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THE FOREST IN MOTION: EXPLORATORY STUDIES IN WESTERN ARNHEM LAND, NORTHERN AUSTRALIA.

BY

JEREMY RUSSELL-SMITH

A Thesis submitted for the degree of Doctor of Philosophy at the Australian National University.

June, 1986
Except where otherwise acknowledged, I have undertaken all the work presented here. One of the constituent papers of this thesis is co-authored. My contribution to that paper is set out clearly in the introduction.

The papers contained in this thesis, and the research upon which they are based, have not been presented as part of the requirements of any other degree.

Jeremy anderson
ABSTRACT

As a contribution to academic debate concerning northern Australian vegetation ecology and history, and as a contribution also to contemporary land management issues in that region, the findings of various biogeographical, ecological and ethnobotanical studies are presented here which, collectively, explore the status of monsoon vine-forest (MVF) vegetation in the western Arnhem Land region of the Northern Territory.

Structurally, the thesis comprises five papers presented in the chronological sequence of their completion, and a brief, explanatory introduction. The first paper, written early in the field-work programme and presented at a northern Australian symposium focusing on current ecological research in the region, describes vegetation changes associated with the advent of European ecological influence in western Arnhem Land (i.e. within the last 100 or so years), at Giina, a traditional Aboriginal camp-site on the edge of the South Alligator River. The paper describes the elimination of MVF at Giina, and its reduction elsewhere in the local area, within the recent historical past. The paper concludes that the destruction of such vegetation is attributable to feral animal impact and changes to the burning regime. These themes are developed in subsequent papers.

Whilst still on field work, and having been approached to present a position paper on MVF in the Northern Territory, the second paper, co-authored with Clyde Dunlop, attempts "to provide an account of the ecology (so far as is known), the condition and the conservation status of monsoon vine-forests in the Northern Territory". This paper challenges the generally accepted view that the scattered distribution of small, discrete patches of MVF across northern Australia is attributable solely to fragmentation of a former closed forest expanse. On the basis of an ecological survey of MVF patches concentrated on the
western Arnhem Land region, but including observations over a wider region of the Northern Territory, it is shown that many MVF patches occur entirely on landforms developed only in the Holocene (i.e. the last 10 000 years) (e.g. coastal riverine floodplain alluvia, coastal beach ridge deposits). Indeed, 70% of the known Northern Territory MVF flora is observed to occur on such landforms. This paper also provides a review of relevant work undertaken on MVF in the Northern Territory at the time of writing, a description of MVF vegetation Habitat Types, an account of the dependent fauna, a checklist of the known flora, and an assessment of the conservation status of MVF in the region.

The third paper, completed at the close of 22 months field studies, was prepared as a consultancy report to the Australian National Parks and Wildlife Service, Canberra. The report details the status, condition, and immediate threats to MVF ecosystems in the vicinity of Kakadu National Park, in the western Arnhem Land region. Special attention is given to the impacts of feral animals, and contemporary and traditional Aboriginal burning practices. The paper also considers the significance of MVF to traditional Aboriginal economy.

The final two papers further develop certain themes outlined in preceding papers. The papers present formal analyses of ecological and biogeographical data, relating the findings to wider academic contexts. On the basis of studies concerning the distribution of MVF in the western Arnhem Land region, and the dispersal capacities and biogeographical affinities of component taxa, the fourth paper considers how these observations may contribute usefully to an understanding of the historical status of MVF in that region. The fifth paper is concerned essentially with the current status of MVF, drawing attention to the ecological ramifications of different burning regimes. To place fire in ecological context, this paper first explores the influence of substrate conditions on MVF distribution. These studies indicate that, in the absence of fire impact, seasonally
xeric, oligotrophic substrates are unlikely to limit widespread development of closed canopy, MVF vegetation.
ACKNOWLEDGEMENTS

The work presented here would not have been possible without the generous support of the Department of Geography (The Faculties, ANU), the Department of Prehistory (Research School of Pacific Studies, ANU), the Australian National Parks and Wildlife Service (Canberra), the officers and owners of Kakadu National Park, and the staff of the Darwin Herbarium (DNA).

