied in more detail in order to ascertain the amount of variability. Here, three extra sub-transects were established and two samples were taken per transect to give a total of 10 replicates within each community.

One soil sample from the forest and one sample from the plains from each transect were analysed for the relationship between soil water potential and moisture content. This analysis took place in the laboratory using the pressure plate technique (M°Intyre 1974). The soil moisture relationships were used to show the available moisture characteristics of the soils and to convert field percent moisture contents to equivalent matric potentials.

4.2.6 Soil temperature and evaporation

The difference in ground surface temperature was measured across the boundaries at transects 4-5. An upright thermometer, with the bulb 2 cm above the soil surface, was placed at the forest, transition and shrubland sites on each of the 5 transects and sub-transects. Change in temperature from sunrise to sunset was measured on several days in

December 1987 (wet season) and July 1987 (dry season). The difference in soil evaporation was assessed across the same boundaries at the same time. A 600-700 gram soil sample was sieved into a plastic container which was buried at each site with the top exposed to the atmosphere. The containers were collected after one week and the moisture content of the soil measured.

4.3 Results

4.3.1 Soil profiles

Figures 3.1.1 to 3.1.6 show the soil profiles from 6 transects. There are generally slight but consistent gradational changes in soil morphology across the forest - plains boundaries. With the exception of transects 2 and 7 the change from forest to transition/shrubland occurs downslope. The change in slope is usually gradual although on transect 3 there is a slight break in slope at the forest - plains boundary (Figure 3.1.3).

All soils have indistinct horizons, with a shallow (<10 cm) organic stained, sandy loam A1 horizon grading to clay loam or loam texture at about 4 metres depth. At depths of between 0.8 and 1.4 metres, light yellow (10YR 3/2) mottles are present. The minimum depth to these mottles usually decreases across the transects from the forest to the plains. There is generally a layer of small (<1 cm) lateritic gravel within each profile. The thickness of the gravel layer varies from 0.5 - 1.7 metres and occurs at depths varying between 2.5 and 6 metres. The gravel layer is often thicker and occurs at lower depths at sites from lower elevations on the same transect (e.g. transect 5, Figure 3.1.4).

There are qualitative differences in soil profiles between those in the east (Mindaloo transects 1, 2 and 3) and the west (Yapilika transects 4, 5, 6 and 7). At Mindaloo, transects 1 and the plains site on transect 2 have a

heavily compacted (impenetrable to the auger) lateritic gravel layer at 4.0 m. This 'rock' layer appears to be associated with striations clearly visible on dry season aerial photographs. The easterly transects (2, 3, 4 and 5) have an orange sand layer, usually beneath the gravel layer, at depths of 6 - 7 metres. Transects 6 & 7, at Yapilika have white clay mottles at depths below 4.0 metres and have white/yellow/orange mottled clays beneath the gravel layer, at depths of 6 - 7 metres. This deep mottled layer was also found at three other sites, not presented here, on the Yapilika side of the plains.

By contrast the *Acacia* shrubland to *Banksia* woodland boundary on the bottom of transect 5, shows relatively abrupt and distinct changes in soil profile morphology. Here, the soil profile from the *Acacia* shrubland site has similar characteristics to the shrubland site at the forest - plains boundary 600 metres away (transect 5). However over a distance of 50 metres the soil profile changes from a gradational red earth to duplex soils with yellow or black A horizons and yellow or gleyed, highly mottled, clay B horizons.

4.3.2 Soil particle size analysis

Particle size analysis by boundary type, community and depth are shown in Table 4.1. All soils have a surface sand (fine + coarse) content of 81 to 90 %, with slight decreases to the lowest depth sampled (one metre). On all transects there is an increase in the percentage of fine + coarse sand from forest to transition to shrubland. T-tests on sites paired across the boundaries show the differences between the forest and the shrubland are significant, while the forest-transition and transition-shrubland differences are not (Table 4.2).

Table 4.1 Means and standard error (in brackets) for soil particle sizes of fine earth faction, by boundary type, community and depth.

	0-15cm					Depth 15-30cm					60-90cm				
	clay	silt	fine*	crse	sands	clay	silt	fine	crse	sands	clay	silt	fine	crse	sands
E.miniata open-forest to _Acacia_ open-shrubland (n = 3)															
Forest	9.7 (0.6)	7.2 (1.2)	55.5 (3.9)	26.0 (2.4)	82.0 (1.3)	16.4 (5.8)	7.5 (1.5)	50.1 (6.4)	28.0 (6.4)	78.1 (4.7)	20.4 (1.2)	3.9 (1.3)	51.3 (6.1)	24.8 (7.3)	76.1 (1.3)
Transition	4.5 (0.9)	17.5 (2.2)	64.5 (4.2)	25.4 (3.6)	89.9 (7.2)	14.1 (1.0)	10.7 (2.7)	64.1 (4.7)	12.4 (3.9)	76.5 (0.7)	28.0 (6.6)	4.9 (1.4)	58.0 (4.6)	9.9 (2.6)	67.9 (7.1)
Open-shrubland	4.8 (1.6)	9.5 (2.2)	62.0 (3.5)	27.0 (3.5)	89.0 (0.7)	13.0 (0.8)	8.4 (1.7)	57.8 (5.6)	23.5 (4.4)	81.3 (1.2)	19.9 (0.3)	4.0 (1.1)	52.4 (5.0)	23.4 (4.8)	75.8 (2.2)
E.tetrodonta open-forest to _Acacia_ open-shrubland (n = 3)															
Forest	8.1 (0.6)	10.2 (3.5)	71.2 (5.3)	14.2 (0.6)	85.4 (9.3)	15.2 (0.7)	8.4 (1.5)	69.0 (3.2)	11.0 (2.2)	80.0 (0.5)	31.5 (7.6)	3.3 (0.6)	51.8 (6.1)	11.8 (3.5)	63.6 (2.0)
Transition	4.4 (1.2)	11.7 (1.3)	73.6 (5.2)	14.3 (2.3)	87.9 (1.4)	12.7 (1.7)	8.1 (1.7)	66.6 (3.1)	15.2 (4.6)	81.8 (1.9)	29.8 (6.5)	3.6 (0.7)	51.0 (5.2)	13.5 (3.6)	64.5 (8.2)
Open-shrubland	6.1 (1.3)	11.0 (2.3)	63.1 (1.4)	23.5 (2.6)	86.9 (2.7)	12.2 (2.8)	8.1 (0.7)	66.6 (3.4)	24.1 (4.2)	90.7 (1.6)	21.0 (0.3)	2.0 (0.4)	53.9 (3.3)	22.8 (2.8)	76.7 (0.5)

cont....

Table 4.1 cont...

	0-15cm					Depth 15-30cm						60-90cm			
	clay	silt	fine	crse	sands	clay	silt	fine	crse	sands	clay	silt	fine	crse	sands

E.miniata open-forest to *G. pteridifolia* woodland
(n = 2)

	clay	silt	fine	crse	sands	clay	silt	fine	crse	sands	clay	silt	fine	crse	sands
Forest	2.7	19.1	71.3	10.1	81.8	23.3	11.9	53.6	11.9	65.5	40.4	7.9	41.1	10.4	51.7
	(0.2)	(0.5)	(4.3)	(2.5)	(1.2)	(0.1)	(1.1)	(5.5)	(9.3)	(10.2)		(0.9)	(4.1)	(0.6)	(0.0) (10.0)
Scrub	0.8	15.1	76.9	11.4	88.3	14.1	11.1	65.6	4.8	74.9	32.9	10.3	6.9	19.1	62.8
	(0.2)	(3.2)	(5.4)	(2.3)	(2.3)	(1.9)	(1.1)	(0.9)	(0.2)	(1.1)	(6.7)	(5.3)	(6.9)	(0.5)	(6.4)

* fine = fine sand. crse = coarse sand. sands = fine + coarse sand.

Table 4.2 Comparison of sand (fine + coarse) content by community. Direction of difference indicates whether content of first community is higher (-) or lower (+) than content of second community. Significance indicates the degree that the difference differs from zero, as determined by paired t-test comparisons across boundary transects 1 - 7.

Community Comparison	Direction of Difference (1st - 2nd)	Significance
Forest to Transition	-	NS
Forest to Shrubland	-	0.04
Transition to Shrubland	-	NS

4.3.3 Soil nutrients

Table 4.3 shows the variation in soil nutrient content across the boundary at transects 4 and 5. The forest has significantly less available sulphur at 1.2 metres depth and surface available aluminium than the shrubland and significantly higher pH, available potassium, available magnesium and percent organic carbon. With the exception of magnesium, the significant differences between the communities are not consistent with depth. The concentration of magnesium significantly decreases from forest, to transition, to shrubland at all depths, although the size of the difference decreases with depth.

4.3.4 Soil moisture

Percent soil moisture content across the boundaries over time is shown on Figure 4.1. General patterns correspond to the seasonal rainfall with maxima towards the end of the wet season, followed by a rapid decline to a minimum recorded in late July 1987. Soil moisture is most variable in the early wet season due to the sporadic storms which occur at this time of the year. The relatively high values in July 1986 are due to the mid dry season rain event in that year (Table 1.1).

Table 4.3 Means for chemical content of soils by depth and community. Samples taken across boundary near transects 4 and 5. The same letters denote row means which are significantly ($p<0.05$) different as determined by Tukey's range test. Rows with no letters indicate that Analysis of Variance showed no significant difference in row means.

Soil Depth (cm) Community	0-15			22-35			100-120		
	*F	T	Sh	F	T	Sh	F	T	Sh
Chemical Attribute									
Conductivity (ms/cm)	.02	.02	.02	.01	.01	.02	.02	.01	.01
pH (1:5)	5.5	5.4	5.5	5.6 A	5.4 B	5.4 B	5.5	5.5	5.3
Total Nitrogen	283	279	299	179	236	201	112	84	98
Phosphorus Avail.ppm.	<5	<5	<5	<5	<5	<5	<5	<5	<5
Potassium Avail.ppm.	12.3 A	10.5 B	8.3 B	11.3	12.8	11.0	5.7	14.8	4.2
%Carbon Avail.ppm.	1.2 A	1.0 B	1.0 B	.75	.67	.75	.27	.25	.23
Calcium Avail.ppm.	18.5 A	6.2 B	2.5 B	2.5	3.1	2.5	2.5	4.1	2.5

cont....

Table 4.3 cont....

Soil Depth (cm)	0-15			22-35			100-120		
Community	*F	T	Sh	F	T	Sh	F	T	Sh

Chemical
Attribute

Magnesium	31.0	10.8	3.6	23.4	10.0	2.5	17.5	16.9	2.5
Avail.ppm.	A	B	B	A	B	B	A	B	B
Copper	.35	.28	.22	.20	.20	.20	.18	.15	.17
Avail.ppm.									
Zinc	.42	.30	.37	.15	.07	.08	.12	.22	.17
Avail. ppm.									
Sodium	54.7	34.8	43.2	19.3	20.7	19.8	11.8	11.8	11.0
Avail. ppm.									
Sulphur	6.4	8.3	8.7	5.2	7.9	3.4	14.6	23.2	12.2
Avail.ppm.							AB	A	B
Aluminium	6.6	14.2	12.2	-	-	-	4.1	5.5	6.7
Avail ppm.	A	B	B						

* F = open-forest. T = Transition. Sh = *Acacia* shrubland.

0-15cm

30-45cm

60-75cm

105-120cm

MOISTURE (%)

20

15

10

5

Au D Ap Au

Au D Ap Au

Au D Ap Au

Au D Ap Au
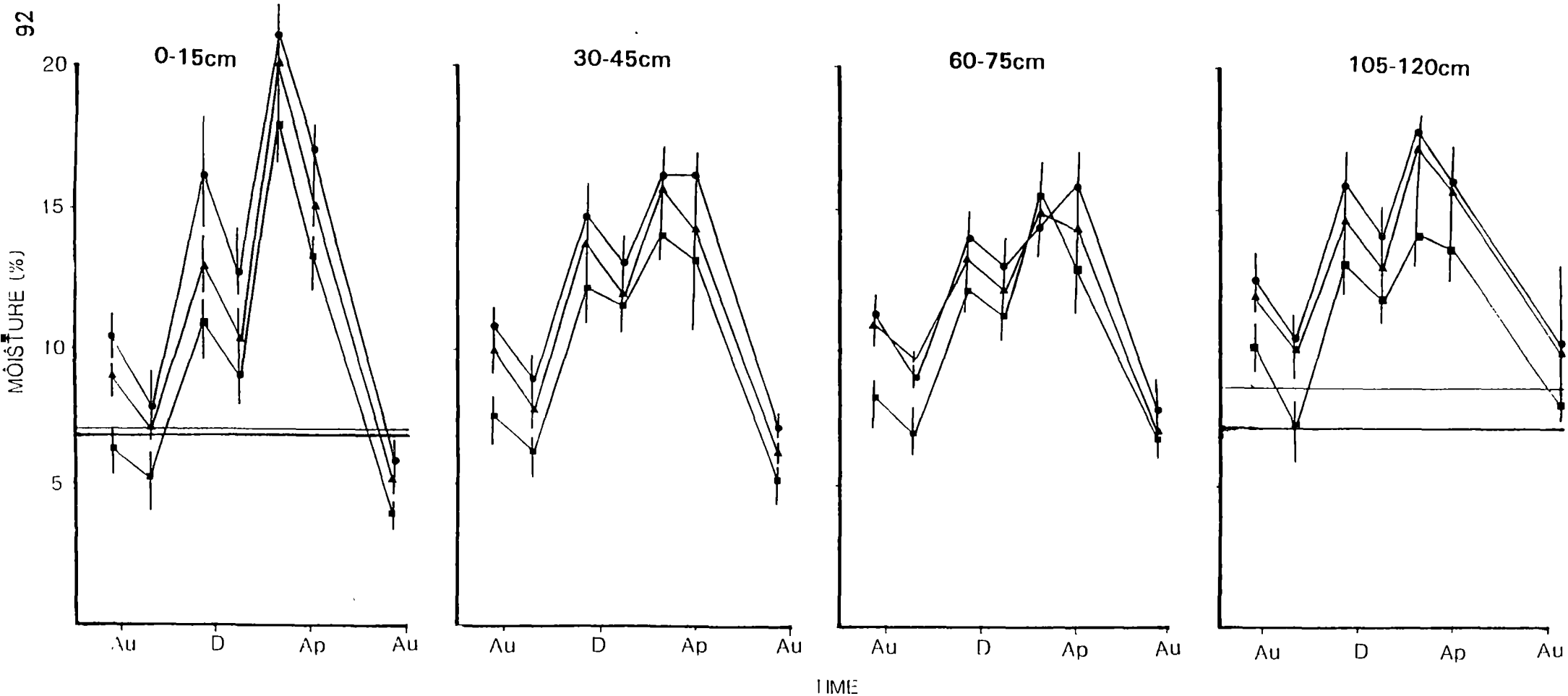
TIME

Figure 4.1.1   Soil moisture (%) by depth over time, across boundary transects. Vertical lines indicate 95% confidence limits.
- *E. tetrodonta* forest to *Acacia* shrubland (transects 4, 5 and 6, n = 12)

FOREST

TRANSITION

SHRUBLAND

-/3 BARS

-15 BARS

93
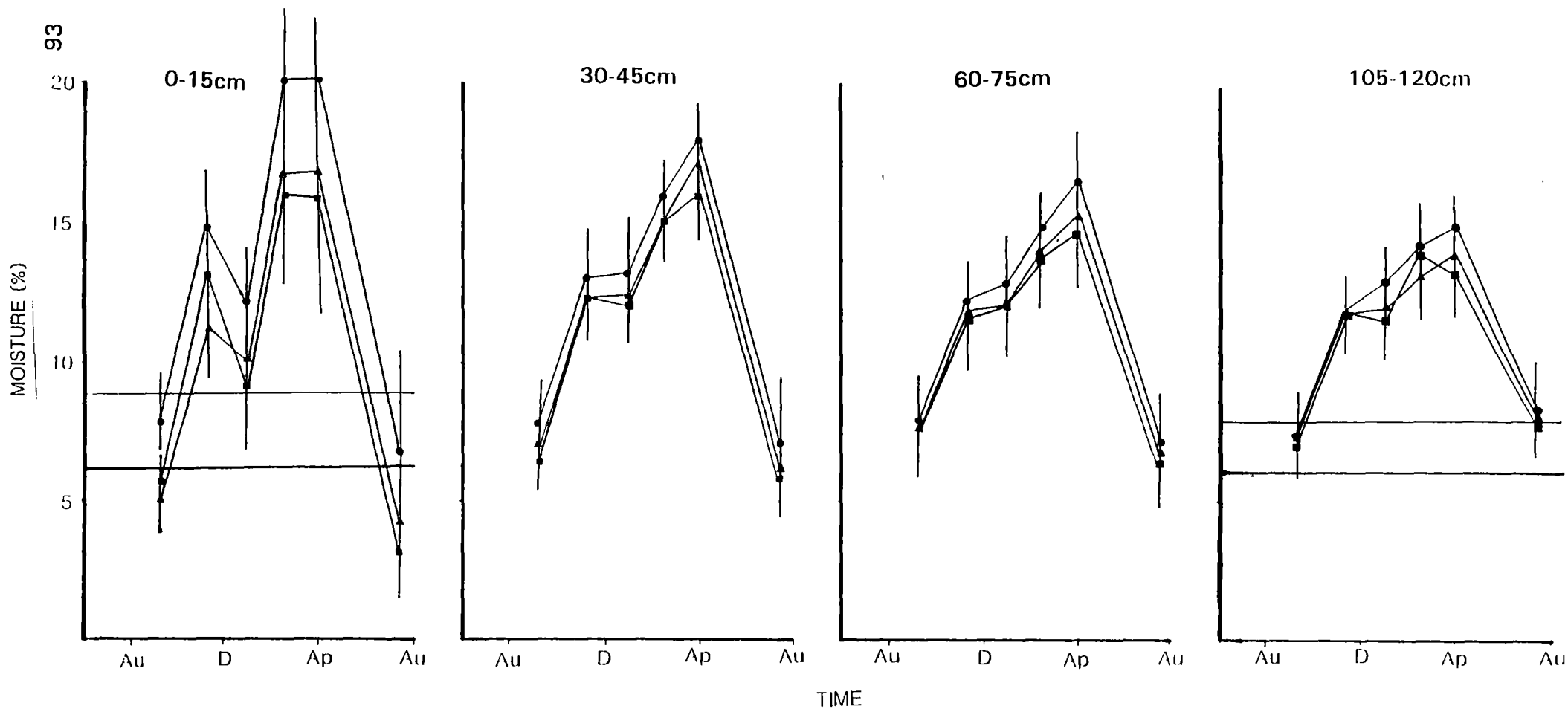
Figure 4.1.2 Soil moisture (%) by depth over time, across boundary transects. Vertical lines indicate 95% confidence limits.
- *E. miniata* forest to *Acacia* shrubland. (transects 1, 2 and 3, n=3)
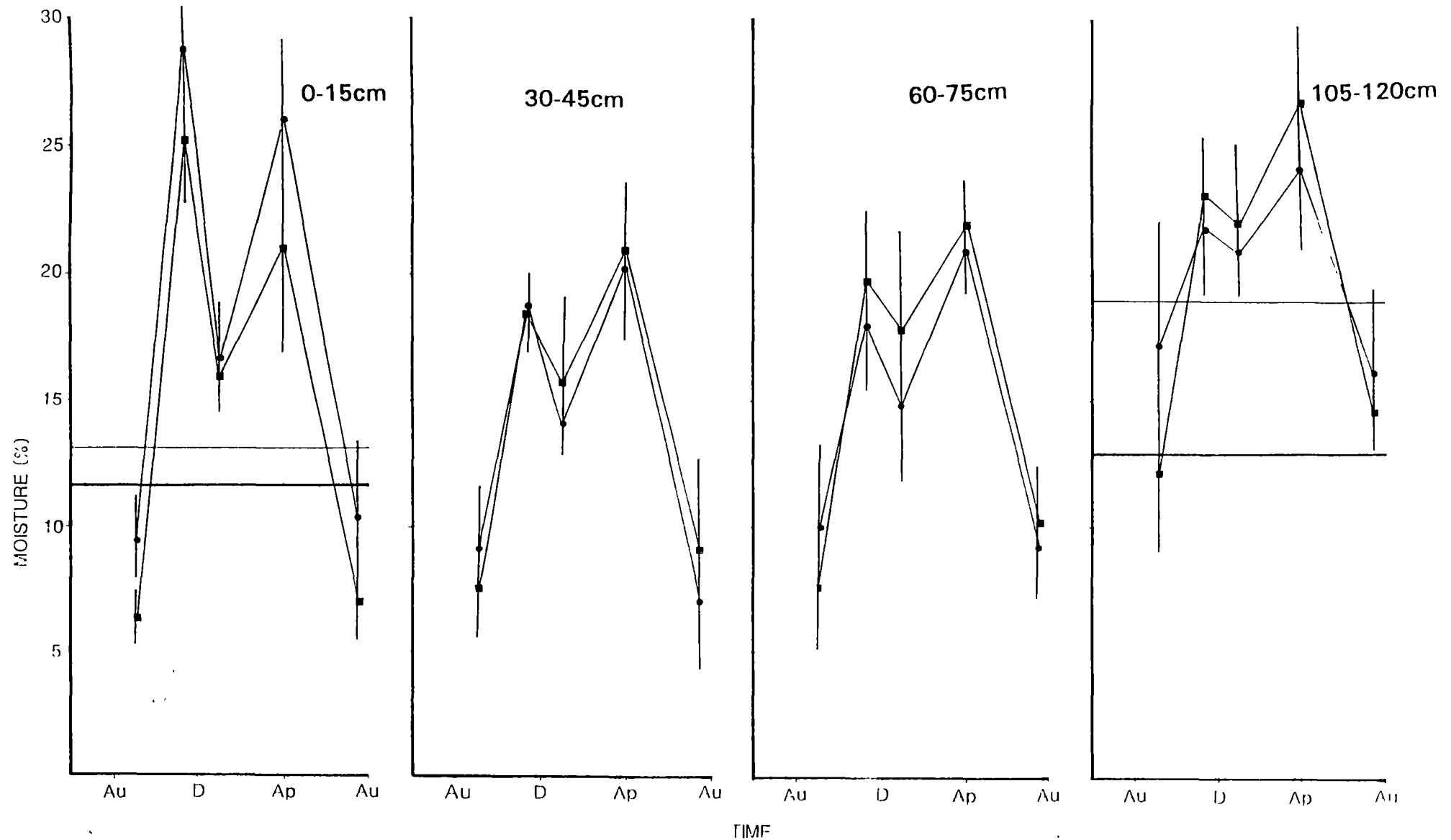
Figure 4.1.3 Soil moisture (%) by depth over time, across boundary transects. Vertical lines indicate 95% confidence limits.
- *E. miniata* forest to *Grevillea* woodland. (transect 7, n = 2)

The general pattern in soil moisture flux is essentially the same for the *E. miniata* forest to shrubland group of transects (1, 2 and 3) and the *E. tetrodonta* forest to shrubland group (4, 5 and 6). There is a distinct gradation in moisture content between communities throughout the year. The forest is generally wetter than the transition, which is generally wetter than the *Acacia* shrubland. Statistical comparison between communities throughout the year at the *E. tetrodonta* forest to plains transects 4-6 (where n = 10), shows that the differences are significant throughout much of the year (Figure 4.1.2). Differences between communities are more pronounced in the upper soil layers and less pronounced in the wet season.