I trust I may be pardoned here if I thank openly only a few people who have given me generous assistances in the final stages of this thesis. Many people have helped me substantially at other times, and I trust that they will accept my gratitude given in the Acknowledgements Sections of the various papers which constitute this thesis. Thus, here, I would like to thank simply: my supervisors, Geoff Hope and Len Webb (for their help, criticism and, above all, tolerance); Val Lyon (for her smiles, grimaces, maps, and unbounded generosity); Penny Wilkins (for so many things over the years); Jan Watson (for deciphering my scrawl); Gary Werren (for the beautiful colour map and his mischief); Val Plumwood (for making her forest home open to me); my mother, Meg Russell-Smith (for her love and support); Mark Allon and Keith Taylor, and the many other inhabitants of Spring Valley Farm; and my dear friend Diane, who, selflessly, has given me the energy to survive this madness.
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INTRODUCTION

In 1981 I was offered the opportunity to participate in an investigation of human prehistory and associated palaeoenvironments in Kakadu National Park, in the western Arnhem Land region of monsoonal, northern Australia. One of the main aims of that research project was to place the archaeological record in palaeoenvironmental perspective. It was envisaged that my participation would involve the undertaking of vegetation-oriented studies which might contribute to a better knowledge of past vegetations, and interactions between people and vegetations, in that local region. It is on this basis that the studies outlined here were initiated.

The archaeological field programme was undertaken over a period of six or so months in the dry season. Initially, it was considered that at least a major component of my studies would entail palynological investigation of archaeological study sites. Fortunately, for I am not a person who relishes being laboratory-bound, the sediments were mostly unsuitable for pollen preservation. With little else to go on, and with precious field-work time slipping by, I determined that an indirect window into the past might be obtained through an ecological investigation of monsoon vine-forest (MVF), or seasonal rainforest, vegetation. A number of factors prompted this optimism.

From preliminary reading I was aware that such vegetation was held popularly to be relict (e.g. Hnatiuk & Kenneally 1981; Kikkawa et al. 1981; Langcamp et al. 1981; Nix & Kalma 1972; Specht 1958; Specht et al. 1977; Stocker & Mott 1981; Webb & Tracey 1979, 1981a,b). Thus, most authors considered the occurrence of widely scattered, disjunct patches of MVF across northern Australia as representing the surviving fragments of a former continuous expanse of closed forest vegetation. It was also generally held that the fragmentation of this vegetation was attributable to late Cainozoic climatic deterioration and/or, in
more recent times, to Aboriginal peoples' burning. However, from my own observations in monsoonal Cape York Peninsula (northern Queensland), and again in the Kakadu region, MVF evidently occurred widely on a variety of land surfaces which could be no older than Holocene in age (i.e. less than 10,000 years old), and, in many instances, on demonstrably very young substrates (e.g. coastal beach dunes, coastal riverine alluvia). J.S. Beard (1976) had made similar suggestions concerning MVF in the Kimberley region of northern, Western Australia. How relict was this vegetation?

As well, in a pioneering study undertaken on Melville Island, off the north-west coast of the Northern Territory, Geoff Stocker (1971) had cleverly demonstrated the retreat of a former large patch of MVF on the basis of the occurrence of remnant earthen incubation mounds built by the megapode bird, the Orange-footed Scrub-fowl (*Megapodius reinwardt* [syn. *M.* *freycinet*]). Stocker excavated a number of mounds and submitted basal shell and charcoal fragments for 

As was shown me in Kakadu, similar occurrences of remnant incubation mounds in localised situations might be amenable for study also.

A third factor in my favour was the interest of a number of Aboriginal people whose enthusiasm to introduce me to their country, and their willingness to instruct me in botanical and burning matters, was to ensure that, if all else failed, the study would be at least enjoyable.

With these new directions I set about making the most of the limited time left me in this first field-work period. Mostly, this involved the development of a field programme for sampling MVF in the western Arnhem Land region, and the necessary learning of Linnaean and Aboriginal taxonomies. Through this work, however, it became readily apparent that many MVF patches were
being, as they still are, affected seriously by contemporary burning and feral animal impacts. Indeed, MVF vegetation is a sensitive and useful barometer of such impacts. With these realisations the focus of my studies became much more concerned with the problems of the present day, and the historical development of those problems with the coming of European society.

In 1982, I worked mostly on an unrelated project, but took the opportunity to visit MVF patches on the Cobourg Peninsula (in north-western Arnhem Land) and, as well, for a couple of months found myself staring down a microscope counting pollen grains from samples collected in association with the greater archaeological project.

In 1983/4, with the generous provision of a grant from the Australian National Parks and Wildlife Service, I resumed field studies in the Northern Territory for a further 14 month period. As well as extending my ecological survey of MVF vegetation to other areas in the 'Top End' of the Northern Territory, and resuming my "ethnobotanical" work, I embarked also on two further studies. As an adjunct to the ecological survey, I undertook various studies aimed at assessing the role of dispersal in a number of different ecological situations. The second study concerned a relatively detailed assessment of the influence of substrate conditions on MVF distribution through an examination of seven MVF/savanna boundaries. This study was prompted by the need to ascertain the extent to which substrates might limit the distribution of MVF in western Arnhem Land.

Since returning from the Northern Territory to Canberra in mid-1984, it has taken two years to bring this study to a satisfactory completion. As a contribution to academic debate concerning northern Australian vegetation ecology and history, and as a contribution also to contemporary land management issues in that region, this thesis provides an account of various studies which, collectively, explore the status of monsoon vine-forest vegetation in the western Arnhem Land region.
Presentation

The thesis comprises a series of five papers presented in the chronological sequence of their completion. This structure has been adopted out of necessity since, by the time I came finally to work up my field data, I had been asked or required to write three papers bearing directly on work undertaken. The final two papers complete that work.

The first paper, presented in 1983 at a northern Australian symposium focusing on current ecological research in that region, describes a local study of vegetation change associated with the advent of European ecological influences in the western Arnhem Land region. This paper introduces a number of themes which are developed in subsequent papers.

The second paper was presented at a conference held in Brisbane, in late 1983, under the theme, "the past, present and future of Australian rainforests". After having been approached to present a contribution from the Northern Territory, I sought the assistance of a friend and chief botanist at the Darwin Herbarium, Clyde Dunlop. We discussed the format the paper should take and wrote it together. Under the examination rules of the Australian National University I am required to indicate the extent of my contribution to that paper. I am responsible for most of the paper with the following exceptions: 1. the section on the flora; 2. the list of species given in the Appendix, and; 3. the section on the conservation status of MVF in the Northern Territory, which we wrote jointly.

The third paper is my consultancy report to the Australian National Parks and Wildlife Service. The paper details the status and condition of MVF in the vicinity of Kakadu National Park, giving attention to the impacts of feral animals, contemporary and traditional Aboriginal burning practices, and the significance of MVF to traditional Aboriginal economy.
The final two papers, as yet unpublished, present formal analyses of certain themes outlined in preceding papers, relating the findings to broader academic contexts. On the basis of studies concerning the distribution of MVF in the western Arnhem Land region, and the dispersal capacities and biogeographical affinities of component taxa, the fourth paper considers how these observations may contribute to an understanding of the historical status of MVF in that region. Various data relevant to this paper, but additional to that given in its Appendices, are provided in a series of Additional Appendices at the end of the paper. The final paper is concerned essentially with the current status and condition of MVF, drawing attention to the ecological ramifications and conservation significances of different burning regimes. To place fire in ecological context, this paper first explores the influence of substrate conditions on the distribution of MVF in western Arnhem Land.