The *E. miniata* forest - *Grevillea* woodland boundary (transect 7) shows a different pattern in soil-moisture flux to the other transects. Here, the plains site is drier on the surface all year round, but wetter in lower layers, particularly during the wet season.

The percent moisture content and equivalent matric potentials across different boundary types is presented in Appendix 3. Wells & van-Cuylenburg (1978) have presented similar data from the Yapilika area, which show similar moisture values for the -15 bar but not at the -1/3 bar level. Unlike the figures presented here these authors show that the moisture content at -1/3 bars is almost double that at -15 bar. It was not possible to re-analysis the soils in this study but a comparison with figures given by Stace *et. al.* (1968) suggest that the -1/3 bar figures given by Wells & van-Cuylenburg (1978) are more accurate and those presented in Appendix 3 are under-estimates. However, only the accuracy of the -15 bar figures are critical to the following discussion.

The percent moisture content and equivalent matric potential (derived from the interpolation of the data presented in Appendix 3) for different boundary types over the driest period of the study, July 1987, are presented in Table 4.4. The trends in matric potential parallel the changes in texture: the loamier forest soils have greater available moisture and a higher moisture percent at a given potential than the

plains. The more clayey soils from transect 7 show higher contents for a given potential than the other transects.

Figure 4.1 show the -15 bar matric potential superimposed on the graph of percent moisture changes. Minimum surface matric potential on the plains are at or below -15 bars for about 1.8 to 3.5 months. At 1.2 metres depth minimum matric potential on the plains is below -15 bars for 0 to 1 month. Matric potential is often higher on the forest site compared to the plains, particularly in the sub-soil, reflecting the greater clay and water content on these sites relative to the plains.

There is a clear difference in soil moisture patterns down the profile between the forest and the plains. This is shown clearly in the moisture profile diagrams for August and November from transects 4-5 (Figure 4.2). The surface soil (0-15 cm) and deeper (105-120 cm) layers of the forest is often substantially wetter than the 45-60 and 75-90 cm layers, thus giving a 'C' shaped profile. By contrast the plains soils generally show a steady increase in moisture content with depth. During the wet season the transition zone and *Acacia* shrubland sites may also exhibit a 'C' profile shape, although not to the same degree as the forest (see November Figure 4.2).

4.3.5 Water table

Figure 4.3 shows the change in water table depths with time across the boundaries. The *E. miniata* forest to plains boundaries (transects 1, 2 and 3) at Mindaloo show variable water table characteristics. No water table was recorded above the bedrock (at 4.0 metres) at transect 1. On transect 3, no water table above 7 metres was recorded at the forest or transition plots and while a minimum water table depth of 6.5 metres was recorded in the shrubland. Transect 2 recorded water tables of up to 1.8 metres below the surface in the forest and 2.2 metres on the plains.
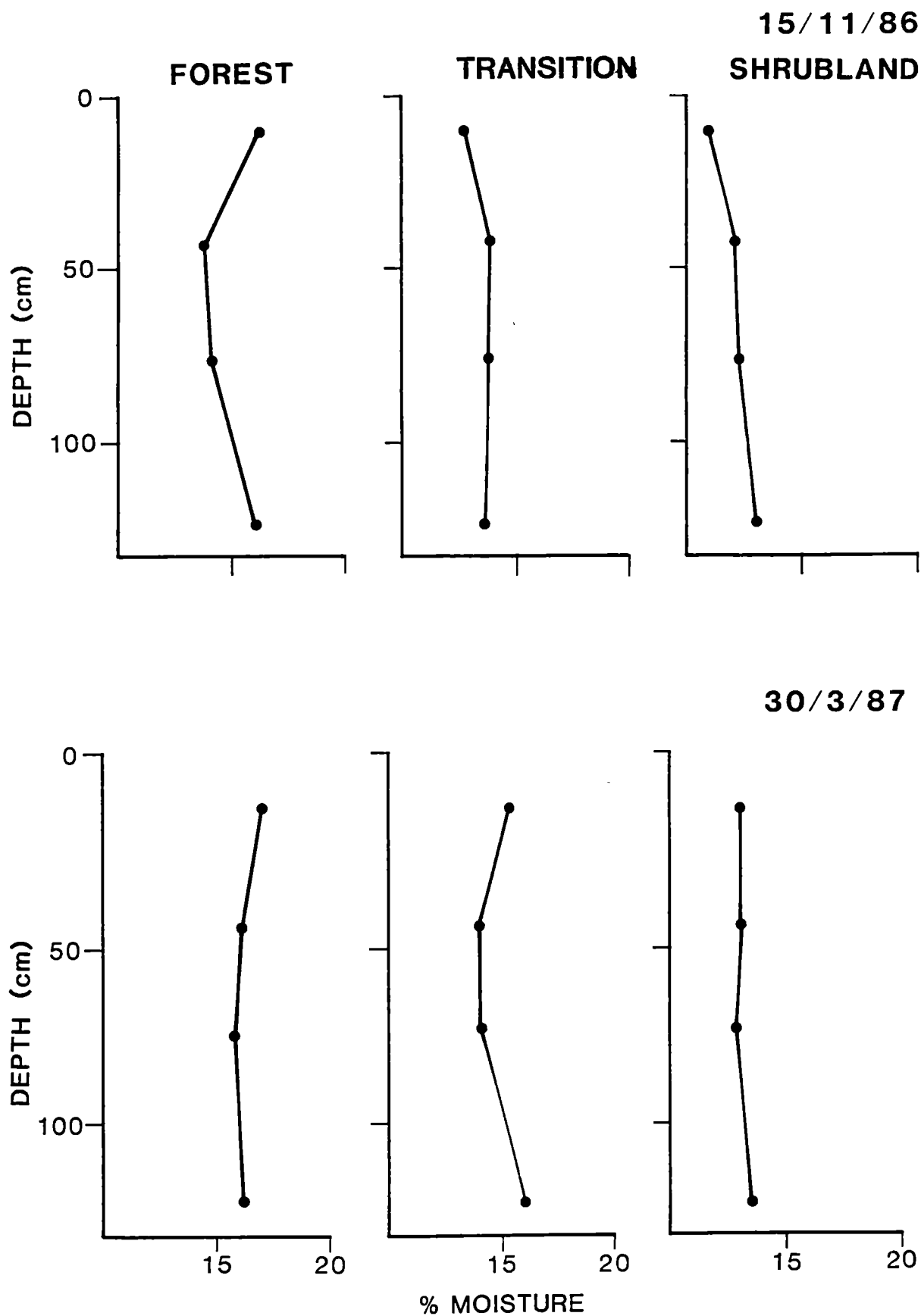
Figure 4.2   Soil moisture profiles for August and November at forest and *Acacia* shrubland sites (transects 4, 5 and 6, n = 12).

Table 4.4 Soil moisture content in July 1987 (%, from Figure 4.1) versus soil matric potential (bar), calculated from interpolation of data in Appendix 3), across different boundary types.

Depth (cm)	%	0-15 U	%	105-120 U
E. miniata open-forest to **Acacia open-shrubland**				
Forest	6.5	<-15	8.1	-13.0
Transition	4.2	<-15	7.4	-1.6
Open-shrubland	3.5	<-15	8.3	-0.5
E. tetrodonta open-forest to **Acacia open-shrubland**				
Forest	6.0	-15	10.3	>0.3
Transition	5.3	<-15	10.0	>0.3
Open-shrubland	4.0	<-15	8.1	-3.0
E. miniata open-forest to **G. pteridifolia woodland**				
Forest	10.3	-7.5	16.1	-8.0
Woodland	6.7	<-15	14.6	>0.3

The *E. tetrodonta* forest shrubland boundaries (transects 4, 5 and 6) showed more uniform water table characteristics. Changes in water table depth mirrored the rainfall, with an abrupt rise in water table in January to a peak in February, followed by a more gradual, although still rapid, decline. The minimum water table depth recorded for these transects was 1.8-2.0 metres in the forest, 1.8-2.0 metres in the transition and 1-1.2 metres in the shrubland. There was always a gradual increase in depth, paralleling topographic position, from the plains to the forest.

Figure 4.3 Depth of water table over time, across boundary transects. Vertical lines indicate ranges. Depths below vertical axis indicate water table below bottom of well.

Transect 7 showed a different pattern of water table flux to the other transects. During the wet season the water table was inverted relative to topographic position i.e. the water table was closer to the surface at the up-hill woodland site than at the forest site. This inversion was verified at two sites adjacent to transect 7. The peak height of the water table in the forest on transect 7 was 1.3 m.

Water tables across the shrubland to *Banksia* woodland (bottom of transect 5) were consistently high. Here minimum water depths range from 0.5 metres in the shrubland to 0 in the *Banksia* woodland, where the water was flowing on the surface during the wet season. Water table depth at the *Acacia* shrubland site on the bottom of transect 5 reached 0.5 metres below the surface and was constantly higher than the same community at the top of transect 5.

4.3.6 Soil temperature and evaporation

Figure 4.4 shows the change in temperature across the boundary at transects 4 and 5. Although mean maximum temperatures reached are the same for all communities, the *Acacia* shrubland and the transition have significantly ($p < 0.05$) higher temperatures in the morning compared to the forest. The between community differentiation is greater in the dry season compared to the wet.

Figure 4.5 shows how the percent moisture content of soil isolated in plastic containers varies across the boundary. The forest soils are significantly wetter than the plains soils and the transition soils are wetter than the shrubland soils although not to a significant extent. The difference between communities is more pronounced in the dry season than the wet season.
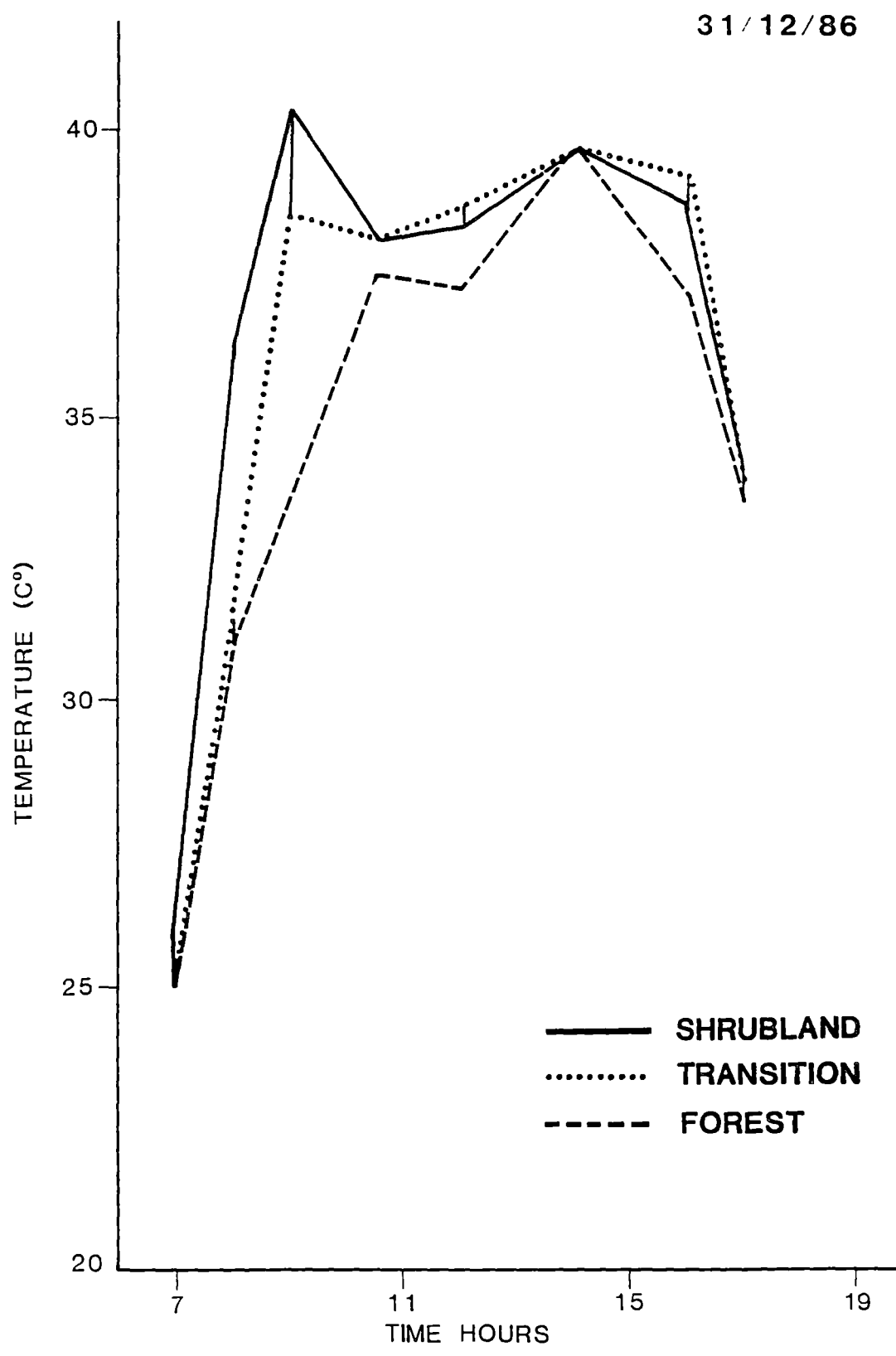
31/12/86

Figure 4.4.1 Surface temperature by community, across boundary transects 4 and 5 (n = 5). Vertical lines join communities not significantly different at the p < 0.05 level, as determined by Tukeys range test - 31/12/86
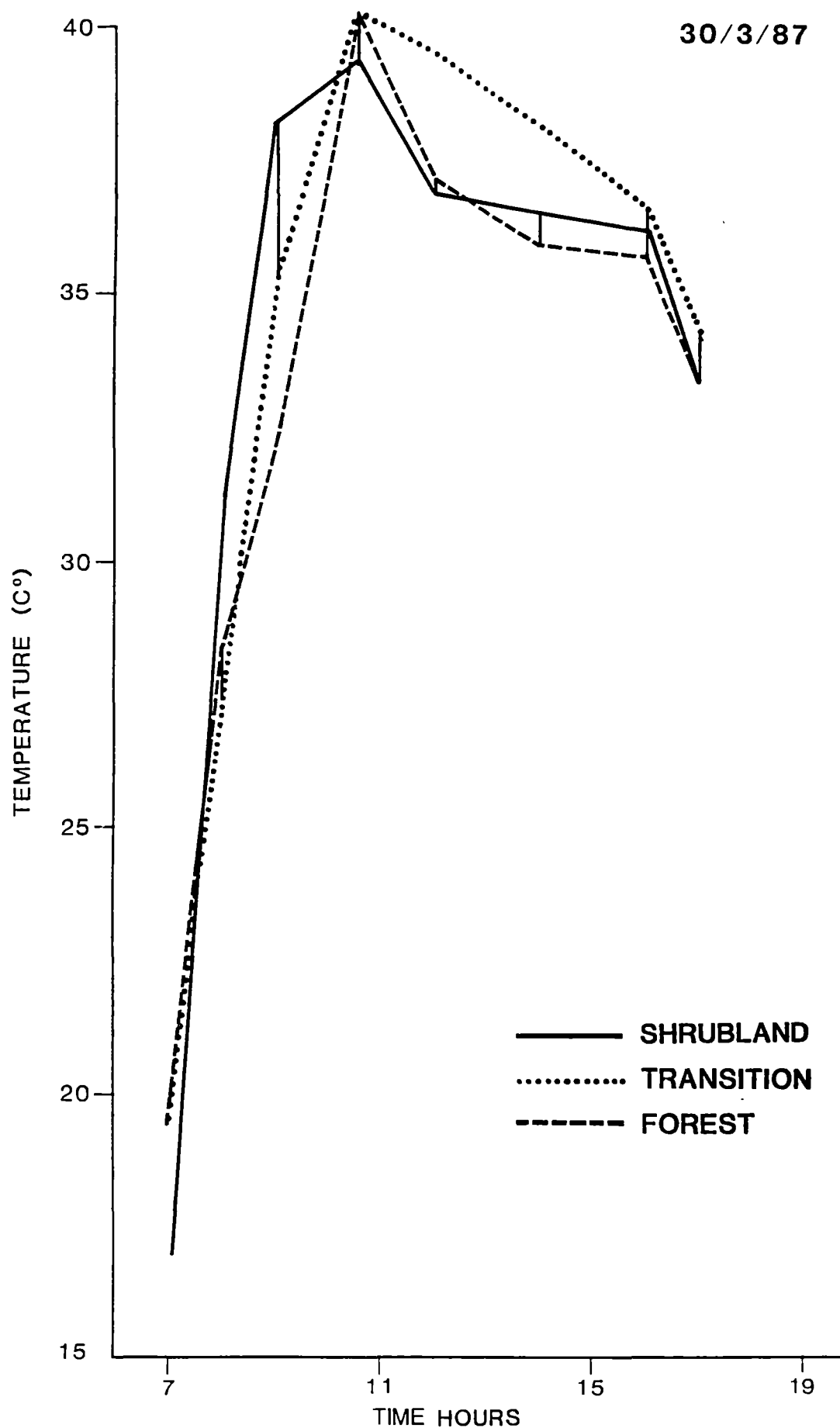
30/3/87

Figure 4.4.2   Surface temperature by community, across boundary transects 4 and 5 (n = 5).   Vertical lines join communities not significantly different at the p < 0.05 level, as determined by Tukeys range test - 30/3/87
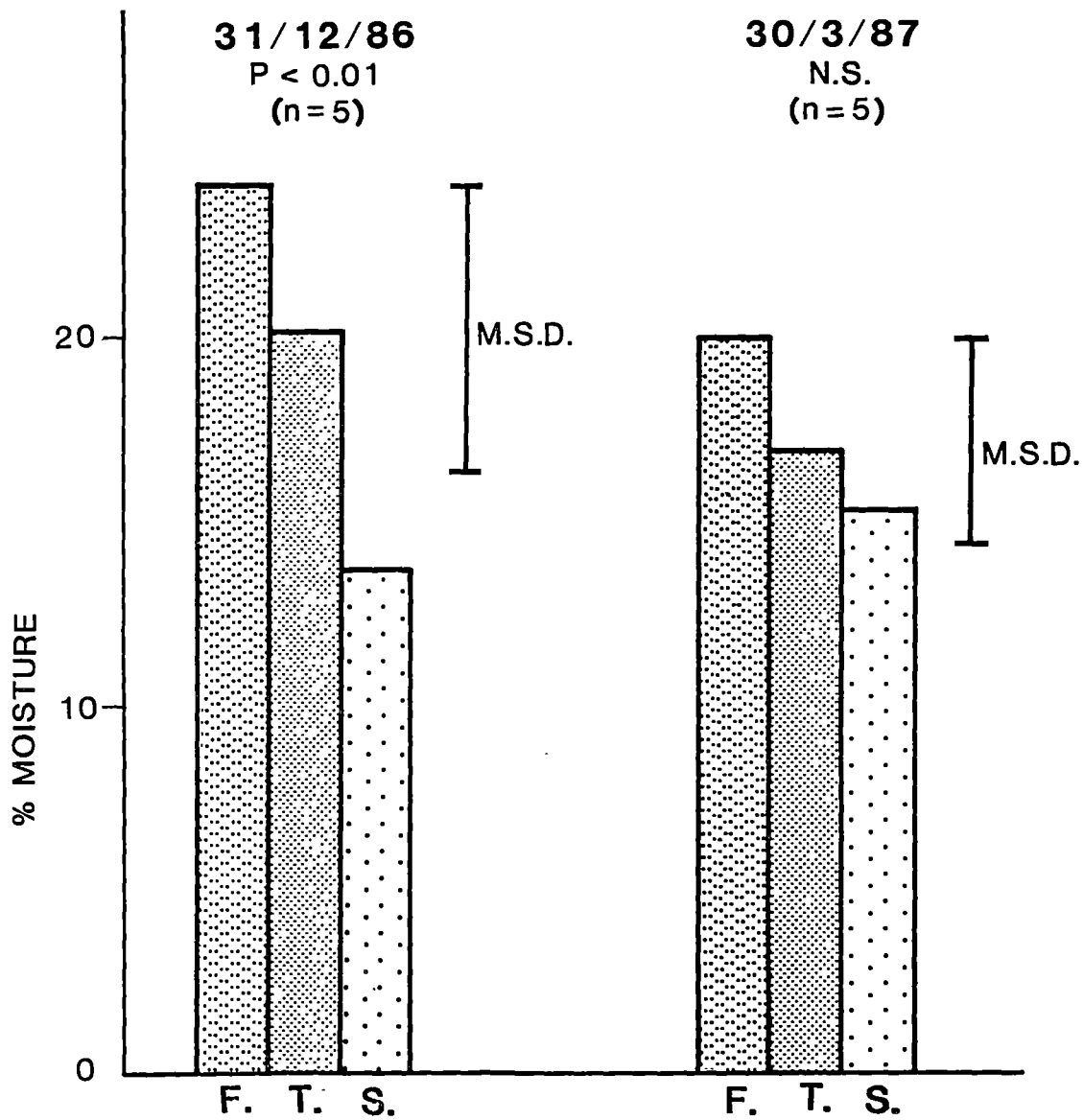
Figure 4.5   Moisture content of surface soil isolated in plastic containers on two days, across boundary transects 4 and 5 (n = 5).

4.4 Discussion

In the following discussion, the environmental factors are assessed in comparison to other soils supporting similar vegetation types in tropical regions of the world to determine if they could be limiting tree growth and in relation to the vegetation patterning described in Chapter 3.

4.4.1 Soil particle size analysis

The data presented in this study show that soils supporting the open-forest generally have significantly lower percent sand contents than adjacent treeless areas. Table 4.5 shows the % sand contents of a range of other red earth soils supporting eucalypt forests and woodlands in northern Australia. It is apparent that the soils from the Melville Island plains and adjacent open-forests have relatively high sand contents

Table 4.5 Sand content (fine and coarse sand as % of fine earth faction) of soils supporting eucalypt open-forests in northern Australia.

Area	Sand %	Reference	Identifier
NT	75	Calder & Day 1982	Emu
Daly Rv	65		Tindale
	92		Blain
NT	81	Day & van-Cuylenberg 1988	loamy
	89		sandy
	93		lateritic
Nth Qld	66	Isbell & Smith 1976	t96
	88		t128
	92		t178
	86		t150
	94		t120
	68	Coventry & Williams (1984)	H
	88	Isbell et al. (1976)	red earth

compared to other loamy red earths which generally support eucalypt open-forest and similar sand contents to sandy red earths which generally support eucalypt woodlands.

Other red soils with high (>85%) sand contents on Cape York Peninsula support heath vegetation (Pedley & Isbell 1971). Soils with high sand contents, but varying drainage, in the Northern Territory are associated with a wide range of vegetation types. For example a study of rainforest, woodland and heath vegetation on the sandstone escarpment near Jim Jim Falls, lists associated soils with surface sand contents between 84 and 90% (Bowman *et al.* 1990). However most comparisons are confounded by other factors such as gravel content and soil depth. Any causal links between soil texture and vegetation are likely to be indirect through other related properties such as soil moisture or fertility.

4.4.2 Water tables

Water table depths have been invoked as a critical determinant of vegetation patterns in northern Australia (Specht *et al.* 1976, Bowman 1986). However, there are few data directly relating water tables to vegetation from which to infer critical heights and periods which limit tree growth. Braithwaite *et al.* (1984) reported modal ground-water heights in the Alligator Rivers region of 16-20 metres with a range of 4.4 to 147 metre, but it is not clear what season these measurements were taken and which plant communities they supported (which ranged from eucalypt and *Melaleuca* forests to wet monsoon forests). Red earth soils in the Torrens Creek area of Queensland are saturated on average once in 3 years to a minimum depth of between 3.8 and 1.4 metres, for less than 5 weeks (Coventry & Williams 1984; Figure 4, profile F and Figure 5). Thus, in addition to being smaller than the adjacent open-forests, the minimum depths to the water table recorded on the Melville Island plains, appear to be less than other red soils supporting eucalypt forests and

woodlands in northern Australia.

However, current water table depths alone cannot account for the position of the forest plains boundaries at Yapilika. The forests were found on sites with minimum water table depths of 1 - 1.5 metres, while Fensham (1990) found forests on Melville Island growing on rocky sites where water tables rose to within 20 cm of the surface. Furthermore, minimum wet season water table depths in the forests adjacent to the plains were not consistent and varied between 2 to 7 metres.

The depth to red/brown mottles in red, yellow and grey earths from northern Queensland coincided with the minimum water table depth observed over a 9 year period (Coventry & Williams 1984). In Katherine yellow mottles in red soils were also found to be related to minimum depth of soil saturation for at least 18 days in any one year (Lucas & Hester 1988). In this study yellow mottles were found in the red soils at depths of 1.5 metres in the forest decreasing to < 1 metres on the plains, while minimum water table depths varied from 1.8 metres to >4 or 7 m. If the mottle/water table depth relationships can be applied to the Melville soils, the yellow mottling may indicate that minimum water table depths have been as low as one metre, even at sites where current minimum water tables are 4-7 metres below the surface (transect 1 & 3).

The yellow mottles which occurred at 1-2 metres depth are not characteristic of red earth soils in general, although similar features have been reported from some 'higher rainfall' soils on Cape York Peninsula (Isbell & Smith 1976). In north Queensland (Coventry & Williams 1984, annual rainfall 585 mm) and Katherine (Lucas & Hester 1988, annual rainfall 864 mm), red-brown/yellow mottles in red earths were found at depths below 3 metres.

Lucas & Hester (1988) and Coventry & Williams (1984) showed that

water table levels varied greatly in response to variations in rainfall. The annual rainfall recorded at Pularumpi does show variation, although not to the same extent as the (more arid) Katherine and North Queensland regions. It is difficult to determine how water table depth would change with variations in rainfall, on Melville Island. The sandy soils at Yapilika drain rapidly, as indicated by the rapid increase and decrease in water table at the beginning and end of the wet season. This suggests that water table height may only vary slightly with a change in rainfall and any increase would drain away rapidly at the end of the wet season. This is supported by the observation that water tables were at a similar height in March 1988 to peak 1987 levels even though rainfall was significantly higher in 1988 compared to 1987 (Table 1.1). It is not known what effect an annual rainfall of 2791 mm (which occurred in the 1974-75 wet season) would have on water tables, although the c 2200 mm which fell in the 1990/91 wet season appeared to have only short term effects on the water tables of the plains and no noticable effect on the vegetation (Greg Sutton pers. comm.).

It may be that hot moist conditions, combined with low oxygen levels, could create reducing conditions causing mottle formation in the absence of complete profile saturation (Ross Coventry & John Williams pers. comm. 1988). Thus, it is difficult to determine whether the yellow mottles on Melville Island are indicating current or past water regimes or are relicts from soil forming processes.

It has been suggested that deep rooted evergreen trees in the wet dry tropics continue to grow throughout the year where they have access to the water table in the dry season (Medina 1982, Bowman 1986). On Cape York Peninsula, Specht *et al.* (1976) considered that *E. tetrodonta* roots probably penetrated to depths of 10 metres and were thus able to exploit deep moisture reserves. In the Mindaloo area root penetration would be limited to 4 metres by the compacted laterite layer. On the

remainder of the plains there appears to be little impediment to roots penetrating even deeper. Thus the water tables in the Yapilika area at least, might aid rather than impede tree growth by providing a source of moisture through the early and mid dry season.

4.4.3 Soil moisture

On transect 7 the water table appeared to directly influence moisture content measurements in the upper 1.2 metres of the soil profile at the peak of the wet season. However, soil moisture contents increased with increasing sand content and forest soils had higher moisture contents and moisture potential values than the adjacent plains.

The between community moisture differential was exaggerated in the surface soils which is at least partly due to the greater surface temperature and evaporation which the plains experience relative to the forest. This probably results from the shade of the tree canopy and may also be accompanied by increased litter accumulation (Kelly & Walker 1976) as was found in *A. aneura* woodlands in central Australia (Slatyer 1961).

The soil moisture retention properties of the Melville soils are typical of other studies on red earths (Calder & Day 1982). These soils show large decreases in percent moisture content from the saturated state with small decreases in matric potential followed by small decreases in moisture content with matric potential as the soils dry out. This pattern causes the rapid drainage and moisture content decrease that is shown by the Melville Island soils at the end of the wet season.

There are few data on temporal changes in moisture flux in northern Australia to allow any determination of critical moisture limits for tree growth on the plains. Russell-Smith (1986) studied forest/monsoon

thicket boundaries where gravimetric soil water contents from a eucalypt forest were in the order of 1-3 % corresponding to soil matric potential of -500 to -100 bars. However, the soils in this study were rocky and thus likely to have very different moisture properties to the Melville Island soils.

Soil matric potential is a measure of the suction required to remove water from the soil matrix. A soil matric potential of -15 bars is often used as measure of the permanent wilting point of a soil (Sarmiento 1984). Water is not considered to be a primary limitation to tree growth in Central America where sub surface (below one metre) soil matric potential does not get below -20 bars (Medina 1982, Goldstein & Sarmiento 1987). Although an arbitrary value, unlikely to be relevant to the permanent wilting point of native vegetation in northern Australia, it is useful as a comparative benchmark. By the end of the dry season the surface layers of the sandy Melville soils have water potential lower than wilting point, but the subsoil (90 cm depth) soil matric potential was above -15 bars or only fell below that figure for less than a month. This indicates that at depth of greater than 90 cm, moisture levels are unlikely to be limiting tree growth.

In South America, different savanna types can be recognised by variations in the degree of waterlogging and drought present at a site (Sarmiento 1984). The Melville Island *Acacia* shrubland communities correspond to Sarmiento's (1984) 'semi-seasonal' savanna. Soil moisture is not considered a major limiting factor in these South American communities which are usually open-woodlands. Other parts of the plains with higher wet season water tables (*Banksia* woodland, *Lophostemon* scrub and parts of the *Grevillea* woodland) correspond to 'hyper-seasonal' savanna categories where drainage is considered a limiting factor.

Thus although the forest soils had significantly greater soil % moisture contents and corresponding soil moisture potential than the plains, it appears that the subsoil on the plains may possess adequate moisture for tree growth throughout the year.

4.4.4 Soil nutrients

The results of the chemical analysis of the soil from across the boundary show similar patterns to studies on Cape York, where soils supporting heath had significantly lower levels of calcium, magnesium and a corresponding higher level of aluminium, than adjacent forest soils (Isbell *et al.* 1976). These authors also found that exchangeable calcium decreased with depth, which mirrors the situation at Melville Island. In pot trials using *Stylosanthes*, the Cape York red earths showed more marked deficiencies of calcium and copper on soils supporting heath than those supporting woodland (Isbell *et al.* 1976).

Chemical analysis of other red earths from northern Australia are listed in Table 4.6 (Note: figures for the Melville Island plains in this table are from bulked samples analysed by a slightly different method to those presented in Table 4.3). In general red earth soils are low in most nutrients, but have extremely low levels of calcium, magnesium, potassium, and sodium (Mott *et al.* 1985). The Melville soils appear to be particularly deficient in calcium, have higher levels of aluminium and low Ph values compared to other red earths from northern Australia. Comparable soils in Brazil, which are acidic and have low CEC and high aluminium levels, support a range of savanna vegetation known as 'Cerrado' (Furley & Ratter 1988).

The relatively high aluminium and low pH and calcium levels of the Melville soils may be contributing to the vegetation patterning of the area. High aluminium levels have been implicated as a negative influence on

Table 4.6 Chemical analysis of selected red earths from northern Australia.

Ph	Org C %	Org N %	Avl P* (ppm)	CEC (meq)	Exch Ca meq%/ 100gm	Reference
5.6	1.00	.078	<5	0.68	1.25	Melville Island, *Acacia* shrubland
6.1	1.01	.08	4.5	8.7	3.09	Mott *et al.* (1985)
6.4	1.7	.09	9.2	6.0	1.47	Day (1977) - Emu
6.5	0.9	.04	4.2	3.0	1.39	- Blain
6.2	1.3	0.0	65*	5.4	1.5	Isbell & Smith 1976
6.1	1.4	.06	4.9	8.4	3.5	Day & van-Cuylenberg (1980) - loamy
5.9	1.6	.07	2.3	9.2	3.1	- sandy
5.5	1.8	.1	4.6	9.4	2.9	- lateritic

* P is sulphuric acid extracted if indicated with asterix. Otherwise Bicarbonate extracted.

tree growth in Neotropical savannas (Sarmiento 1984). This element can be detrimental to plant growth by two mechanisms (Sarmiento 1984). There is a direct toxic effect caused by the inhibition of root growth and an indirect effect whereby in a very acid medium aluminium ions can lock up phosphate in a non utilisable form. Low calcium levels can exacerbate the effects of aluminium. However, nothing is known about the tolerance of the major eucalypt species from Melville Island, to the direct or indirect effects of high levels of aluminium or low levels of calcium. These factors are investigated further in Chapter 5 of this thesis.

The reasons for the higher nutrient status of the forest soil are unclear. They could be inherent to the site, the sandy plains soil producing lower amounts of weatherable minerals than the loamier forest soils (Tisdale & Nelson 1975). Alternatively there is evidence that tree canopies may enrich sites by trapping nutrients and enhancing recycling in the surface soil. Stocker (1969) invoked a similar argument for explaining the increased nutrient status of monsoon thickets compared to eucalypt forests on Melville Island. Kellman (1979) and Weltzin & Coughenour (1990) have shown that the surface soil beneath trees in American and African savannas are enriched by various nutrients compared to soils away from trees. The fact that many of the chemical advantages of the forest soil at Yapilika, including carbon, decrease with depth supports the notion of vegetation-induced change.

Seymour (1981) describes a series of studies on vegetation succession on beach dunes in south-east Queensland, which provide an alternative view of the interaction between vegetation and soil nutrient accumulation. Here a change in vegetation from scattered trees and shrubs through shrubland and low woodland to tall eucalypt open-forests, is associated with a progressive soil nutrient accumulation and profile development. However, in this system it appears that the older, deeper soils lose nutrients, through leaching, at a faster rate than they

accumulate. The oldest soils therefore support woodland or heathland.

Thus, a causal mechanism for the low nutrient status of the plains soils could be the large water surplus, which occurs during the rainy season, promoting the downward transport of ions and clay through the deep sandy soil profiles, resulting in an impoverishment of the soil nutrient content (cf Goldstein & Sarmiento 1987). This process would be reinforced by vegetation induced accumulation in the forest. The low levels of nutrients such as calcium, magnesium and associated high levels of aluminium could be a result of these processes.

4.4.5 Spatial patterning of the edaphic changes

The changes in environmental parameters measured occurred gradually over the forest plains boundary compared to the abrupt changes that occurred over the plains to *Banksia* woodland boundary. The soil moisture, texture and morphological values of the transition zone were always intermediate between the forest and the shrubland. It might be argued that the placement of 3 sites across the boundary does not allow an accurate assessment of the spatial patterning of factors. However, the extra sites on transect 5 illustrate that the trends in soil morphology (depth and thickness of gravel layer, depth of yellow mottles) continue in a gradual manner into the forest and across the plains. The fact that the soils of the plains formed from deposition of sediments on the slight topographic gradient (Hughs 1976) supports the notion that the changes in edaphic factors across the boundary occur gradually rather than abruptly.

4.4.6 Vegetation environmental relationships

The independence of structure and floristic patterns noted in Chapter 2 and 3 could be explained by differential resource partitioning between the

strata. Thus the transition in understorey across the forest plains boundary could be caused by a gradual change in surface factors while the overstorey is responding to more abrupt changes at depth. The decrease in soil moisture with depth in the forest also gives indirect evidence of differential utilisation of resources with depth and could be due to tree roots in the forest extracting more sub-surface moisture than the shrubs/grasses on the plains.

In the introduction to this thesis (Chapter 1) it was pointed out that the resource partitioning of woody and herbaceous growth is a central focus of many savanna studies (Sarmiento 1984). In a study on a dry (600 mm/annum rainfall) African savanna, Knoop & Walker (1985) have suggested that the ratio of woody:grassy vegetation on a site can be predicted by the ratio of surface to sub-surface soil moisture. These authors found that sites with low top:sub soil moisture ratio were associated with a greater abundance of woody vegetation compared to sites with higher ratios. The ratio of surface:sub soil (0-15:105-120 cm) moisture was about 1:3 on the plains and 1:1 in the forest (Figure 4.2). This suggests that the ratio hypothesis does not hold or that the plants are responding to factors other than moisture.

The *E. miniata* to *Grevillea* woodland boundary (transect 7) showed similar structural characteristics but a different floristic patterning to the other transects (Chapter 3). This implies that there may be corresponding differences in environmental factors affecting floristic composition across this boundary. The higher water table and corresponding soil moisture content on this transect may account for the different pattern. This is supported by the fact that floristic variation across the boundary on this transect tended across the first axis of the survey ordination (Chapter 2) which was interpreted as a water table gradient. Furthermore, the floristic survey showed that the *Grevillea* woodland community (group 4) had significantly higher water tables, than the forest (groups 1 and 3) and *Acacia* shrubland (group 2) communities.

Sharp structural boundaries may coincide with sharp or gradual floristic boundaries (Wardle 1981, Hobbs 1986). Sharp changes in species composition have been related to sharp changes in soil nutrients and texture (Werger *et al.* 1983) and gradual changes have been related to gradual changes in edaphic factors (Werger *et al.* 1983, Hobbs 1986). Similarly gradual structural changes have been associated with gradual changes in environmental gradients (Cole 1982, Bowman 1986), whereas abrupt structural changes often coincide with steep environmental gradients (Hobbs 1986). Thus, the lack of correspondence of the sharp structural boundary with a sharp floristic boundary on Melville Island is not unusual but, because it is not accompanied by an equally abrupt change in environmental factors, cannot be explained by edaphic factors alone.

Van der Maarel (1976) has hypothesised that abrupt boundaries could be the result of disturbance agencies such as herbivores or humans. Canny (1981) puts forward a similar hypothesis in the terms that a sharp boundary is associated with 'boundaries in the flow of external energy' (page 18). More gradual transitions may result when two different environments blend together (van der Maarel 1976) in the absence of changes in external energy (Canny 1981). Thus sharp structural boundaries have been associated with ecological disequilibrium (Wardle 1981) or with the differential effects of disturbance factors such as fire (Clayton 1958, Blasco 1983, Gillison 1983) or grazing (Hobbs 1986).

Thus while the lack of trees on the plains might be due to an edaphic factor such as nutrients, a disturbance factors such as fire may be responsible for the sharpness of the structural boundary. Alternatively an infrequent lethal event (e.g. extreme waterlogging) may have created the boundary which is maintained by soil characteristics and fire. These arguments are discussed further in Chapter 6.

CHAPTER 5 <u>THE EFFECTS OF ENVIRONMENTAL FACTORS ON THE</u>
<u>GROWTH OF SEEDLINGS AND ROOT SUCKERS</u>

5.1 Introduction

The previous chapters investigated the vegetation and associated environmental patterns on the plains and adjacent forests which enabled a discussion of the environmental factors which may or may not be limiting tree growth on the plains. This chapter seeks to measure the growth response of plants to variations in some of those environmental factors previously discussed.

Practical constraints limit the experimental manipulations to seedlings and root suckers rather than fully mature individuals. Thus the results cannot be readily extrapolated to fully grown trees, although they are directly relevant to the establishment and growth of juveniles and provide insights into the regeneration processes operating on or adjacent to the plains and to Top End eucalypt forests in general.

The discussion in Chapter 4 hypothesised that the sharp forest boundary may be the result of an interaction between fire and differential growth rates of eucalypts across the boundary. Nutrients were implicated as a possible limiting factor. This hypothesis is investigated here by measuring the height growth of *E. miniata* and *E. tetrodonta* seedlings in response to changes in site and fertiliser applications. Pot trials designed to help interpret the growth of seedlings in the field, by measuring the growth response of plants to changes in soil type and moisture regime (flooding and droughting), were also carried out. Data are also presented on the effects of fire on seedling growth and survival.

The occurrence of *E. tetrodonta* root sucker and eucalypt lignotuberous growth on and adjacent to the plains has been referred to several times in

this thesis. These lifeforms are common throughout the Top End (Lacey & Whelan 1976) and may provide a potential source of trees (Wilson & Bowman 1987). By contrast, eucalypt germinants appear to be rare in the Yapilika area and throughout Top End forests (B. Wilson pers. ob.) In this chapter the potential of *E. tetrodonta* root suckers to respond to fire protection and fertiliser addition is tested. Field dispersal and germination of eucalypt seed is also investigated.

5.2 Methods

5.2.1 Growth of *E. tetrodonta* and *E. miniata* seedlings across the forest plains boundary

E. miniata and *E. tetrodonta* seed were collected from Melville Island in October 1986. The seeds were germinated immediately and pricked out into tubes containing sieved soil which had been collected from a forest site at Yapilika. The seedlings were planted out in late January 1987 on the forest, transition and shrubland sites adjacent to transect 5 (Chapter 3). The forest plantings were located in an existing canopy gap, about 50 metres in diameter. All sites were cleared of woody growth greater than one metre high, before planting. At each site there were four treatments:

1. no weeding or fertiliser (control)
2. vegetation removal (referred to as the weeded treatment).
3. weeded + complete fertiliser mix (referred to as the complete treatment).
4. weeded + dolomite fertiliser. (referred to as the dolomite treatment).

Table 5.1 presents the fertiliser constituents and rates of application used in the trial, which were determined to approximate those used in pine

plantation operations at Yapilika (Merv Haines pers. comm.). In addition to direct inputs of Calcium and Magnesium, the dolomite application also reduces the activity and solubility of aluminium and manganese (Tisdale & Nelson 1975).

Fertiliser was applied once, one month after planting. Weeding of fertiliser treatments was necessary as it was considered likely that fertilising unweeded plots would stimulate the growth of established grasses and shrubs at the expense of the target plant, thus confounding the fertiliser effects. Weeding was carried out by killing all herbaceous and woody ground cover with 'Roundup' contact herbicide (which neutralises on contact with soil) before planting and, hand weeding regrowth after planting.

Table 5.1 Amount and composition of fertilisers used in field trials (percentage figures refer to elements in italics)

Dolomite: 289 kg/ha (700 gms/25 m.sq.)

Calcium carbonate 14%
Magnesium carbonate 14%

Complete = NPK + Micronutrients

NPK: 240 kg/ha (600 gms/25 m.sq.)

Nitrogen 13%
Phosphorus 6%
Potassium 16%
Sulphur 1%

Micronutrients: 380 kg/ha (950 gms/25 m.sq.)

Iron sulphate 12%
Manganese sulphate 2.5%
Zinc sulphate 1%
Copper sulphate 0.5%
Sodium borate 0.1%
Sodium molybdate 0.005%
Sulphur (from sulphate) 15%

To reduce the effects of fertiliser on adjacent treatments, application was randomly applied to blocks of seedlings rather than randomly applied to individuals. Each site was divided into eight rectangles measuring six by one half metres. A one metre gap was left between each rectangle to further reduce the effects of fertiliser on adjacent treatments. Each rectangle was planted with 26 *E. miniata* or 26 *E. tetrodonta* seedlings in two rows 0.5 metres apart. In subsequent data analysis these blocks were treated as replicates.

Thus at each site a total of 208 seedlings were planted in a 12 x 6 metres area. Height growth of seedlings was measured at regular intervals over an 18 month period. Dry season surface soil moisture content was periodically measured, using the procedures described in Chapter 3.

5.2.2 Seed dispersal, field germination and early growth of *E. miniata* and *E. tetrodonta* seedlings

Dispersal

The potential seed dispersal distance of the major eucalypt species was estimated using the theoretical relationship developed by Cremer (1977), which relates seed dispersal distance to seed weight, canopy height and wind velocity by the following formulae:

$D = V_w H / V_t$ where

D = Dispersal distance (m)

V_w = Wind speed (m/s)

H = Height of tree (m)

V_t = Terminal velocity of seed (m/s)

The terminal velocity of the seed was estimated by the formula

$V_t = 4.27 \, W0.27$

where W = seed weight (gms). The mean seed weight was determined by weighing 50 *E. tetrodonta* and 50 *E. miniata* seeds.

Field germination and early growth

One hundred *E. miniata* and one hundred *E. tetrodonta* seeds were sown at the forest, transition and shrubland sites in November 1986. At each site half (50 of each species) the seed were sown into a weeded (as per the seedling growth experiment) area and half were sown into an unweeded area. The seed was pressed into the ground and covered with a small amount (<2 mm) of soil. The germination and height growth of resulting seedlings were recorded at periodic intervals.