I trust these studies may be of use to you.

References


NIX, H.A. & KALMA, J.D. 1972. Climate as a dominant control in the


A RECORD OF CHANGE: STUDIES OF HOLOCENE VEGETATION HISTORY IN THE SOUTH ALLIGATOR RIVER REGION, NORTHERN TERRITORY.

Jeremy Russell-Smith
May, 1983

A record of change: studies of Holocene vegetation history in the South Alligator River region, Northern Territory

J. RUSSELL SMITH

Geography Department, Australian National University, P.O. Box 4, Canberra, A.C.T. 2601

Abstract

A multidisciplinary investigation of human prehistory and associated palaeoenvironments in the southern section of Kakadu National Park, western Arnhem Land, was carried out by the Department of Prehistory, Research School of Pacific Studies, Australian National University in 1980-82. This paper relates specifically to two studies of vegetation history undertaken in the vicinity of Kiina, on the South Alligator River, 80 km from the present coastline. The first study concerns a reconstruction of Holocene vegetation history based on the pollen analysis of wetland sediments. The analysis highlights the relatively recent development of freshwater wetland communities (<1500 years B.P.), and a marked reversion to saline influences in very recent times. The second study examines the spatial retreat of a nearby patch of closed monsoon forest vegetation. Preliminary C¹⁴ dating suggests that this retreat has occurred in very recent times also.

The development of the freshwater wetlands over the longer term is due to continuing terrigenous sedimentation following mid-Holocene flooding by the sea. The marked vegetation changes that have occurred at Kiina in the last 110 years however, may be attributed to the impact of feral animals, especially water buffalo, and to changes in fire regime.

Introduction

In the course of a multidisciplinary investigation of human prehistory and associated palaeoenvironments in Kakadu National Park, two studies of vegetation history were undertaken in the vicinity of Kiina, close to the South Alligator River.

The first study concerns a reconstruction of Holocene plant assemblages associated with coastal riverine sediments, based on pollen analysis. While the investigation of late Quaternary vegetation history has progressed rapidly over recent years in south-eastern Australia (see Fig. 2.2 in Walker & Singh 1981), the northern, central and western sectors of the continent have received little attention. In Northern Australia a notable exception to this has been the work of Kershaw (1976, 1978) on the Atherton Tableland, north-eastern Queensland. In the markedly seasonal tropics, however, only one other study besides that reported here has been undertaken: that being an investigation of coastal vegetation history associated with Holocene landforms at Princess Charlotte Bay, Cape York Peninsula (Grindrod 1983).

The second study investigates the elimination of monsoon vine-forest vegetation in the vicinity of Kiina. This study is based on the excavation of incubation mounds of the megapode scrub fowl, Megapodes reinwardt, and the subsequent radiocarbon dating of charcoal fragments incorporated within the mound fabric, following the procedure pioneered by Stocker (1971a). Because the prime habitat of the scrub fowl is monsoon vine-forest, the occurrence of disused incubation mounds in eucalypt dominated vegetation of the present indicates...
of the loss of monsoon vine-forest from these sites. While the exploratory nature of both these studies is emphasised, the results have important implications for contemporary environmental management practices throughout the Top End coastal/sub-coastal region.

Study area

Kiina is the traditional Kakadu name for a small headland that abuts the floodplain on the eastern bank of the South Alligator River; Lat. 12°51'; Long. 132°33' (Fig. 1). The headland is part of an extensive deeply weathered laterite plain that rolls westwards from the Arnhem Land escarpment, termed the 'Koolpinyah Surface' by Williams (1969). Rivers have incised deep valleys into this plain which, during periods of high sea level such as prevail at present, become infilled and form extensive riverine and coastal plans (Clarke et al. 1979; G. Hope unpublished; Williams 1969).