5.2.3 Leaf water potential of *E. tetrodonta* and *E. miniata* seedlings grown across the forest plains boundary

A pressure bomb was used to measure the amount of force required to extract water from the severed leaves of seedlings planted across the forest plains boundary. Measurements were taken of five *E. miniata* and five *E. tetrodonta* seedlings, 18 months after planting, from the complete and unfertilised weeded treatments at the, forest, transition and shrubland sites, at midday, on two consecutive days.

5.2.4 The effect of fire on the growth of *E. tetrodonta* and *E. miniata* seedlings

All sites used in the seedling trial were protected from fire until April 1988 (14 months after planting) when the unweeded treatments were burnt. The height and number of living seedlings were recorded 0 and 10 months after burning.

5.2.5 The effect of soil type and mycorrhizal inoculation on the growth of seedlings in pots

General

Unless otherwise stated the seedlings used in the pot trials outlined in Sections 5.2.5 and 5.2.6 were established under the following procedures which will be referred to as 'standard nursery conditions'. Soil was collected from 0-20 cm depth at the forests and shrubland site adjacent to transect 5. The soil was pushed through a large diameter (1 cm) sieve, into 15 cm diameter pots. Seed was collected from Yapilika on or adjacent to the plains area. The seedlings were germinated in seedling trays and pricked out into pots about 4 days after germination.

The pots were placed under shade for one month, after which they were left in full sunlight and watered twice a day for fifteen minutes to keep soil moisture content at or near field capacity. Pots were individually identified and regularly shuffled to avoid differential effects of nursery position confounding the treatments. Thus individual pots were treated as replicates.

Soil type

Forty *E. tetrodonta* and forty *E. miniata* seedlings were grown in pots filled with forest or shrubland soil. After 7 months the pots were emptied, the soil carefully removed from the roots and the weight of the shoot and root of individual seedlings were measured.

Mycorrhiza

Fifty *E. tetrodonta* and fifty *E. miniata* seedlings were grown in pots filled with heat sterilised potting mix made from coarse river-bed sand, peat-moss and peanut shell. Twenty-five pots of each species were inoculated with 40 gms of open-forest soil and twenty-five pots with shrubland soil at 0 and 4 months after pricking out. A small amount of

slow release 'Osmocote' fertiliser was added to the pots to negate any differential nutrient effects of the soil used as inoculum. After 7 months the pots were emptied, the soil carefully removed from the roots and the weight of the shoot and root of each seedling was measured.

5.2.6 The effect of flooding and drought on the growth of seedlings in pots

Flooding

Forty *E. tetrodonta*, forty *E. miniata* and forty *Grevillea pteridifolia* germinants were pricked out into pots filled with forest soil. The seedlings were grown under standard nursery conditions for four months at which time twenty pots of each species were placed into tubs filled with water to a level one centimetre below the soil surface. The height growth and survival of the plants were recorded for seven months and compared with control seedlings which were grown in equivalent soils under standard nursery conditions.

Drought

Twenty *E. tetrodonta*, twenty *E. miniata* and twenty *G. pteridifolia* seedlings were grown in pots filled with forest soil. Pots were grown under standard nursery conditions for four months, until January 1987 when they were placed under cover and watering was stopped. Each day after watering was stopped the pots were weighed and the death of plants recorded. After all individuals had died, the soil and plant remains from each pot was oven dried and weighed to allow calculation of soil moisture content throughout the experiment. The experiment was repeated in July 1988, on 7 month old *E. tetrodonta* and *E. miniata* seedlings.

During the second droughting experiment extra seedlings were periodically measured for pre-dawn xylem pressure using a sap pressure

bomb. This enabled the determination of leaf moisture stress levels in relation to soil moisture and plant death.

5.2.7. Variation in leaf transpiration rates between *E. miniata*, *E. tetrodonta* and *Grevillea pteridifolia*.

Leaf transpiration testing was carried out following the methods of Bannister (1964) and Gloagheun (1987). Pots with *E. tetrodonta*, *E. miniata* and *G. pteridifolia* seedlings were saturated for 24 hours to ensure all individuals were at full turgor. Testing was carried out at midmorning (1030 hrs), when seedlings were photosynthesising, in a laboratory where the temperature was 24°C and relative humidity was 50%. Leaves were cut from the stems of plants and measured for weight loss over a 25 minute period.

5.2.8 Growth of *E. tetrodonta* suckers

This trial was established on a 0.5 ha area at Yapilika, which had a relatively uniform cover of dense *E. tetrodonta* root suckers. All ground layer vegetation at the site was burnt back to ground level by a fire in August 1986. Five treatments were applied and each treatment was replicated once (ie. n = 2). The treatments were.

1. Fire protection.
2. Weeded so only one shoot sprout per square metre remained + fire protection.
3. Fertilised with complete fertiliser mix + fire protection.
4. Fertiliser + weed treatment + fire protection.
5. Burnt.

The fertiliser application rates were those used in the seedling trial (see Table 5.1). Treatments were applied to five by five metre squares of

suckers, with at least 5 m distance between adjacent squares. Roots were severed with a sharp spade to a depth of 30 cm around the perimeter of each treatment to avoid fertiliser application effecting adjacent treatments. The fertiliser was applied in November 1986 and December 1987.

In November 1986, the tallest 15 stems in each 25 m^2 block were marked and their height measured to give an estimate of 'top height' per treatment. In June 1988 the height of, the marked shoots which still had live foliage and, the tallest 15 shoots in each plot, were measured. The density of clumps and number of suckers per clump were measured in the control and burnt treatments in June 1988.

To compare the growth of suckers on the plains to suckers in the forest, the height of *E. tetrodonta* suckers at a nearby forest site and the unburnt treatments on the plains trial, were measured periodically over the duration of the experiment.

5.3 Results

5.3.1 Growth of *E. tetrodonta* and *E. miniata* seedlings across the forest plains boundary

Data analysis

The mean height growth of the seedlings planted across the forest plains boundary, broken down by treatment, species and site are presented graphically in Figure 5.1. All seedlings show increasing height until the 1987 wet season, after which some treatments (e.g. the *E. tetrodonta* seedlings with the complete fertiliser treatment on the transition site) show decreasing mean height. It is unclear whether the decreases are due to competition between adjacent seedlings or differences in site factors and the fertiliser effects. Thus the analysis of variance of
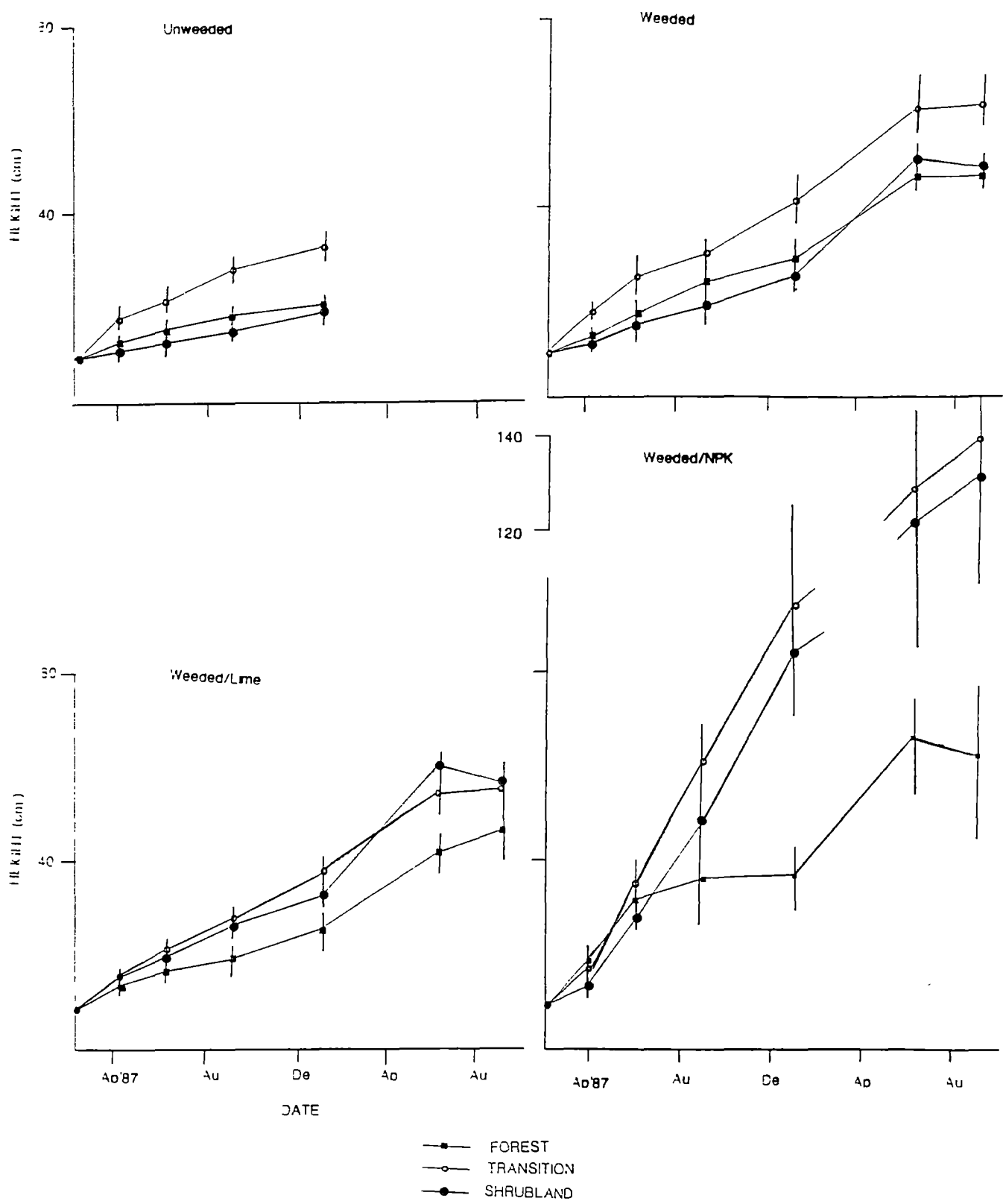
Figure 5.1.1   Height of seedlings planted across the forest plains boundary over time.
Vertical lines indicate 95% confidence limits.
- *E. miniata*

Unweeded

Weeded

HEIGHT (cm)

80

40

Weeded/Lme

Weeded/NPK

HEIGHT (cm)

80

40

Ap'87   Au   De   Ap   Au

DATE

Ap'87   Au   De   Ap   Au

DATE

FOREST
TRANSITION
SHRUBLAND
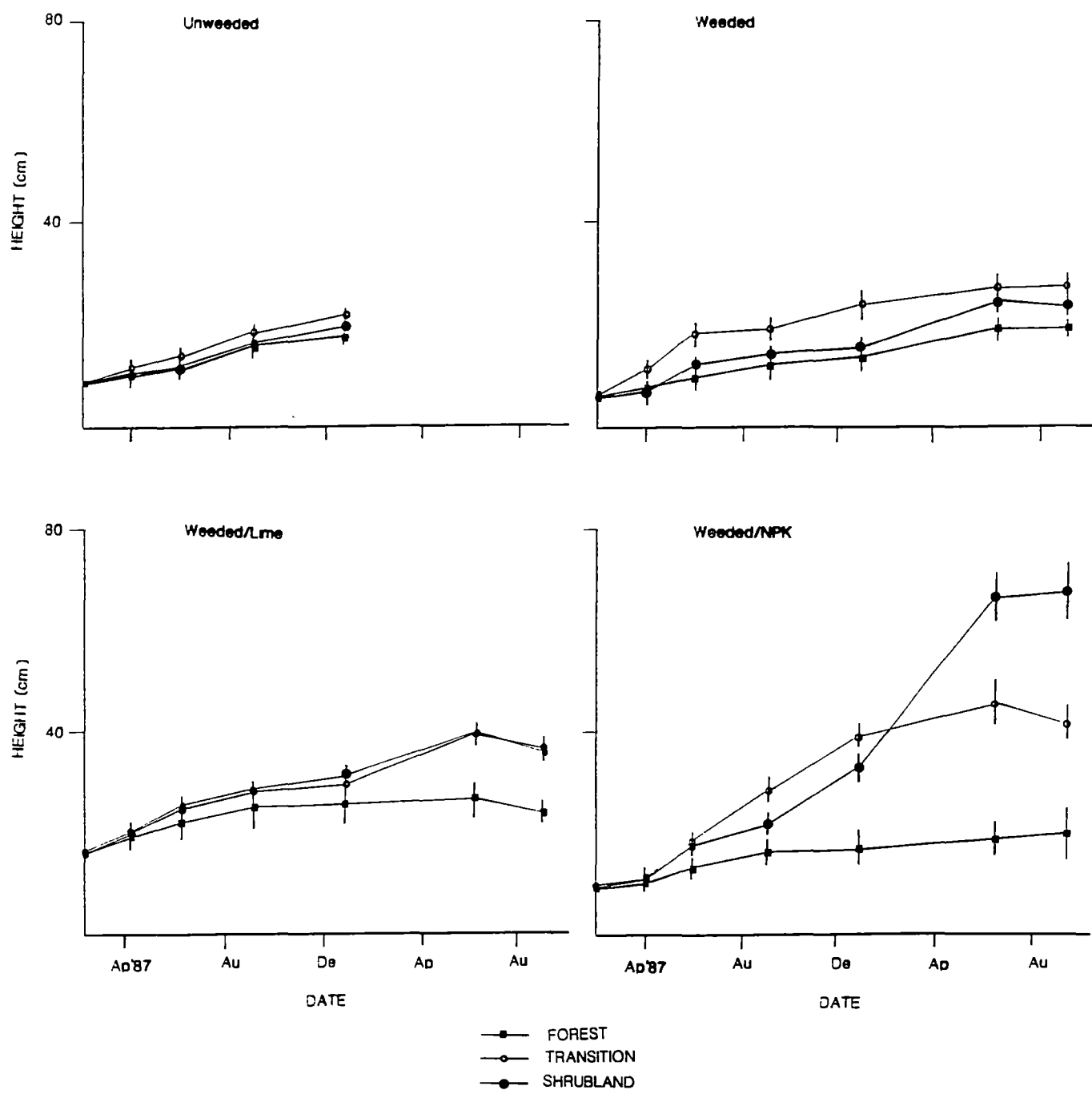
Figure 5.1.2   Height of seedlings planted across the forest plains boundary over time. Vertical lines indicate 95% confidence limits.
- *E. tetrodonta*

seedling height growth is carried out on December 1987 figures, when differences between treatments were maximal.

The height growth of seedlings in the forest was lower than seedlings on the shrubland and transition sites (Figure 5.1). In general the weeding or fertiliser treatments are associated with an increase in height growth. However these increases are generally smaller or not significant on the forest site. As the forest site has higher surface soil levels of moisture and nutrients than the other sites (Chapter 3), it is concluded that the residual canopy was suppressing the seedlings on the forest site. This result has several implications for seedling establishment which will be taken up in the discussion. However, it also confounds the effects of the other treatments and therefore the following analysis of variance uses data from the transition and shrubland sites only.

The treatments were applied to rectangular blocks of 26 seedlings (see section 5.2.1). The analysis of variance treats these blocks as replicates. The error bars on Figure 5.1 are derived from 26 seedlings within each treatment by site by species block. These individual seedlings are 'pseudo-replicates' because they are not randomly located with respect to each other. The small size of each planting site (12 x 6 metres) and the dry season surface moisture measurements suggest that conditions within the study site were uniform. However, these error bars are erroneous if there was any environmental variation within the 12 x 6 metre sites.

Results

Table 5.2 shows the analysis of variance of seedling heights, for the shrubland and transition site in December, broken down by the factors species, site and treatment. The main effects show highly significant ($p < 0.001$) differences in F values (Table 5.2). Thus the *E. miniata* seedlings grew quicker than *E. tetrodonta* seedlings in the same

treatment. Height growth decreased from transition to shrubland sites. The complete fertiliser treatment is associated with the tallest seedlings, the unweeded the shortest and the weeded and dolomite treatments are associated with intermediate mean heights, although the addition of dolomite does not appear to induce substantial increase in height growth compared to the weeded treatment.

There is a significant (p<0.001) treatment by site interaction (Table 5.2). The December 1987 heights of seedlings in the unweeded and weeded treatments on the transition site, are substantially higher than the corresponding treatments on the shrubland sites (Figure 5.1). There is no significant difference between the heights of seedlings treated with complete and lime fertiliser on the shrubland and transition sites. Thus, it appears that the fertiliser treatment induced a differential effect on the two sites.

Table 5.2 Analysis of variance of December 1986 seedling heights (transformed by Log10 to equalise variances), planted across the forest plains boundary on the transition and shrubland sites. Mean heights are presented in Figure 5.1.

Effect	DF	Significance
Species	1	0.001
Treatment	3	0.001
Site	1	0.001
Species* Treatment	3	0.001
Species* Site	2	NS
Treatment* Site	6	0.001

The species by site interaction is not significant (Table 5.2), although *E. tetrodonta* appears to grow relatively better than *E. miniata* on the shrubland site compared to the transition site, particularly in the unfertilised treatments (Figure 5.1). The species react significantly differently ($P < 0.001$ species by treatment interaction, Table 5.2) to the treatments. *E. miniata* appeared to have a proportionally larger response to the complete treatment than *E. tetrodonta* (Figure 5.1). There is no significant site by species by treatment interaction (Table 5.2).

Table 5.3 shows the percent survival of seedlings, broken down by species, treatment and site. Table 5.4 pools the percentages across factors. The trends in survival parallel the height growth data. *E. miniata* has a greater survival rate than *E. tetrodonta*. The transition site has the greatest number of seedlings surviving and the forest the least. Although the complete fertiliser treatment has the highest and the unweeded the lowest, survival rates, there is no significant difference in survival rates between treatments.

5.3.2 Seed dispersal, field germination and early growth of *E. miniata* and *E. tetrodonta* seedlings

Dispersal

The weights of *E. tetrodonta* and *E. miniata* seed were found to average 3.00 and 2.84 10^{-3} gms respectively. Mean tree height in the area was measured as 25 metres and average wind velocity was estimated at 10 km/hr. Using Cremer's (1977) formula for wingless seed it is calculated that, *E. tetrodonta* seed would disperse 6.32 metre and, *E. miniata* seed would disperse 6.59 metre, from the mother tree.

Table 5.3 Survival (% out of 26) for seedlings in December 1986, planted across the forest plains boundary broken down by species, site and treatment.

	E. miniata	*E. tetrodonta*
Forest		
Unweeded	84.6	35.9
Weeded	65.4	61.5
Weeded/complete	80.8	57.7
Weeded/lime	73.1	30.8
Transition		
Unweeded	88.5	73.1
Weeded	92.3	80.8
Weeded/complete	92.4	100.0
Weeded/lime	73.1	57.7
Shrubland		
Unweeded	61.5	73.1
Weeded	76.9	53.8
Weeded/complete	84.6	80.8
Weeded/lime	96.2	92.3

Table 5.4 Survival (% out of 26) for seedlings in December 1986, planted across the forest plains boundary, pooled by species, site or treatment. Different letters denote row means significantly (p<0.05) different as determined by Tukey's range test. Analysis of variance showed that F values for all row means were significant (p<0.05).

E. miniata	*E. tetrodonta*		
80.8	66.4		
A	B		

Forest	Transition	Shrubland	
61.1	82.2	77.4	
A	B	AB	

Unweeded	Weeded	Weeded/ complete	Weeded/ lime
69.3	71.8	82.7	70.5
A	A	A	A

Field germination and early growth

Two months after sowing, no germinants were found on the forest site or on the unweeded treatments on the shrubland or transition site. At this time, 15 (15% of seed sown) *E. miniata* and 3 (3% of seed sown) *E. tetrodonta* germinants were found on the weeded transition and shrubland sites. No *E. tetrodonta* germinants were found in the following dry season. Eighteen months after sowing 7 *E. miniata* seedlings were still surviving, of which 6 were on the shrubland site. Seed from the same batches as that sown in the field, germinated within 4 - 7 days at a rate of 60 - 70% when placed on germination trays under moist shady conditions in the nursery.

The height growth of the 6 *E. miniata* germinants on the shrubland site

over time is shown in Figure 5.2. It is apparent that 18 months after sowing, the height growth of *E. miniata* germinants is similar to the height growth of *E. miniata* transplants on the unweeded shrubland site (cf. Figure 5.1).

5.3.3 Leaf water potential of *E. tetrodonta* and *E. miniata* seedlings grown across the forest plains boundary

Gravimetric measurements of soil moisture within the experimental sites throughout the duration of the experiment, indicated that between site moisture regime conformed to the general trend shown in Chapter 2. That is the moisture content of the forest was wetter than the transition which was wetter than shrubland and, the differences were greater in the surface layers. At the time of the moisture potential measurements reported below, the surface soil percent moisture contents were 5.6, 4.9 and 4.1 at the forest, transition and shrubland sites respectively.

Table 5.5 shows the mean midday leaf water potential measurements of seedlings in the complete fertiliser and weeded treatments by site. The mean potentials presented in Table 5.5 are pooled across the days, because the analysis of variance showed that there was no significant difference in leaf moisture potential between the two days. The analysis of variance also shows a significant (p<0.001) difference in potential between species, treatment and community factors and a significant (p<0.01) interaction between species and treatment. *E. miniata* generally shows a lower potential (lower stress) than *E. tetrodonta*. Seedlings from the complete fertiliser treatment generally have a lower potential than the unweeded treatment. Seedlings from the transition site have lower potential (lower stress) than the other sites, while the forest seedlings have equal or slightly higher potentials than the shrubland.
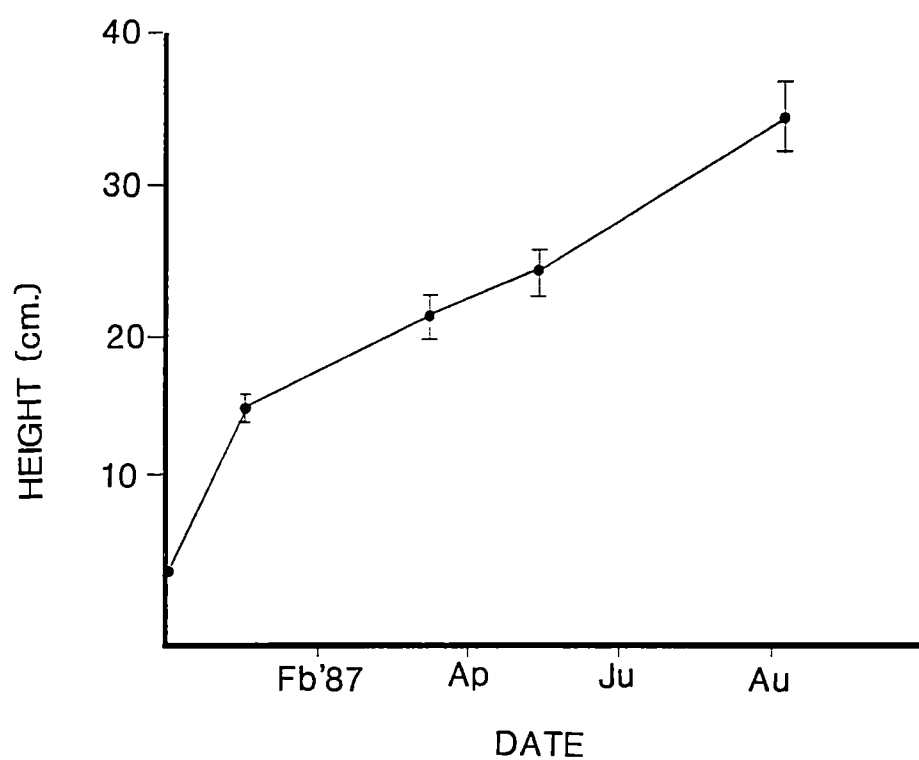
Figure 5.2   Height of *E. miniata* germinants sown at the weeded shrubland site over time.   Vertical bars represent 95% confidence limits.

Table 5.5 Means of leaf moisture potential (kPa) of seedlings planted across the forest plains boundary by community (n = 5). Measurements were taken on August 27, 1030 hrs and August 28, 1200 hrs. Different letters denote means significantly (p < 0.05) different within each species, as determined by Tukey's range test. Analysis of variance showed that F values for all row means were significant (p < 0.05).

Community	Weeded/ complete fertiliser	Weeded
E. miniata		
Forest	2405 A	2498 A
Transition	1884 B	2239 A
Shrubland	2349 A	2225 A
E. tetrodonta		
Forest	2567 A	2842 A
Transition	2050 B	2463 AB
Shrubland	2136 B	2877 A

Analysis of variance

Effect	DF	Significance
Species	1	p < 0.001
Treatment	1	p < 0.001
Site	2	p < 0.001
Species* Treatment	1	p < 0.01
Species* Site	1	NS
Treatment* Site	1	NS

Table 5.6 shows mean pre-dawn leaf potential measurements of *E. miniata* and *E. tetrodonta* seedlings on the second measurement day. These seedlings had potentials of between 620 and 827 kPa, with no consistent difference between treatments.

5.3.4 The effect of fire on the growth of *E. tetrodonta* and *E. miniata* seedlings

The fire in April 1988 removed the shoots of all the 15 month old seedlings. By September 1988 72% of *E. tetrodonta* and 85% of *E. miniata* had resprouted (Table 5.7). There is no estimate of the size of seedlings at the time of burning, although the mean height of seedlings in the preceding December which did not resprout, was significantly less than the corresponding heights of seedlings which subsequently survived (Table 5.8). Two sampled Chi-squared tests showed that there is a significant (p<0.05) positive association between survival and the transition site and significant (p<0.05) negative association between survival and the forest site, paralleling the trend in seedling heights.

Table 5.6 Means and standard errors (in brackets) for pre-dawn leaf matric potential (kPa) of *E. miniata* seedlings planted across the forest plains boundary (N=5). Analysis of variance showed no significant difference between treatments or sites.

Treatment	Weeded/complete fertiliser	Weeded
Community		
Forest	620 (289)	861 (276)
Transition	654 (145)	654 (76)
Shrubland	861 (324)	551 (331)

Table 5.7 Survival (% out of 26) for seedlings in September 1987 on unweeded treatment, after being burnt in April 1987.

Species	E. miniata	E. tetrodonta
Community		
Forest	72.7	44.4
Transition	95.7	78.9
Shrubland	87.5	84.2
Total	85.2	72.3

Table 5.8 Means for height (cm) of seedlings in December 1986, which were alive or dead in September 1987 after being burnt in April 1987. Significance of F values from analysis of variance is indicated.

	E. miniata	E. tetrodonta
Dead	20.0	14.9
Alive	26.1	18.7
Significance	$P < 0.05$	$P < 0.05$

5.3.5 The effect of soil type and mycorrhizal inoculation on the growth of seedlings in pots

Soil type

Table 5.9 shows the root, shoot and total weights and ratios of *E. miniata* and *E. tetrodonta* seedlings grown for seven months in forest or shrubland soil. Seedlings grown in forest soil have higher mean root, shoot and total weights and lower mean root:shoot ratios than seedlings

grown in shrubland soil. However, Table 5.10 shows that only the root weights are significantly different between treatments. Root/shoot ratios and shoot weights showed significant species by treatment interactions (Table 5.10). Thus the differences between soil types in these attributes is greater for *E. miniata* than *E. tetrodonta*.

Mycorrhiza

Table 5.9 also shows the root, shoot and total weights and ratios of *E. miniata* or *E. tetrodonta* seedlings grown for seven months in sterile potting mix inoculated with small amounts of forest soil or shrubland soil. *E. tetrodonta* seedlings grown in forest soil inoculated pots have higher root and shoot weights than *E. tetrodonta* seedlings grown in pots inoculated with shrubland soil. However, the analysis of variance showed no significant difference in any of the measured parameters between treatments (Table 5.10).

5.3.6 The effect of flooding and drought on the growth of seedlings in pots

Flooding

Figure 5.3 shows the death rate of seedlings placed in saturated pots by species. After 7 months some seedlings from all species were still alive although survival rates varied. Two sampled Chi-square tests show significant positive association between survival rate and *Grevillea* seedlings.

Table 5.9 shows that root, shoot and total weights of seedlings grown in the flooded soils were substantially lower than seedlings grown under normal nursery conditions. It was not possible to do an analysis of variance between the treatments on these data because the variances could not be homogenised by any transformations tried. However, qualitative comparisons between species show clear differences in
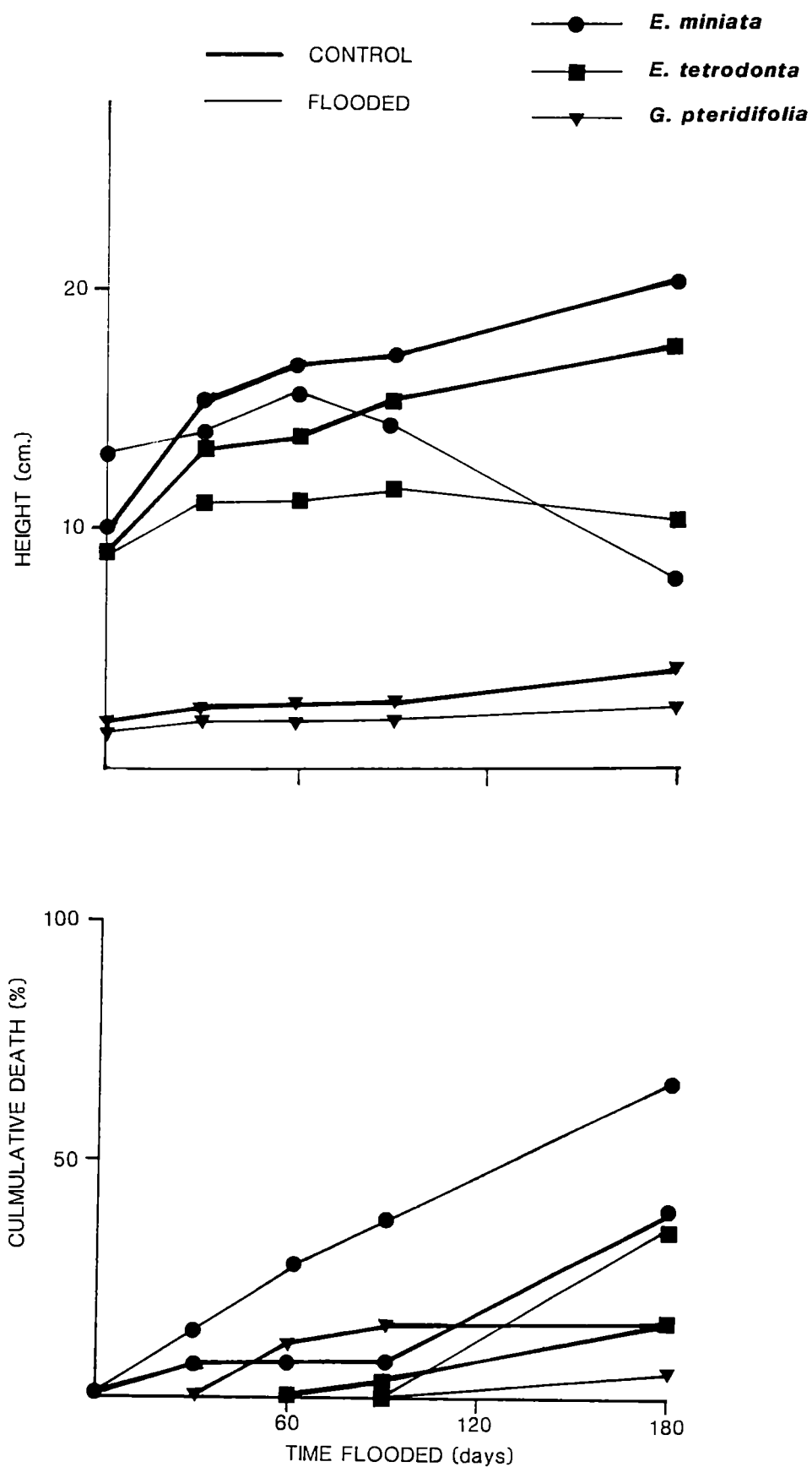
Figure 5.3 Death (cumulative percent) and height of saturated seedlings over time. Vertical bars represent 95% confidence limits. Control = normal nursery watering conditions. Flooded = Normal nursery watering conditions plus saturation to 1cm below soil surface.

Table 5.9 Means for root, shoot, root/shoot ratio and total weight (gms, with standard error in brackets) of plants grown in various soil types and moisture conditions.

Treatment	Root	Shoot	Root/ Shoot ratio	Total weight
E. miniata				
Forest soil	1.00 (.22)	2.10 (.34)	0.53 (.09)	3.10 (.52)
Shrubland soil	0.60 (.26)	0.69 (.27)	1.12 (.30)	1.29 (.52)
Mix + Forest inoculation	1.22 (.22)	5.28 (.90)	0.26 (.03)	6.71 (1.11)
Mix + Plains inoculation	1.28 (.26)	5.40 (.98)	0.23 (.04)	7.20 (1.36)
Forest soil/ saturated	0.17 (.10)	0.17 (.13)	1.38 (.35)	0.35 (.17)
E. tetrodonta				
Forest soil	1.75 (.15)	1.40 (.17)	1.36 (.12)	3.15 (.28)
Shrubland soil	0.95 (.18)	1.13 (.21)	0.91 (.14)	2.08 (.37)
Mix + forest inoculation	2.60 (.36)	6.67 (.75)	0.43 (.05)	9.40 (1.01)
Mix + shrubland inoculation	1.82 (.21)	4.08 (.57)	0.50 (.05)	6.04 (.74)
Forest soil/ saturated	0.35 (.12)	0.25 (.12)	1.56 (.18)	0.59 (.06)
G. pteridifolia				
Forest soil	1.68 (.19)	2.63 (.24)	0.63 (.04)	4.30 (.40)
Forest soil/ saturated	1.44 (.15)	1.57 (.17)	1.70 (.87)	3.00 (.15)

Table 5.10 Analysis of variance of mean root, shoot, root/shoot ratio and total weight of plants grown in various soil types and moisture conditions (presented in table 5.9)

Forest soil vs Shrubland soil (n is variable with mean of 10).

Source	DF	Shoot	Root[1]	Root/ Shoot ratio	Total weight
Species	1	**	**	NS	***
Treatment	1	NS	**	NS	NS
Species* Treatment	1	*	NS	**	NS

Potting mix + forest inoculation vs. potting mix + shrubland inoculation (variable n with mean of 20).

Source	DF	Shoot	Root[1]	Root/ Shoot ratio	Total weight
Species	1	***	***	***	NS
Treatment	1	NS	NS	NS	NS
Species* Treatment	1	NS	NS	NS	NS

[1] $Log10(x+1)$ transformed to homogenise the variances.

response patterns of shoot height growth by species through time (Figure 5.3). *Grevillea* always maintained a positive growth in the saturated treatment while the eucalypts suffered shoot dieback and negative height growth. The reduction in height growth between the flooded and control seedlings was greatest for *E. miniata*. The *Grevillea* also showed less difference in root and shoot weights between the flooded and control treatments compared to the eucalypts (Table 5.9).

The saturation of the seedlings in pots was accompanied by morphological changes. The foliage of the *Grevillea* turned yellow, although leaf loss was minimal compared to the eucalypts. As well as losing their leaves much of the foliage of the eucalypts was reduced in size compared to the controls. There was no apparent change in root morphology between treatments.

Drought

Figure 5.4 shows the moisture regime imposed in the droughting experiments. The first experiment, which was carried out in the dry season, had a rapid reduction in soil moisture content (with a rise in moisture at day 4 due to the pots inadvertently receiving a light watering) from a lower initial moisture status compared to experiment two, which was carried out in the humid wet season. The mean size of the eucalypts was larger in experiment two compared to experiment one (Table 5.11). Both experiments show that *E. miniata* died significantly quicker (Fig. 5.4) and at a significantly higher moisture content (Table 5.12) than *E. tetrodonta*. *Grevillea* died quicker than *E. miniata* although the difference was not significant in the second experiment.

The terminal moisture content and pattern of deaths of species, varied with the conditions of the experiment. In the second experiment, the bigger seedlings died at higher moisture contents, and more suddenly, than the smaller seedlings droughted in the first experiment.

The plot of pre-dawn leaf moisture potential versus moisture content of *E. miniata* and *E. tetrodonta* (Figure 5.5) seedlings in pots shows that both species reached maximum potentials of about 2760 kPa before dying.

EXPERIMENT 1
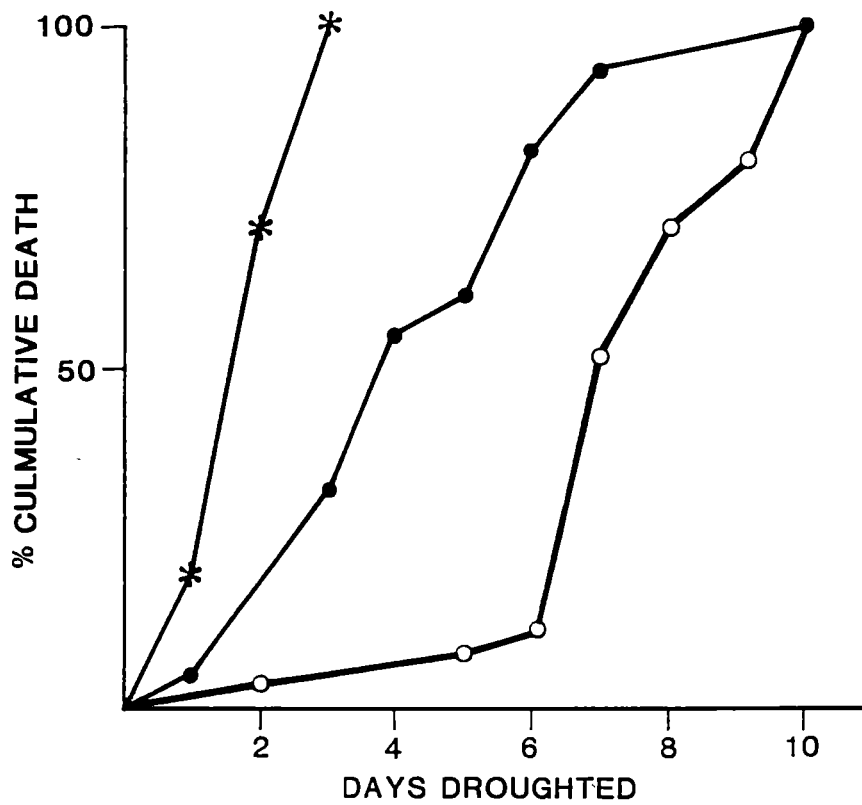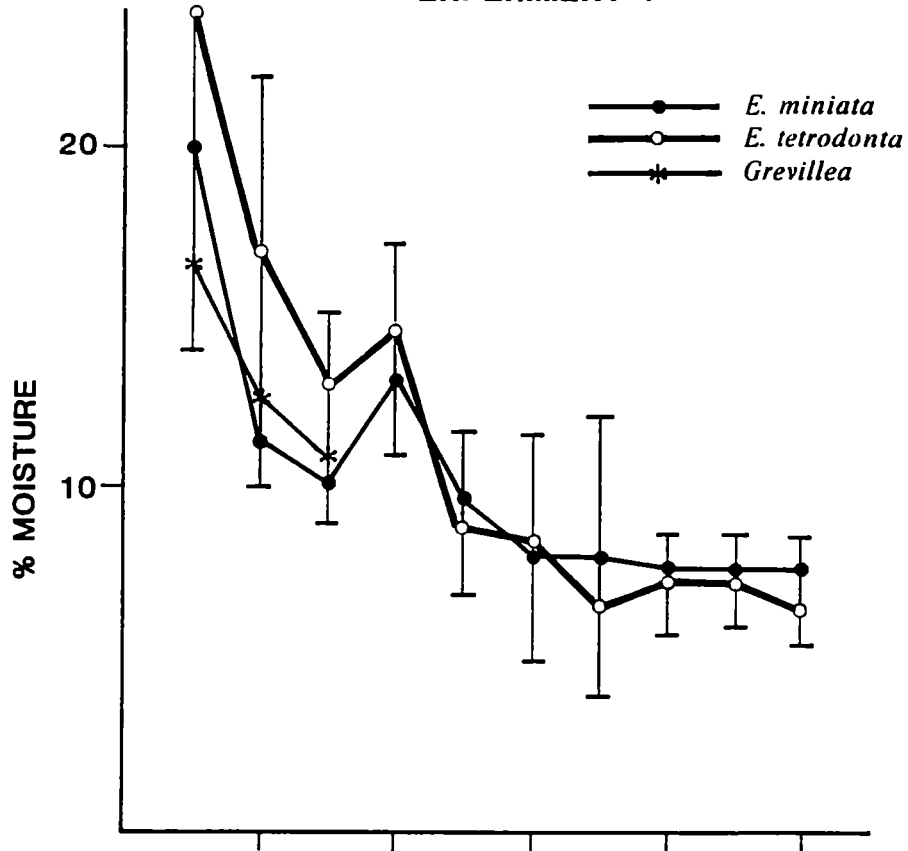
Figure 5.4.1   Soil moisture versus death of droughted seedlings - experiment 1
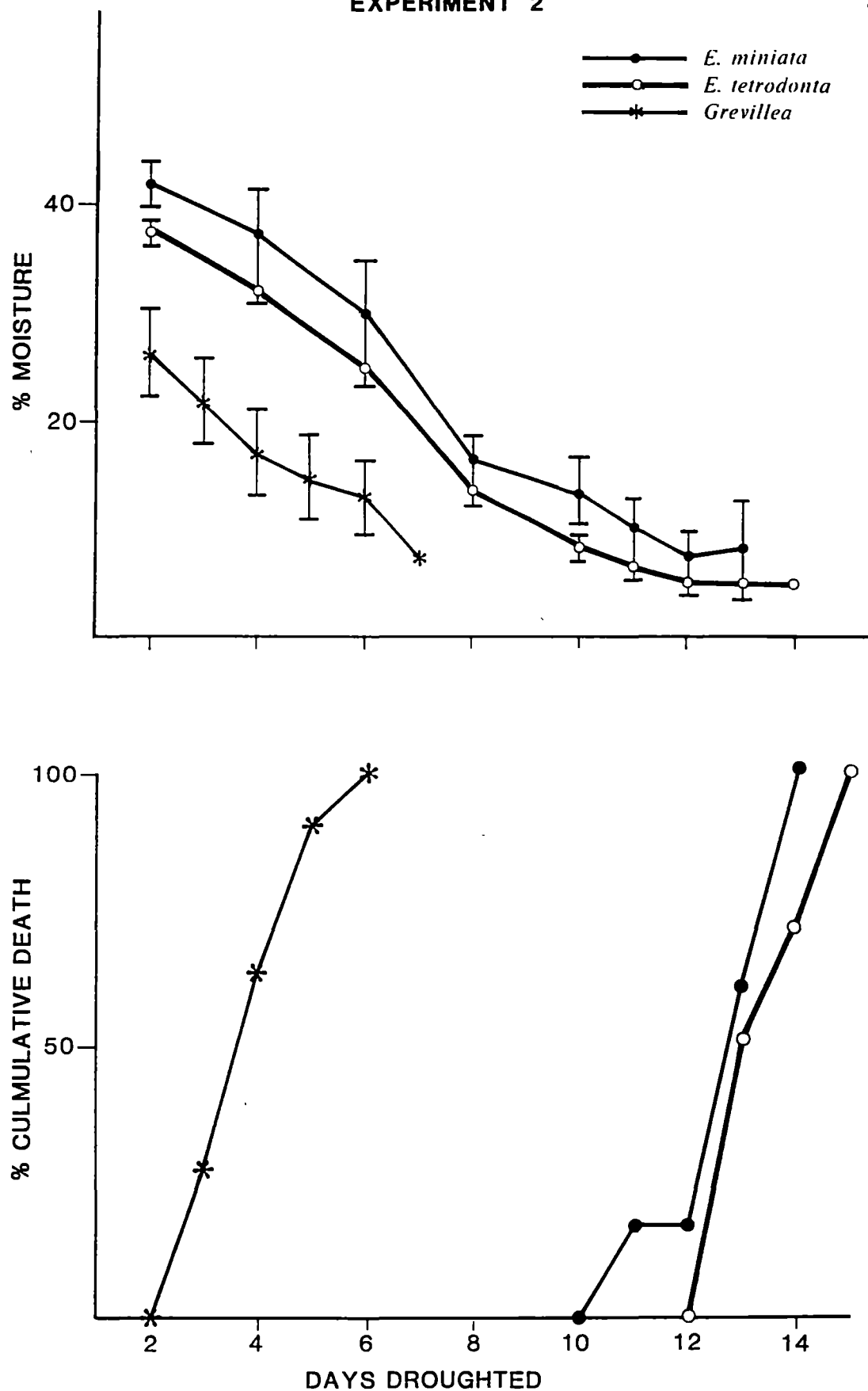
Figure 5.4.2 Soil moisture versus death of droughted seedlings - experiment 2

Table 5.11 Means and standard errors (in brackets) for height (cm) and total weight (gm) of seedlings used in drought experiments 1 and 2.