The South Alligator River drains the southwestern sector of Arnhem Land. The river skirts the escarpment in the south and then, leaving the escarpment, it forms a braided stream as it passes through the laterite lowlands. Just to the south of Kiina the river becomes incompetent (at high flow) (Williams 1979) and empties into a vast freshwater floodplain. Directly to the west of Kiina a number of small channels fuse to establish single river channel which then proceeds to the sea (Fig. 1). This main channel is tidal throughout its length.
About 50 m west of the Kiina headland an extensive natural levee system borders a remnant river channel and cuts off low lying lagoons, marginal to the laterite plain, from tidal influences. During the wet season, typically from November to March, these areas of the floodplain are inundated by sheets of freshwater. With the onset of the dry season, these areas dry out progressively, leaving surface water only in the deepest depressions.

The floodplain next to the main tidal channel of the South Alligator River, to the west of the levee system bordering the remnant river channel (Fig. 1), is characterised by subtle topographic heterogeneity. Shallow channels, often only 30 cm deep and 2.5 m wide, and bordered by sandy levees up to 50 cm high, take seasonal freshwater outflow from the marginal lagoons to the river. During the dry season, as the tidal limit progresses upstream, these same channels facilitate the lateral overflow of tidal waters during spring tide phases. The limit of dry season tidal inundation at the present day occurs immediately south of Kiina (Fig. 1).

The riverine floodplain is formed of surficial black organic clays which overlie grey to bluish-grey clays of estuarine origin. These latter sediments date from the time of rising Holocene sea level. Geomorphological features pertinent to floodplain evolution and landforms in the vicinity of Kiina have been studied in detail by G. Hope (unpublished).

Climate

Major climatic features of the region are described by MacAlpine (1976). The climate is markedly seasonal with an almost rainless dry season from May to September, and a wet season from November to March. Rainfall data collected for over 60 years at Oenpelli, 50 km to the north, indicates that mean annual rainfall is 1340 mm, 98.3% of which occurs during the wet season. Temperature data from the same station, collected over a ten-year period, indicate that mean annual maximum and minimum temperatures are 33.8°C and 21.7°C respectively, with October and November being the hottest months.

Vegetation

Published accounts of vegetation in the region are provided by Story (1969, 1976), and by Williams (1979) for floodplain vegetation. For the purposes of this paper, however, the vegetation in the vicinity of Kiina may be described conveniently as comprising six broad types as follows. The general distribution of these in the study area is shown in Fig. 1.

Eucalypt woodland. This is the predominant vegetation of the laterite plain. The tree stratum, varying in height from 12 to 18 m, is dominated by eucalypts, especially Eucalyptus conferriflora, but includes a variety of other species such as Erythrophloeum chlorostachys, Gardenia megasperma, Planchonia carnea, Syzygium subhospiculare, Terminalia catapetiae and T. ferrandiana. During and immediately following the wet season ground cover approaches 100% and is from 30 cm to 1 m in height. Dominant species comprise the exotic labiate annual, Hyptis suaveolens, and the grasses Chrysopogon fallax, Digitaria biennis, Eriachne triseta, Eragrostis spp., Eulalia leschenaultia, Heteropogon contortus, Panicum minoanaense and Schizachyrium fragilis. This community is subject to frequent dry season burning, often on an annual basis, and at such times ground cover is characteristically sparse and patchy.

Closed monsoon vine forest. Monsoon vine forest vegetation occurs in small, discrete and often widely disjunct patches, occupying a variety of ecological situations from the Kimberleys to Cape York Peninsula (Kikawa et al. 1981; Webb & Tracey 1981). While floristically related to other rainforest types, which exist along the eastern fringe of Australia, monsoon vine forest is distinguished by its generic affinities with dry tropical floras in Indo-Malesia, Africa and South America (Ibid.). This suggests a common origin for this vegetation in a megathermal Gondwanaland environment (Nix 1982).