	Experiment 1	Experiment 2
E. miniata		
height	19.3 (3.5)	20.2 (2.2)
weight	4.5 (0.1)	2.7 (0.3)
E. tetrodonta		
height	13.8 (0.6)	17.5 (0.7)
weight	1.8 (0.3)	2.3 (0.4)
G. pteridifolia		
height	2.5 (0.1)	
weight	3.3 (0.4)	

Table 5.12 Means for soil moisture content (%) at the time of death of seedlings in drought experiments 1 and 2. The same letters denote column means not significantly different at $p < 0.05$ level as determined by Tukey's range test. Analysis of variance showed that F values were significantly ($P < 0.05$) different at each experiment.

Species	Experiment 1	Experiment 2
E. miniata	9.1 A	7.3 A
E. tetrodonta	6.0 B	4.4 B
G. pteridifolia	12.0 C	8.2 A
Significance	0.001	0.001

40 ⎤

30

E. miniata

SOIL MOISTURE (%)

20

10

1378   2756

LEAF MOISTURE POTENTIAL (kPa)
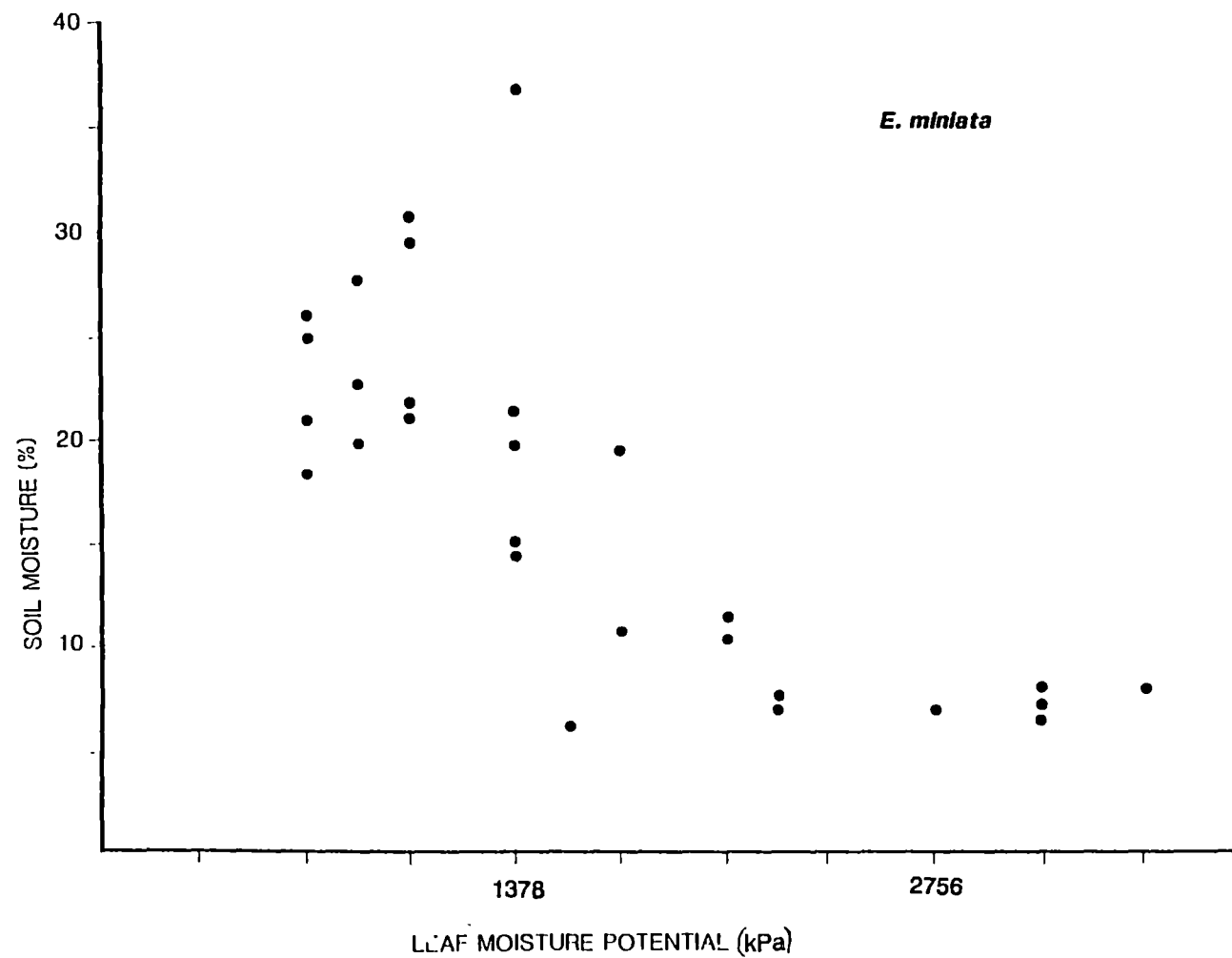
Figure 5.5.1   Pre-dawn leaf matrix potential versus percent moisture content of droughted seedlings grown in pots - *E. miniata*

E. tetrodonta

SOIL MOISTURE (%)

LEAF MOISTURE POTENTIAL (kPa)

1378   2756   4134
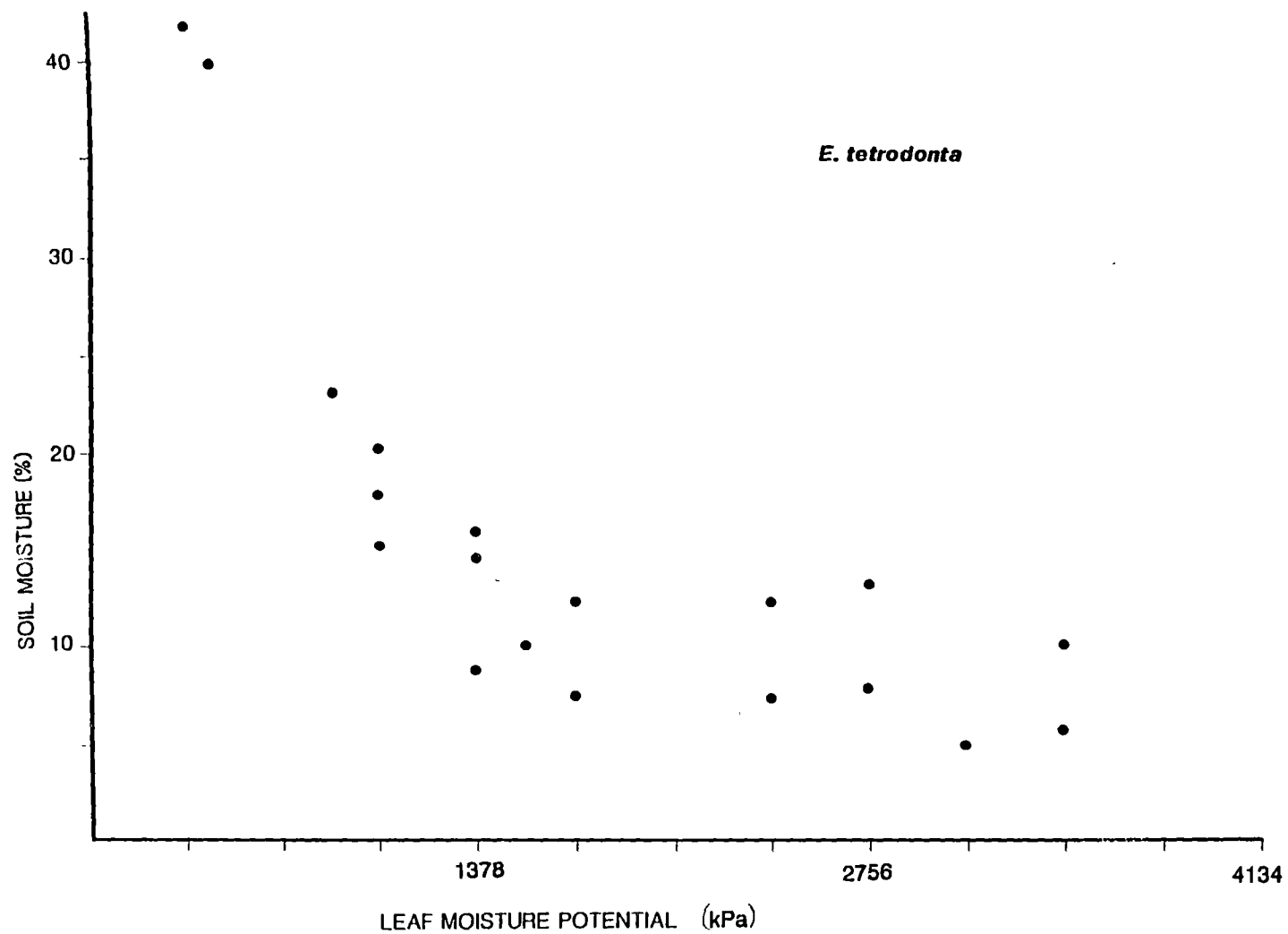
Figure 5.5.2   Pre-dawn leaf matrix potential versus percent moisture content of droughted seedlings grown in pots - *E. tetrodonta*

5.3.7 Variation in leaf transpiration rates between _E. miniata, E. tetrodonta_ and _Grevillea pteridifolia._

Weight losses from cut leaves over 25 minutes for _E. miniata, E. tetrodonta_ and _G. pteridifolia_ are shown in Table 5.13. The results parallel the trend of seedling response to drought in pots. All species show significantly different weight losses over the period in descending order, _G. pteridifolia, E. miniata_ and _E. tetrodonta_. This result coincides with the trend in fresh-leaf percent moisture content which show _E. miniata_ and _G. pteridifolia_ have significantly higher values than _E. tetrodonta_.

Table 5.13 Means for weight loss (% of initial) of leaves by time since cut from stem and moisture content of fresh leaf (% of dry weight). The same letters denote column means not significantly different at $p<0.05$ level as determined by Tukey's range test. Analysis of variance showed that F values were significantly ($P<0.05$) different for all row mean.

Species (n = 115)	Time (minutes) 5	10	15	25	leaf moisture content (%)
E. miniata	2.5 A	6.3 A	9.3 A	16.9 A	238 A
E. tetrodonta	0.5 B	1.3 B	2.6 B	4.3 B	174 B
G. pteridifolia	0.7 B	1.8 B	15.0 A	24.1 A	233.9 A

148

5.3.8 Growth of *E. tetrodonta* suckers.

Table 5.14 shows the mean top height of suckers measured in November 1986 and June 1988 and percent and mean height of the shoots marked in 1986 which survived until 1988, pooled across the replicates by treatment. The results of the analysis of variance of the means of top height in 1986 and 1988, the differences between dates, and the height of shoots in June 1988 which had originally being measured in November 1986 (excluding the burnt treatment where all original shoots were destroyed) presented in Table 5.15, show that there were no significant differences in any mean heights between treatments.

Table 5.14   Means of height (cm) and survival (%) of *E. tetrodonta* suckers by treatment (n = 30). Analysis of variance showed that F values were not significant (p < 0.05) for any row.

Treatment	Top height Nov. 1986	Top height June 1988	Percent of original shoots surviving	Mean height of shoots surviving
Unburnt	64.2	83.0	23.3	50.7
Fertiliser/ Unburnt	67.7	69.7	15.0	50.3
Weeded/ Unburnt	70.2	62.4	52.5	60.6
Fertiliser/Weeded/ Unburnt	71.4	80.6	60.5	76.5
Burnt	66.2	97.7	0.0	0.0
Forest/ Unburnt	99.8	74.0	65.7	74.3

Table 5.15 Analysis of variance of means for height of *E. tetrodonta* on the plains (presented in Table 5.14)

Top height in November 1986

Effect	DF	Significance
Treatment	4	NS
Replicate	1	NS

Top height in June 1988

Effect	DF	Significance
Treatment	4	NS
Replicate	1	NS

Differences between top heights in November 1986 and June 1988

Effect	DF	Significance
Treatment	4	NS
Replicate	1	NS

Height in June 1988 of shoots which had originally being measured in November 1986 (burnt treatment excluded as all original shoots were destroyed)

Effect	DF	Significance
Treatment	3	NS
Replicate	1	NS

The mean top height of shoots on all plains treatments in November 1986 were similar (Table 5.14). At this time the height of the forest shoots was substantially higher than those on the plains (Table 5.14). Most of the treatments on the plains showed slight increases in mean top height

between 1986 and 1988 (Table 5.14). Shoots in the burnt treatment appeared to show more, and the weeded treatment less, shoot growth relative to the other treatments between 1986 and 1988. The mean height of shoots at the forest site showed a between measurement decrease compared to the plains sites which showed an increase (Table 5.14).

Less than 66% of shoots measured in 1986 survived between measurement dates on any treatment (Table 5.14). Suckers in the forest showed the highest percentage survival rate over the measurement period (Table 5.14). Apart from the burnt treatment where all shoots were burnt back to the ground each year, the control and fertilised treatment on the plains had the lowest survival rate (Table 5.14). With the exception of the fertilised/weeded/unburnt treatment there is a decrease in the mean height of shoots surviving between the measurement periods (Table 5.14), although these differences are not significant (Table 5.15).

Figure 5.6 shows the growth of individual suckers which survived the measurement period at the unburnt sites on the plains and the forest, over time. Suckers on both sites show similar growth patterns with an initial pre-measurement dry season growth burst, followed by little growth in the first wet season, die back in the dry season, and regrowth in the following wet. Individual shoots on the plains which survived the measurement period were less in number and less likely to increase their height compared to individuals from the forest.

Table 5.16 shows the comparison of the stocking of sprout clumps and shoots between the burnt and unburnt treatments on the plains. Burning was associated with a significant increase in the number of shoots per clump and the density of clumps.

FOREST

HEIGHT (cm)

120

60

Nov '86   Mar '87   Jul '87   Nov '87   Mar '88   Jul '88
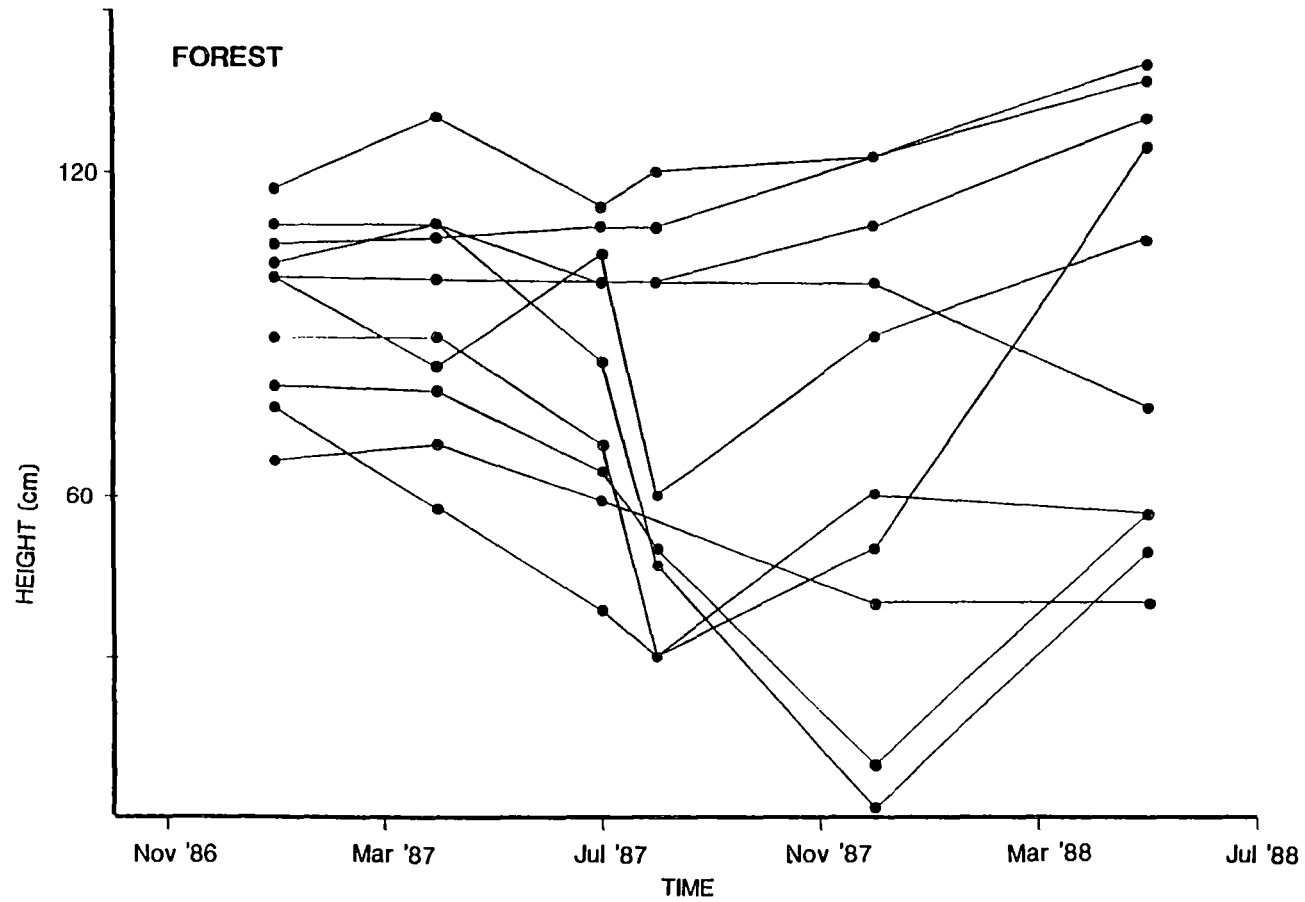
TIME

Figure 5.6.1   Height of individual *E. tetrodonta* root sucker shoots, which survived for 18 months, over time - forest site
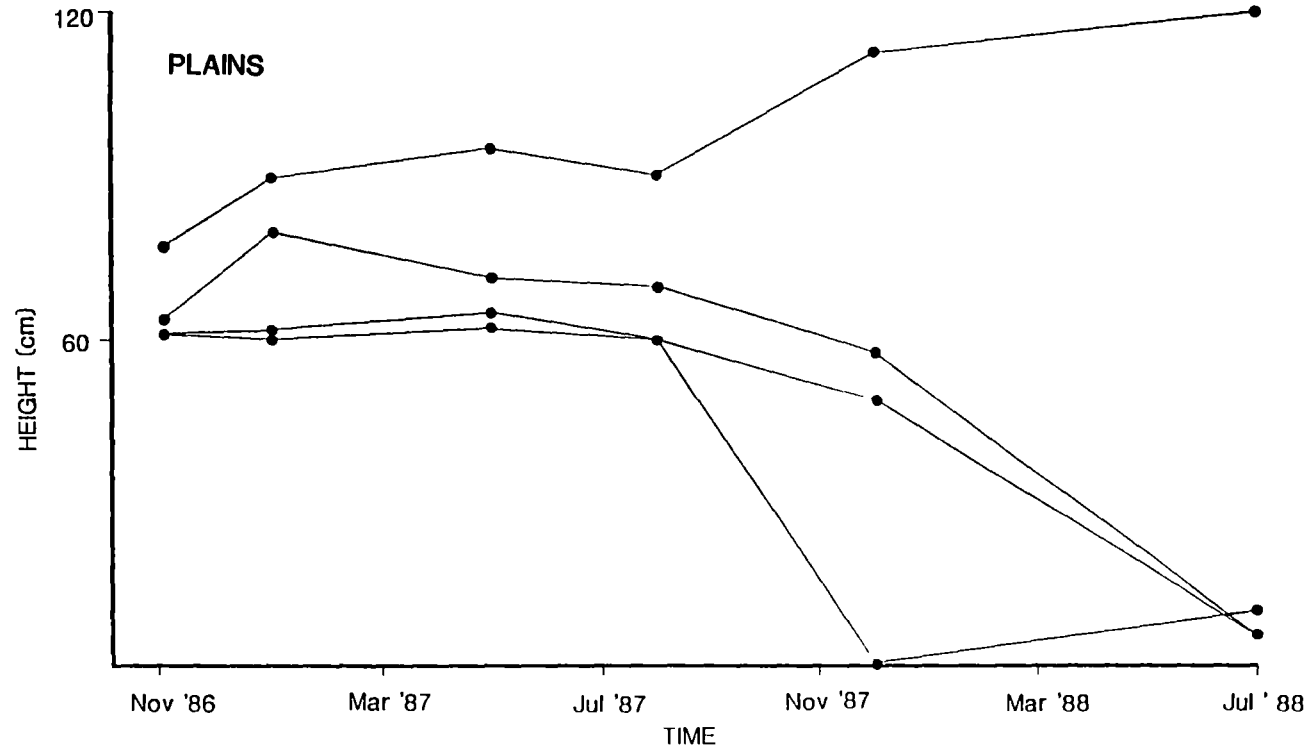
Figure 5.6.2   Height of individual *E. tetrodonta* root sucker shoots, which survived for 18 months, over time - plains site

Table 5.16 Means for number of clumps and shoots per clump, between a burnt and unburnt area of *E. tetrodonta* suckers on the plains. Significance of F values from analysis of variance is indicated.

	Nos. shoots/clump 4 m. sq. plot (n = 10)	Nos. clumps/ 4 m. sq. plot (n = 10)
Burnt Area	4.0	8.3
Unburnt Area	1.4	4.5
Significance	p<0.001	p<0.001

5.4 Discussion

5.4.1 Seedling growth in response to environmental factors

Seed dispersal and germination

The lack of eucalypt juveniles on the plains (Chapter 3) could, in part, be due to the poor seed dispersal of the dominant tree species. Temperate eucalypt species possess light seed which (on flat terrain under light wind conditions similar to the Melville Island situation) is potentially dispersed one times the height of the parent tree (Cremer 1977). The northern Australian eucalypt seed are 10 times as heavy as the biggest seed reported by Cremer (1977) and theoretical dispersal distances are less than 7 metres. Furthermore, the prevailing winds in the Yapilika region at the time of seed shed (September - December) are from the north-west. As many of the forest to plains boundaries studied run west to east (Appendix 2), the wind would further reduce potential seed dispersal onto the plains.

It is not clear what caused the paucity of eucalypt germinants under the forest canopy and the low field germination rate of sown seed observed at Yapilika. Ants are abundant in northern forests (Anderson & Lonsdale 1991) and have been heavily implicated in the removal of eucalypt seed in southern forests (Ashton 1976). However, Major and Lamont (1985) indicate that ants do not remove eucalypt seed in northern forests. Furthermore the seed sown at Yapilika was buried under a small amount of soil. Therefore it seems unlikely that ants can be implicated in the low germination rates.

Removal of ground vegetation at Yapilika appeared to promote seedling germination and establishment. This suggests that competition from grasses may be a factor affecting seed germination. Such competition has been shown to affect the establishment of tree seedlings in African savannas (Strang 1969, Knoop & Walker 1985). The poor soil fertility and moisture content of the plains soils relative to the forest soil (Chapter 4) may also affect number of seedlings, directly through an effect on germination or indirectly by causing low flowering of adult trees.

Mott *et al.* (1985) raise the possibility of episodic germination events being an important mechanism in seedling establishment in northern Australian forests and woodlands. Thus the tropical eucalypt species may have developed a strategy whereby their seed has the ability to germinate and develop rapidly if subjected to good early rains, to maximises their chances of surviving the subsequent dry season, at the expense of failing to develop if early rains are poor. Thus the exceptionally dry December (94 mm compared to an average of 304 cm, Table 1.1) during this study could have resulted in the desiccation and death of seed and young germinants.

In support of the episodic hypothesis the large seeded *E. miniata* and *E. tetrodonta* were observed to germinate rapidly under moist conditions in

the nursery, as do southern eucalypt species with large seed (Grose 1963). However, little is known about factors affecting the early germination and growth of the eucalypts in northern Australia. In the absence of further work, it is thus difficult to conclude whether the flowering, germination and seedling densities observed on Melville Island are atypical of the northern eucalypt forests and woodlands.

Forest canopy

The suppression of eucalypt seedlings under a forest canopy of the same species, has been reported many times from temperate eucalypt forests (Henry & Florence 1966, Incoll 1979, Rotheram 1983, Bowman & Kirkpatrick 1986b). Bowman & Kirkpatrick (1986a) have shown that *E. delegatensis* juveniles were only suppressed directly under tree crowns while other eucalypts in southern Australia have been shown to suppress regrowth 1 to 3 crown diameters from the tree stem (Rotheram 1983). These studies indicate that canopy gaps are generally required to enable eucalypt seedlings to develop into trees.

Similarly it has been suggested that tropical eucalypts require relief from overwood suppression to regenerate successfully (Bowman 1986, Wilson & Bowman 1987, Bowman *et al.* 1988b). The size of the gap required for unimpeded growth would be expected to vary with site quality. The results from this study (Section 5.3.1) suggest a gap size of at least 50 metres is required on forest sites adjacent to the treeless plains, to avoid suppression of eucalypt seedling growth.

Bowman & Kirkpatrick (1986b) have shown that adult *E. delegatensis* trees in Tasmania, suppress juveniles largely through their effect on soil moisture. The very subdued response to the fertiliser treatments in the forest compared to that from the transition and shrubland sites suggests that at Yapilika, the competition from the overwood may not be primarily for nutrients. The greater moisture stress shown by seedlings from the

forest compared to those from the plains suggests that competition here may also be for moisture. If this is so then it would appear that seedlings in the forest are competing with the more extensive roots of the overstorey for sub-surface (<30 cm) soil moisture, because surface moisture in the upper layers of the forest was higher than that on the plains. This suggests that seedlings on the plains may be tapping sub-surface water with little impedance.

Fensham (1990) has presented results from Melville Island studies, which point to a possible inhibition of seedling growth due to chemical releases from adult eucalypts. Similar 'allelopathic' effects have been implicated in many studies of temperate eucalypts (e.g. Florence & Crocker 1962, Evans *et al.* 1987) although its existence in the field has not been satisfactorily established (May & Ash 1990). Such a mechanism would explain the lack of seedling establishment in northern forests and is worthy of further investigation.

Soil nutrients

The seedling transplant experiment clearly showed that seedlings on the plains grew more slowly than those planted on the transition site and that growth varied with fertiliser addition and removal of ground layer competition. However, the effects of treatments may only be indirectly related to their apparent primary cause. For example, Grime & Curtis (1976) have shown grasses are more vulnerable to desiccation when root penetration is limited by nutrient deficiency.

The increased height growth associated with the fertiliser treatment on the plains was also associated with a significant reduction in leaf moisture stress of seedlings in the dry season. This could be a result of increased root growth which allowed greater uptake of moisture by the plants, although it is doubtful that the root:shoot ratios of seedlings from the fertilised treatments would have exceeded those from the unfertilised

treatments. The decrease in height growth during the 1988 dry season may indicate that, at this time, something other than nutrients had become limiting. An alternative explanation is that the initial fertiliser application, which was not repeated, had been leached or absorbed from the soil at the time of negative growth.

However, the results from the fertiliser trial showed that there was a differential response to nutrient application across the boundary. Furthermore, the seedlings treated with the complete fertiliser mix on the shrubland site were under greater moisture stress than those on the equivalent treatment on the transition site, indicating that there was an increased response to nutrients alone. There appeared to be a greater response to the dolomite application on the shrubland site compared to the transition site, although the application of this fertiliser did not increase seedling growth significantly above the unfertilised treatments. Thus, it is possible to conclude that the addition of nutrients increased eucalypt seedling height growth more on the shrubland site than the transition, but there was no evidence that calcium and magnesium were more limiting than other nutrients.

Soil type and mycorrhiza

The pot trials showed that seedling roots grew significantly slower in plains soils than the forest soils when given plenty of water. This gives some support to the results of the soil analysis and the field trials, that the soils from the plains were nutrient poor compared to the forest. These results warrant the establishment of further pot trials to test the effects of soils from different depths and the role of specific nutrients.

Studies on heaths in Victoria have shown that growth response of eucalypts to fertiliser is improved by the addition of mycorrhiza (Groves and Specht 1981 quoting Burrell 1968). However, the pot trials reported in this thesis (Section 5.3.5) showed no significant difference in

the growth rates of seedlings grown in sterile and inoculated potting mix. Furthermore the seeds sown directly into the shrubland appeared to grow as well as the adjacent planted seedlings. Thus there is no evidence that mycorrhiza are responsible for the differential growth rates of seedlings across the forest plains boundary.

Flooding

Generally waterlogging pot trials, similar to the one reported here, have yielded results which conformed to field observations of species resistance to flooding (e.g. Bannister 1964; Ladiges & Kelso 1977; Gill 1985, Gloagheun 1987, although an experiment by Parsons (1968) yielded inconclusive results). Thus, *Grevillea pteridifolia* grown in pots, was found to be more resistant to water saturation than *E. tetrodonta* which in turn was more resistant than *E. miniata*. In the field, *Grevillea pteridifolia* was found on sites which are often saturated in the wet season, while the eucalypts were generally found on sites where water tables did not get within 1.5 metres of the surface for substantial periods (Chapter 2). The results are broadly similar to findings in southern Australia, that eucalypts which dominate well drained sites are not generally capable of growing on water-logged sites (Ladiges & Kelso 1977.)

The reasons for reduction in growth in the saturated treatments may be directly due to the anaerobic conditions reducing root respiration, growth, and translocation. Indirect effects can be caused by the reduced availability of nutrients in the soil (Ladiges & Kelso 1977), which may be particularly relevant on nutrient poor soils or when different species have different nutrient requirements. Water-logging can increase the levels of more soluble ions in soil which can then become toxic to plants. Thus water-logged plants often contain high levels of iron (Jones & Etherington 1972); Ladiges & Kelso 1977) and manganese (Jones 1972). The effects of such nutrient changes is determined by the plants resistance to

toxicity and the amount of ions initially in the soil. Further indirect effects would result from the reduction in shoot biomass, which reduces the plants ability to absorb nutrients and moisture and survive subsequent dry seasons.

Factors other than the direct ability to tolerate saturation will determine a plants survival in the field. For example *Grevillea* shrubs appear to be more shallow rooted than the eucalypts thus increasing their ability to survive under saturated conditions. Similarly *E. tetrodonta* can survive on areas where the surface is saturated in the wet season, by adopting the root sucker lifeform which have shallow roots and a growing season largely restricted to the dry season.

However, although the eucalypts showed a poor growth rate associated with water logging compared to the *Grevillea*, they did survive for a relatively long period of time (cf. Gill 1985). Thus it is doubtful that the wet season water tables observed in the Yapilika/Rola plains area (Chapter 2 and 4) would exclude eucalypt growth and establishment on the plains boundary.

Drought

The rates of leaf weight loss from the transpiration experiment, are a measurement of the amount of moisture escaping through the stomata before stomatal closure, which often occurs between half and one hour after cutting (Bannister 1964). It is assumed weight loss represents variation in water loss from the leave's stomata and cuticle and that there is no evaporation from the cut petiole. Similar measurements have been used in the past to give approximate insights into the water relations of plants (Gloaghuen 1987) and have corresponded to the observed trends in species drought resistance. Thus *E. tetrodonta* seedlings appear able to maintain a lower moisture content and potential in their leaves and a lower transpiration rate than *E. miniata* and *G. pteridifolia*, under

abundant moisture conditions. This may be partly explain *E. tetrodonta* seedlings showing lower susceptibility to desiccation in the pot trials.

The result that *E. tetrodonta* seedlings are more tolerant to drought than *E. miniata* corresponds to the field observations that the former species is more prominent on drier sites than the latter (Chapter 2). However *Grevillea pteridifolia*, which showed lower drought resistance than the eucalypts, occurs on the transition sites which are drier than the forests (Chapter 4) in addition to seasonally wet sites (Chapter 2). In this case either the response of the mature plant differs greatly to the seedling, or the physiological amplitude of the species is modified by environmental factors resulting in a different ecological amplitude. Thus the *Grevillea* may be growing on the transition site due to a lack of competition from a eucalypt overstorey, which is absent due to factor(s) other than drought.

However, there is other evidence that drought alone is not restricting the growth of eucalypts on the plains. The lowest pre-dawn leaf potentials reached by the seedlings in droughted pots were lower than those recorded at midday from seedlings growing in the field (Section 5.3.3). Also, the terminal soil moisture content in pots, was equal to or lower than field surface moisture contents measured and substantially lower than sub-soil measurements. Furthermore, well watered seedlings grown in plains soil under nursery conditions did not grow faster than unfertilised seedlings on the plains field site, indicating that water was not limiting seedling growth.

Thus the data presented in this Chapter support the results obtained in Chapter 4, that seedlings planted on the plains, although under greater moisture stress than those on the ecotone site, appeared to be receiving adequate water at the end of the dry season to survive and grow.

Fire

The ability of seedlings to withstand the effects of fire is seen as of fundamental importance to regeneration of north Australian forests (e.g. Lacey & Whelan 1976). However published data relevant to this issue is scarce. The data presented in this thesis, relating to the effects of burning on seedling survival, are in agreement with an unpublished report by Stocker (Conservation Commission of the Northern Territory Forestry E.P. 261, 1969). This report showed that *E. tetrodonta* and *E. nesophila* seedlings planted at Gunn Point had survival rates of 35 and 100% when burnt 6 months after planting and 94 and 100% when burnt 18 months after planting. The higher survival rates reported in the Stocker experiment may be due to the fact the seedlings used had been grown in potting mix under nursery conditions for a substantial period before planting out, and thus were bigger than the seedlings used in the trials at Yapilika.

The data presented in this thesis indicate that eucalypts of the region may only require one fire free dry season after germination to survive burning. Much of the open-forest and plains on Melville Island are burnt off as soon as possible each dry season. These early season burns are cooler than those occurring late in the year and go out at night leaving small patches of unburnt areas. This is likely to be similar to the fire regime manufactured by Aboriginal people over much of northern Australia before European settlement (Haines 1986) and implies that eucalypts are likely to be able to sexually reproduce under current fire regimes.

It has been emphasised that the ability of juveniles to escape the effects of fire and grow on to trees is dependent on both fire regime and the growth rate of the seedlings which in turn is at least partly determined by site factors (Lacey & Whelan 1976, Bowman 1986, Bowman & Minchin 1987). The net result of site factors at Yapilika was that seedlings on

the plains grew slower than those in the transition zone and thus would have less chance of escaping the effects of fire. However, the results also indicate that, on the shrubland and transition sites, a fire free interval of greater than 2 years would be required before seedlings could obtain sufficient height to avoid the removal of their above ground parts by fire. Thus, although seedlings could establish in the transition zone, the current fire regime would preclude their continued height growth.

The results from thirteen years of fire exclusion in an *E. miniata, E. tetrodonta* open-forest, suggest that little eucalypt regrowth develops under an open-forest canopy in the absence of fire (Bowman *et al.* 1988b). This is supported by the result in this thesis that seedlings in the forest grew slowly. Thus fire would also tend to prevent the recruitment of these seedlings in the absence of a release from the factors inhibiting their growth.

The intensity of fires is related to vegetation type in northern Australia (Bowman 1986, Bowman *et al.* 1988a, Bowman & Wilson 1987). The absence of canopy on the plains would result in stronger winds, greater evaporation and drier fuels and be expected to cause more intense and/or frequent fires than in the adjacent forest. This is supported by the authors observations that many early dry season fires in the area, are more intense on the plains or stop burning at the forest/ plains boundary. Thus the vegetation on the plains tends to create a more fire prone environment which would tend to retard seedling establishment and growth and reinforce the vegetation pattern.

5.4.2 *E. tetrodonta* sucker growth in response to environmental factors

The results presented here are in agreement with the observations of Lacey & Whelan (1976) that most of the growth of *E. tetrodonta* suckers occurs in the first few months after burning and that little growth occurs

in the following wet season.   Jones & Laude (1956) related similar seasonal variation in the sprouting of plants in Californian Chamise vegetation to seasonal variation in plant physiology.   Fire has been shown to promote sprouting in savanna species (Hopkins 1965). On the Melville plains, old shoots are replaced in the absence of fire, but are not as numerous or vigorous as sprouts stimulated by fire.   Suckers protected from fire did not respond dramatically to fertilising and/or weed control. Thus, the suckers tested appear to be a physiologically incapable of advanced growth, at least over the 18 month measurement period.

The lack of sucker growth could be due to site constraints, such as a lack of adequate moisture supply, although the relatively dramatic response of the seedling growth on a similar site to the same fertiliser treatment (Section 5.3.1) indicates otherwise. The loss of sprout vigour could be related to the physiological deterioration of the plants with age (Lacey & Whelan 1976).   Connor & Wilson 1(968) have reported that fertiliser treatment stimulated the growth of the *Angophora* (Myrtaceae) coppices sufficiently to escape the effects of the triennial fire regime and develop into low trees, in wet heathlands in southern Queensland. However, in this case there was little significant response reported in first years (see also Specht *et al.* 1977) indicating the Melville Island experiment may have produced different results if run for a longer period of time.

The better growth of the suckers in the forest compared to the plains is probably due to a combination of better site conditions and better physiological condition of the plants.   These plants may be able to respond with an increase in growth rate to the removal of the overstorey. Lacey & Whelan (1976) quoted *E. miniata* growing 4 metres in 4 years in a fire protected clear-felled area. Wilson & Bowman (1987) suggest that relatively dense, small size eucalypt trees in an area adjacent to Darwin developed from regrowth following the removal of the overstorey by a strong cyclone (Tracey) in 1974.   However, Fensham (1990) has

presented data showing a slow and patchy response of eucalypt sucker growth to canopy removal or fertiliser addition. Thus it appears that, although numerous, only a small proportion of lignotuberous and root suckers have the physiological potential to develop into trees. Furthermore they require a relatively long fire free interval to do so, as indicated by their slow growth rate compared to seedlings.

Clumps of suckers on the Melville Island plains rarely exceed half a hectare. Lacey & Whelan (1976) observed that similar clonal clumps in the Northern Territory were limited to 55 m^2 and often originated from trees. It is not clear whether *E. tetrodonta* clumps can develop from lignotuberous growth of seedlings or must originate from the roots of trees. However, as the seeds cannot spread far from a tree it is likely that the isolated lignotuber patches on the plains originated from trees and therefore may indicate a contraction of the forests.

CHAPTER 6 SUMMARY AND CONCLUSIONS

The introduction to this thesis put forward the hypothesis that a lack of trees in tropical regions is often associated with environmental constraints which preclude tree growth by retarding, the successful establishment of tree species or, the development of established individuals to trees. Although the forest plains boundary on Melville Island is not associated with environmental changes which are obvious on initial inspection, detailed examinations presented in Chapters 2 - 5 showed several interrelated biotic and abiotic elements that may limit tree growth. These elements, and the relationships between them, are summarised in Figure 6.1. The remainder of this chapter discusses these factors in relation to vegetation patterning across the forest plains boundary and to some of the general models that have been put forward to explain the differential growth of tree and grasses, particularly in tropical savannas.

The structure and composition of the vegetation of the plains is qualitatively different to the common vegetation types of northern Australia (Chapter 2). However, the major environmental parameters associated with the vegetation patterning in the area are similar to those found in many phytosociological studies of the region. Many of the environmental factors which differentiate the plains from the adjacent open-forests and are associated with a lack of tree growth (Figure 6.1), can be related to the geomorphogenesis of the plains. Thus the formation of the plains by the deposition of colluvium in a low lying basin has resulted in higher water tables and sandier soils with inherently lower moisture and nutrient contents (Chapter 4).

Although detailed field measurements showed that the soil moisture content (percent and potential) of the plains was consistently lower than the adjacent open-forests, there appeared to be adequate moisture at
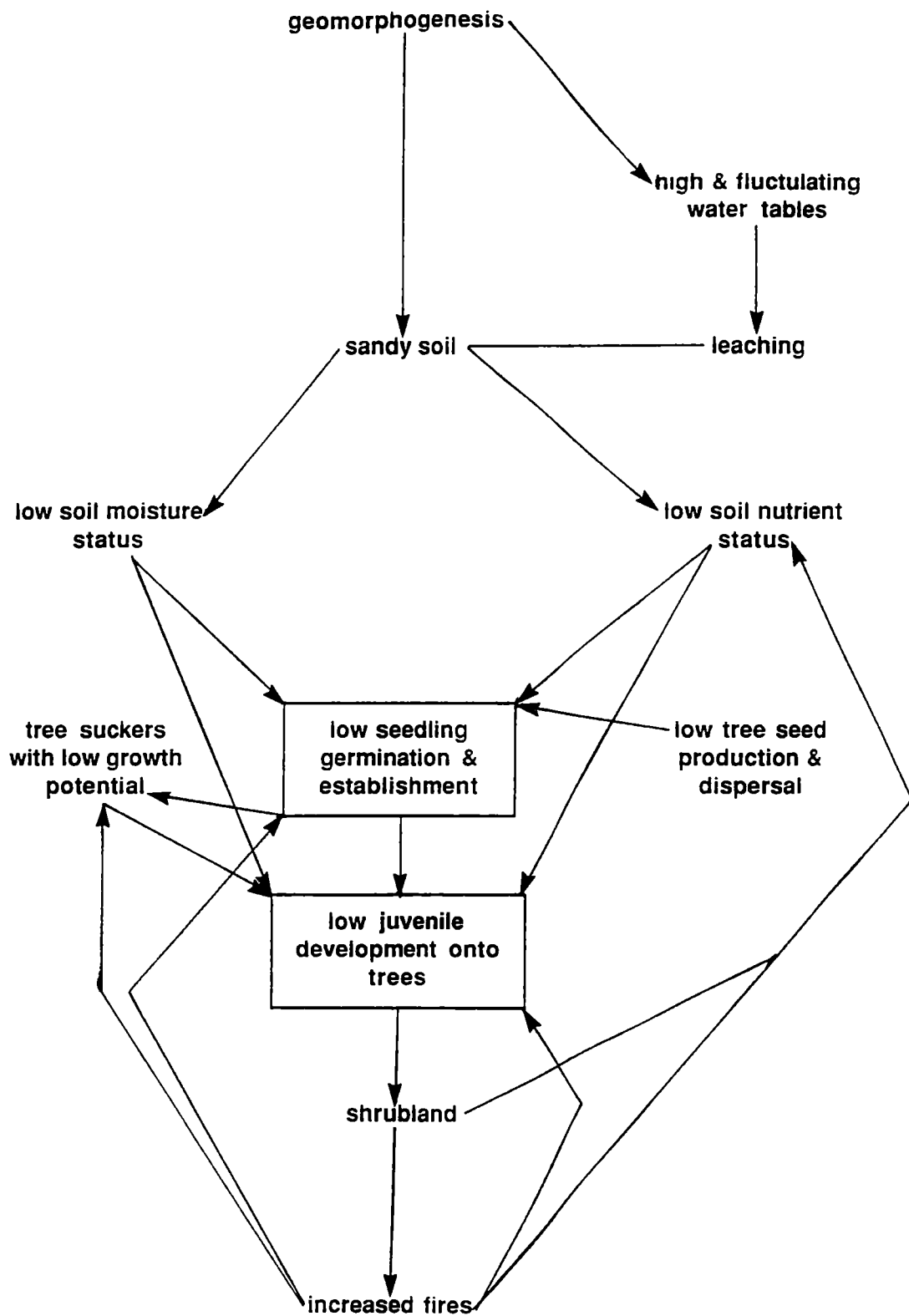
Figure 6.1 The relationship between major environmental factors which act to reduce tree establishment and growth on the Melville Island plains.

depth to support tree growth throughout most of the year (Chapter 4). Thus, fertilised seedlings planted on the plains grew 5-10 times faster than adjacent unfertilised seedlings, probably because they were able to develop extensive root systems which could tap sub-surface moisture reserves throughout the year. By comparison, well watered seedlings planted in pots did not grow substantially faster than unwatered seedlings growing on the plains. The field plantings and associated pot trials also reported in Chapter 5 gave further support to these observations by showing that seedlings could grow under conditions of higher moisture stress than those recorded in the field.

Depth to the water table was generally lower on the plains than adjacent forest sites, although minimum water table depths varied widely across the different boundaries studied. Drainage is normally invoked as a major determinant of vegetation patterning where water tables perch on a shallow (<1.0 m) clay layer. By contrast, the deep sandy soils at Yapilika appear to be able to drain excess water rapidly at the end of the wet season (Chapter 4). Thus, although drainage appeared to be limiting tree growth on the wetter parts of the plains (Chapter 2) and across the forest to *Grevillea* woodland (boundary transect 7, Chapter 3 & 4), present and past water table levels did not appear to be directly limiting tree growth over the forest shrubland boundaries studied.

Nutrients were implicated as exerting a significant effect of the growth of tree seedlings across the forest plains boundary. The sandy plains soils had significantly lower nutrient levels compared to the adjacent open-forests (Chapter 4). The differentially greater response of seedlings planted on the plains to the addition of fertiliser, suggested that nutrients were more limiting to growth on the shrubland compared to the transition sites (Chapter 5). Pot trials showed that soils from the plains were associated with a lower growth rate than forest soils and that the differential growth rates were not due to variations in mycorrhizal

distribution (Chapter 5).

The higher nutrient status of the forest soils may be partly due to vegetation induced accumulation by trees and losses due to the hotter, more frequent fires associated with the shrublands of the plains. However nutrient losses on the plains are possibly a consequence of the deep sandy soils combined with the relatively high rainfall and water table levels of the area. These factors tend to promote leaching of chemicals down the profile leading to impoverishment of soil fertility levels. It is suggested that the particularly low levels of calcium and magnesium and the associated high levels of aluminium could be important limiting factors to tree growth on the plains. However, the addition of calcium and magnesium to seedlings growing across a forest plains boundary did not stimulate growth compared to adjacent unfertilised seedlings (Chapter 5). Further work on the effects of these nutrients on the growth of eucalypts is necessary to give more conclusive results in relation to Yapilika and may also provide useful insights into eucalypt patterning throughout northern Australia.

The suggestion that nutrients play a more important role than dry season soil moisture, contrasts with many previous studies in northern Australia which have implicated soil moisture as the overriding determinant of vegetation patterning. However, in this and other tropical savanna regions of the world, soils with high water holding capacity are also generally those with high nutrient levels, making it difficult to separate these elements. Thus, although one may play a greater role than the other in determining vegetation patterns in certain situations, generally both factors will be included in any environmental-vegetation model (e.g. Figure 6.1).

Several treatments were imposed on root suckering *E. tetrodonta* plants, on and adjacent to the plains, in attempts to stimulate growth (Chapter

5). There was no response after two years to the addition of various fertilisers in combination with thinning and fire protection treatments. These results were in marked contrast to the large and rapid increases in seedling growth on the plains which were associated with comparable fertiliser treatments (Chapter 5). Thus although common under the forest canopy and to a lesser extent the plains, most of the eucalypt root suckers in the area appear to be physiologically retarded from developing into trees, irrespective of the edaphic and other environmental conditions they are exposed to. Root suckers on the plains could have originated from vegetative spread from the forest, but are possibly the remnants of a retreating tree cover.

The association of the sharp structural boundary with a gradual environmental boundary (Chapter 3 and 4) indicates that the forest plains boundary on Melville Island cannot be explained by edaphic factors alone (Chapter 4). Furthermore the field plantings (Chapter 5) indicate that tree seedlings can grow on shrubland sites, albeit at reduced rates compared to transition sites. Thus the limitations to tree growth on the plains are not absolute with no clear overriding causal agent, but involve several vegetation-environmental interactions (Figure 6.1).

The ability of seedlings to withstand the effects of fire is seen as of fundamental importance to regeneration of north Australian forests (Chapter 5). The data presented in Chapter 5 indicate that eucalypt seedlings growing at Yapilika, rapidly develop the ability to renew their aerial parts after removal by fire and may only require one fire free dry season after germination to survive burning. However, the current fire regime on the plains would prevent seedlings growing onto trees. The interaction between fire and the differential seedling growth rates across the forest plains boundary, would result in higher seedling establishment and growth on sites close to the forest compared to sites on the plains. This relationship is compounded by the promotion of more intense and

frequent fires by the more open plains vegetation. Thus, in the absence of fire, eucalypt seedlings may be capable of successfully establishing and growing on to trees on some plains sites. In such a fire free environment it is hypothesised that tree growth would diminish across the current 'transition' zone, resulting in a gradual structural boundary paralleling the gradual floristic boundary (Chapter 3).

Field and nursery trials indicated that the seed of the dominant eucalypt species of the area appear to be able to germinate and develop rapidly if subjected to good early rains, but fail to develop if early rains are poor (Chapter 5). Furthermore, although not specifically studied, it was apparent that the eucalypts in the Yapilika area flowered and seeded sporadically and that seed shed took place immediately (within 2-3 weeks) after seed ripening at the end of the dry season. These facts suggest that episodic germination events may be an important mechanism in seedling establishment in northern eucalypt forests and may partly explain why few germinants were found in the Melville Island forests (Chapter 3). The sporadic germination combined with the low dispersability of the seed of the dominant eucalypts (Chapter 5) and the low ability of suckers to develop onto trees, would result in a potential low colonisation rate of the plains by the dominant eucalypt species. This inherently conservative ability to colonise the plains would reinforce the edaphic and fire induced patterns discussed above.

Changes in vegetation across the forest plains boundary have the potential to exert direct effects on seedling establishment and growth. The more open vegetation of the plains promotes higher surface evaporation rates (Chapter 4) which could reduce germination of eucalypt seeds compared to the shaded forest sites. However the field studies reported in Chapter 5 showed that germination and growth under the forest was lower than on adjacent plains sites. This could be explained by the confounding effect of competition from the tree canopy on the

relationship between edaphic factors and seedling growth rates and implies that tropical eucalypts require relief from overwood influence to regenerate successfully. The results from this study (Section 5.3.1) suggest a gap size of at least 50 metres is required on forest sites adjacent to the treeless plains, to avoid suppression of eucalypt seedling growth. Further from the plains, on less sandy soils (i.e. with higher moisture and nutrient status), the number of tree saplings increased (Chapter 2), which could be due to higher growth rates and lower gap size requirement on these sites.

The decrease in soil moisture with depth found in forest, but not adjacent shrubland soils (Chapter 4), gave indirect evidence of resource partitioning between the strata. It is suggested that trees in the Melville Island forests thrive by developing deep and extensive root systems which can tap sub-soil resources all year round, while the herbaceous and low shrub components rely mainly on the surface layers of the soil for the majority of their resources. The differential resource partitioning of woody and herbaceous growth is a central focus of many savanna studies (Chapter 1), but has not been considered to great extent in tropical eucalypt forests where many studies have confined environmental measurements to 'easy to measure' surface parameters (e.g. Chapter 2). This study has given some indirect evidence that the differential distribution of resources and their interactions with fire could be an important determining factor of vegetation patterns in north Australia. Thus there is a need to differentiate under and overstorey floristic composition and their associations with surface and sub surface edaphic factors, to adequately describe vegetation patterning and environmental correlates in the region.

The distribution of savannas throughout the world is generally associated with climatic factors while regional variations have been related to edaphic or disturbance regimes (Chapter 1). There is a general

consensus that tree growth is absent from areas with clay soils which are saturated in the wet season (Chapter 1 & 3), as was concluded on the wetter areas of the Melville Island plains (Chapter 2). It appears that fewer generalisations are possible on sandier, drier soil types. For example, the models presented by Walker & Noy-Meir (1982) and Johnson & Tothill (1985) which relate increases in woody vegetation to increases in sand content or decreases in soil moisture content, are not applicable to the Melville Island situation where woody vegetation decreased with increasing sand content. Models which are more widely applicable to drier savanna types, incorporate all possible environmental factors influencing vegetation structure in broad non-qualitative ways and accept that different factors will be more important in different situations. In this context, Figure 6.1 can be seen as a modification/sub-set of such a model put forward by Walker (1987).

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APPENDIX 1

Mean abundance and frequency of all species by community

Abundance is given in the following percent projected foliage cover categories

1: 0-1%
2: 1-5%
3: 5-25%
4: 25 -50%
5: 50 -75%
6: 75 -100%

Frequency (in brackets) is given in the following percent categories

1: 0-10%
2: 1-20%
3: 20 -30%
4: 30 -40%
5: 40 -50%
6: 50 -60%
7: 60 -70%
8: 70 -80%
9: 80 -100%

Collecting numbers of species lodged in the Darwin hebarium given in brackets after taxa not identified to the species level (BW = B. Wilson).

Group	1	2	3	4	5	6	7

Species

Mature lifeform tree or shrub

Species	1	2	3	4	5	6	7
Acacia aulacocarpa	2 (6)	-	1 (1)	1 (1)	-	-	-
Acacia difficilis	-	3 (8)	2 (7)	3 (7)	1 (1)	4 (9)	1 (2)
Acacia gonocarpa	-	3 (9)	1 (3)	1 (1)	-	2 (8)	-
Acacia dimidiata	-	-	-	-	2 (2)	-	1 (2)
Acacia latescens	2 (5)	2 (4)	2 (4)	2 (3)	2 (2)	3 (9)	1 (2)
Acacia oncinocarpa	3 (7)	2 (5)	4 (9)	3 (6)	3 (7)	1 (1)	1 (2)
Alphitonia excelsa	2 (5)	2 (3)	1 (3)	1 (2)	1 (2)	2 (9)	1 (2)
Ampelocissus acetosa	1 (2)	-	-	-	-	-	-
Banksia dentata	1 (1)	1 (1)	2 (2)	2 (3)	2 (6)	-	1 (4)
Buchanania obovata	1 (4)	1 (1)	2 (7)	2 (8)	1 (6)	-	1 (3)
Calytrix exstipulata	-	2 (5)	1 (1)	1 (1)	1 (1)	3 (7)	1 (1)
Cassia mimosoides	1 (1)	-	-	1 (2)	-	1 (2)	-
Cycas armstrongiana	1 (2)	-	-	-	-	-	-
Distichostemon hispidulus	1 (3)	3 (9)	2 (8)	2 (9)	2 (4)	-	1 (1)
Erythrophleum chlorostachys	2 (2)	-	1 (1)	1 (2)	-	-	-

Group	1	2	3	4	5	6	7

Species

Species	1	2	3	4	5	6	7
Eucalyptus confertiflora	-	1 (1)	-	-	-	-	-
Eucalyptus grandifolia	-	-	-	1 (2)	1 (1)	-	1 (2)
Eucalyptus latifolia	1 (1)	-	-	-	-	-	-
Eucalyptus miniata	4 (7)	2 (1)	2 (2)	-	-	1 (1)	-
Eucalyptus nesophila	4 (9)	1 (1)	3 (9)	1 (3)	2 (3)	1 (5)	1 (2)
Eucalyptus polycarpa	-	1 (1)	-	-	-	1 (1)	1 (2)
Eucalyptus porrecta	-	2 (1)	-	1 (2)	-	-	2 (3)
Eucalyptus ptychocarpa	1 (1)	1 (1)	-	2 (4)	2 (4)	-	2 (2)
Eucalyptus tetrodonta	3 (6)	1 (1)	4 (9)	2 (6)	-	-	1 (1)
Gardenia megasperma	1 (2)	1 (1)	1 (1)	-	1 (2)	2 (1)	1 (2)
Gardenia suffruticosa	1 (4)	1 (1)	1 (4)	1 (3)	1 (4)	-	-
Grevillia heliosperma	2 (7)	1 (1)	2 (2)	2 (4)	-	1 (2)	1 (2)
Grevillea pteridifolia	2 (5)	3 (5)	3 (8)	1 (9)	2 (7)	1 (8)	1 (8)
Grevillea goodii	3 (6)	3 (9)	3 (9)	2 (6)	3 (9)	-	1 (1)
Hibbertia cistifolia	2 (8)	3 (8)	3 (9)	1 (6)	2 (9)	1 (3)	1 (3)
Indigofera saxicola	1 (1)	-	-	-	-	-	-

Group	1	2	3	4	5	6	7
Species							
Ixora tomentosa	-	-	-	-	-	1 (1)	-
Jacksonia dilatata	-	1 (1)	-	-	1 (1)	3 (8)	1 (1)
Livistona humilus	3 (9)	2 (6)	2 (4)	1 (3)	3 (9)	2 (4)	2 (5)
Lophostemon lactifluus	-	1 (1)	-	2 (3)	3 (7)	-	3 (6)
Melaleuca nervosum	-	-	-	1 (2)	2 (2)	-	2 (4)
Melaleuca viridiflora	-	-	-	-	1 (1)	-	1 (1)
Osbeckia australiana	-	-	-	1 (1)	1 (1)	-	1 (2)
Pachynema complanatum	1 (5)	2 (9)	2 (9)	2 (7)	2 (6)	1 (1)	1 (2)
Pandanus spirallis	2 (4)	-	1 (2)	-	1 (2)	-	1 (2)
Persoonia falcata	2 (9)	2 (9)	2 (9)	2 (8)	2 (7)	1 (5)	1 (6)
Petalostigma pubescens	-	-	-	-	-	-	1 (1)
Petalostigma quadriloculare	1 (1)	-	-	3 (6)	2 (5)	-	2 (4)
Planchonella pohlmaniana	1 (2)	1 (1)	-	1 (1)	1 (1)	1 (1)	-
Planchonia careya	2 (8)	-	2 (8)	2 (7)	2 (2)	2 (1)	1 (2)
Syzigium eucalyptoides sub. *bleeseri*	1 (1)	-	1 (1)	3 (8)	3 (6)	-	3 (8)
Syzigium suborbiculare	-	-	1 (1)	1 (1)	1 (1)	1 (1)	-

Group	1	2	3	4	5	6	7
Species							
Terminalia ferdinandiana	3 (4)	2 (2)	2 (2)	3 (5)	2 (2)	1 (2)	1 (2)
Verticordia cunninghamii	-	-	-	-	1 (1)	1 (2)	1 (3)
Wrightia saligna	2 (3)	2 (4)	1 (3)	1 (3)	1 (4)	1 (1)	1 (2)

Group	1	2	3	4	5	6	7

Species

Mature lifeform herb vine or fern.

Species	1	2	3	4	5	6	7
Alloteropsis semialata	2 (5)	1 (5)	2 (7)	1 (2)	-	-	1 (1)
Aristida holathera	1 (1)	2 (8)	1 (1)	-	1 (2)	2 (3)	1 (2)
Bonamia breviflora	1 (1)	-	-	-	-	-	-
Borreria breviflora	3 (8)	3 (7)	2 (6)	2 (3)	1 (3)	2 (7)	-
Borreria exerta	-	-	-	-	-	1 (1)	-
Borreria sp. (BW 56)	-	-	-	-	1 (1)	-	-
Brachiaria holosericea	1 (1)	1 (3)	1 (2)	-	-	2 (6)	-
Buchnera gracilis	1 (2)	1 (2)	1 (4)	1 (2)	1 (2)	1 (1)	1 (2)
Buchnera linearis	-	-	-	-	1 (1)	-	-
Burmannia juncea	-	-	-	-	-	-	1 (1)
Cassytha filiformis	-	1 (2)	-	1 (1)	1 (1)	1 (1)	1 (2)
Cheilanthes tenuifolia	1 (1)	-	-	-	1 (1)	-	-
Chrysopogon latifolius	2 (5)	-	-	-	-	-	-
Coelorhachis rottboellioides	-	-	-	-	1 (1)	-	-

Group	1	2	3	4	5	6	7

Species

Species	1	2	3	4	5	6	7
Desmodium brownii	-	-	1 (1)	1 (1)	-	-	1 (2)
Desmodium clavitricha	3 (7)	1 (1)	1 (1)	-	1 (1)	-	1 (1)
Digitaria ciliaris	1 (1)	1 (1)	-	-	-	1 (1)	-
Drosera petteolaris	1 (2)	2 (7)	1 (7)	1 (4)	2 (9)	1 (1)	1 (7)
Eragrostis cummingii	2 (3)	2 (8)	1 (4)	1 (2)	2 (4)	1 (5)	-
Eriachne agrostidea	-	-	-	-	-	-	1 (1)
Eriachne armittii	-	-	-	-	-	2 (2)	-
Eriachne avanacea	2 (9)	4 (9)	4 (9)	3 (9)	4 (9)	2 (2)	3 (7)
Eriachne burkittii	2 (1)	1 (1)	2 (2)	4 (9)	3 (9)	1 (2)	3 (7)
Eriachne ciliata	-	2 (4)	-	1 (2)	-	3 (9)	-
Eriachne obtusa	1 (1)	3 (9)	2 (4)	1 (1)	3 (5)	4 (9)	1 (1)
Eriachne squarrosa	1 (3)	3 (8)	2 (2)	1 (1)	3 (2)	4 (5)	1 (1)
Eriachne triseta	4 (7)	2 (4)	2 (5)	1 (3)	2 (6)	4 (9)	2 (2)
Eulalia mackinlayi	3 (7)	-	2 (4)	3 (9)	3 (5)	-	2 (5)
Euphorbia vachellii	-	-	1 (1)	1 (2)	-	-	-
Eurybiopsis macrorhiza	-	1 (3)	1 (4)	1 (1)	-	-	-

Group	1	2	3	4	5	6	7
Species							
Fimbristylis densa	1 (2)	1 (3)	-	1 (3)	1 (3)	1 (3)	1 (4)
Fimbristylis furva	-	-	-	1 (1)	1 (1)	-	3 (4)
Fimbristylis oxystachys	-	2 (5)	-	-	-	-	-
Fimbristylis sp. (BW 74)	-	-	-	-	-	-	1 (1)
Fimbristylis sp. (BW 78)	-	-	-	-	1 (1)	-	-
Fimbristylis sp. (BW 155)	-	-	-	-	1 (1)	-	-
Fimbristylis sp. (BW 88)	-	-	-	-	-	-	1 (1)
Fimbristylis sp. (BW 89)	-	-	-	-	-	-	1 (2)
Flemingia parviflora	2 (4)	-	1 (1)	1 (3)	2 (2)	-	1 (2)
Galactia tenuiflora	1 (3)	-	-	-	1 (2)	-	-
Germania grandiflora	-	-	-	1 (1)	1 (1)	-	2 (4)
Goodenia leiosperma	-	1 (2)	-	-	1 (2)	-	1 (2)
Habernaria ochroleuca	1 (1)	-	-	-	-	-	-
Haemodorum brevicaule	-	-	1 (1)	1 (1)	1 (2)	-	-
Haemodorum corymbosum	1 (1)	-	-	-	-	-	-

Group	1	2	3	4	5	6	7
Species							
Ipomoea gracillus	-	1 (1)	-	-	-	-	-
Ipomoea graminea	-	-	1 (2)	1 (1)	-	-	1 (1)
Leptocarpus spathaceus	-	1 (1)	-	2 (2)	2 (2)	-	2 (4)
Lomandra tropica	1 (2)	1 (2)	-	1 (1)	1 (2)	-	1 (1)
Mitrasacme arnhemica	-	-	-	-	1 (2)	-	1 (1)
Mitrasacme elata	1 (1)	1 (1)	1 (2)	1 (3)	1 (3)	1 (2)	1 (1)
Mitrasacme exerta	1 (1)	2 (8)	1 (2)	2 (7)	1 (3)	1 (5)	1 (2)
Mitrasacme pygmea	-	-	-	-	1 (2)	-	1 (1)
Mitasacme sp.	1 (7)	1 (4)	1 (7)	1 (2)	1 (1)	1 (1)	1 (1)
Mitrasacme stellata	-	1 (2)	1 (2)	1 (2)	1 (4)	1 (1)	1 (2)
Murdania graminea	-	-	-	-	-	-	1 (2)
Panicum mindanaence	1 (2)	-	1 (2)	1 (2)	1 (2)	-	1 (1)
Patersonia macrantha	-	-	1 (1)	-	-	-	-
Phyllanthus simplex	-	-	1 (1)	-	1 (1)	-	1 (1)
Polygala ericephala	1 (3)	1 (6)	1 (6)	1 (3)	1 (1)	-	1 (1)
Polygala longifolia	-	-	-	1 (1)	1 (2)	-	-

Group	1	2	3	4	5	6	7
Species							
Polygala orbicularis	2 (8)	1 (3)	2 (8)	1 (2)	1 (1)	-	-
Pseudopogonatherum contortum	2 (4)	1 (1)	-	1 (1)	2 (3)	2 (3)	1 (2)
Ptilotis distans	-	1 (1)	-	-	-	-	-
Rhynchospera heterochaeta	-	-	1 (1)	1 (6)	3 (8)	-	3 (9)
Rottboellia formosa	-	-	-	2 (2)	-	-	1 (1)
Sacciolepis indica	-	-	-	-	-	-	1 (1)
Sauropus brunonis	1 (1)	1 (1)	-	1 (5)	-	-	1 (1)
Sauropus ditassoides	1 (1)	-	-	-	-	-	-
Sauropus glauca	1 (2)	1 (4)	1 (7)	1 (5)	1 (3)	-	1 (2)
Schizachyrium fragile	-	1 (1)	1 (1)	-	-	2 (3)	2 (2)
Schoenus sparteus	-	-	-	-	-	1 (1)	-
Scleria brownii	1 (1)	-	-	-	-	-	1 (3)
Scleria novea-hollandise	-	-	-	-	-	-	1 (1)
Scleria sphacelata	-	-	-	-	-	-	1 (1)
SCROPHULACEAE (BW 95)	-	-	-	1 (1)	1 (1)	-	-

Group	1	2	3	4	5	6	7
Species							
Setaria apiculata	2 (2)	2 (5)	-	1 (2)	-	1 (7)	-
Sorghum intrans	2 (1)	4 (5)	3 (4)	2 (2)	2 (5)	4 (3)	4 (4)
Sorghum plumosum	3 (5)	3 (8)	4 (9)	3 (4)	3 (7)	1 (1)	3 (3)
Stackhousia intermedia	-	1 (3)	1 (2)	1 (1)	-	-	1 (1)
Stylidium leptorrhizum	-	-	-	1 (2)	1 (4)	-	1 (3)
Stylidium 'pink' (BW 84)	-	-	-	1 (1)	-	-	1 (2)
Stylidium 'white' (BW 79)	-	-	-	-	1 (2)	-	-
Thaumastochloa major	3 (9)	2 (7)	2 (8)	1 (4)	2 (7)	1 (5)	-
Thysanotus banksii	-	-	-	-	-	-	1 (1)
Trachymene didiscoides	-	1 (3)	1 (1)	1 (3)	2 (3)	-	-
Uraria lagopodioides	1 (1)	-	-	1 (1)	-	-	1 (1)
Utricularia sp. (BW 101)	-	-	-	-	-	-	1 (2)
Vigna vexillata	1 (1)	-	-	1 (1)	-	-	1 (2)
Xyris complanata	-	-	-	-	-	-	1 (2)
Yakirra nulla	2 (1)	1 (4)	-	1 (1)	1 (2)	1 (1)	-

APPENDIX 2

Vegetation Map - Located in envelope attached to back cover.

APPENDIX 3

Soil moisture content (%) by matric potential (lbs/in2) across different boundary types.

Soil Depth (cm)	15-30		75-90	
Potential (Bars)	-1/3	-15	-1/3	-15

E. miniata open-forest to
Acacia open-shrubland
(n = 3)

Forest	10.9	8.8	11.0	7.8
	(2.8)	(2.3)	(1.3)	(0.8)
Shrubland	7.7	6.2	8.1	6.0
	(0.4)	(0.3)	(0.5)	(0.6)

E. tetrodonta open-forest to
Acacia open-shrubland
(n = 2)

Forest	9.0	7.4	9.0	8.2
	(1.4)	(0.8)	(1.0)	(0.8)
Shrubland	8.3	7.1	8.6	7.2
	(1.4)	(0.8)	(0.6)	(0.5)

E. miniata open-forest to
G. pteridifolia scrub
(n = 2)

Forest	13.1	8.7	18.9	15.0
	(1.1)	(0.6)	(0.3)	(0.1)
Woodland	11.5	7.5	12.9	10.1
	(3.2)	(1.7)	(5.5)	(4.2)