A number of small monsoon vine forest patches occur to the north of Kiina, close to Kumunkuwi (Fig. 1). These cover a total area of no more than 4 ha. The occurrence of dispersed scrub fowl mounds in eucalypt woodland around Kumunkuwi and Kiina however indicates that monsoon vine forest was locally more widespread at some past time. Using the terminology of Webb (1959), these extant patches may be described as semi-deciduous notophyll vine forest. Canopy height is from 10-14 m with occasional emergents to 18 m.

Major tree species includes Bombax ceiba, Celtis philippensis, Drypetes lasiogyna, Gonopodium falcatum, Litsea glutinosa, Polyalthia
nitidissima, Strychnos laceda and Wrightia pubescens. An intermittent shrub layer is present, comprising species such as Alphylus cobbe, Glycosmis pentaphylla, Micromelum minutum. Vines are especially prominent and include Dioscoea transversa, Flaggella indica, Jasminum simplicifolium, Malatia scandens, Pachygone ovaia and Steumone elliptica.

Paperbark forest. Paperbark forest is well developed along the edge of the floodplain, on the levee opposite Kiina, and in some low lying areas of annual swamp. Tall paperbarks, Melaleuca leucadendron and M. cajuputi, up to 20m in height, overtop a dense stratum of Barringtonia acuta and Cathormion umbellatum to 10m in height. On the levee opposite Kiina dense thickets of Bamboo, Bambusa arnhemica, to 14m in height, are associated with paperbark forest vegetation.

Annual swamp. Williams (1979) defines annual swamp as being areas still immersed by freshwater in August (mid dry season) but to a depth less than 40 cm, and with bottom vegetation dominated by vascular plants. This definition is useful also in describing low lying swamp situations in the vicinity of Kiina. These swamps are dominated by dense stands of the sedge Eleocharis dulca, up to 2.5m in height, and more locally by the legume Sesbania cannabina. Other component species include Convolvulus aquatica, Ludwigia ascendens, Marsilea mutica, Monochoria cyanea, Nymphoides gigantea, Nymphoides indica and Vallisneria spiralis. By the end of the dry season these annual swamps have dried out completely, leaving vast areas of bare, cracked black soil.

Mixed herbfield. This vegetation type occupies relatively elevated situations on the black soil floodplain. There is a low cover, to 50cm, of broadleaved annual herbs, dominated by Hygrophila salicifolia, Melochia corchorifolia, Meschysma polysachyon, Phyla nodiflora, and graminoid species, Cypus spp., Eriocholoa procer, Puprena ciliaris, Leptochloa neetii, Oryza meridionalis and Paspalum scrobiculatum. This vegetation is reduced to a straw mat by the late dry season.

Saline grassland. In the vicinity of Yjina this vegetation type occupies extensive areas of the floodplain which receive occasional dry season tidal inundation. The low dense graminoid vegetation is composed predominantly of Sporobolus virginicus, with Paspalum scrobiculatum of more restricted occurrence. As well, two mangrove species, Avicennia marina and Sonneratia caseolaris occur sporadically along most major tidal channels.

Fieldwork and laboratory methods

In the late dry season of 1981, a backhoe was used to dig a series of pits across the Kiina floodplain in connection with a study of floodplain stratigraphy and landform evolution (G. Hope, unpublished). Sediment samples for pollen analysis were collected from the walls of two pits located 200m (Hole 3) and 400m (Hole 4) east of the main river channel respectively (Fig. 1). While Hole 3 was selected initially to provide a continuous depositional record, the stratigraphy of the top metre exhibited evidence of disturbance and so an undisturbed surficial section from Hole 4 was sampled. In Hole 3, samples were collected in relation to stratigraphic strata. Two samples were collected also from these holes for 14C dating; mangrove wood from Hole 3 at a depth of 290cm and fine organic remains from Hole 4 at a depth of 72cm. In the laboratory, sediment samples were prepared for pollen analysis employing standard procedures as outlined by Faegri & Iversen (1975).

For the purpose of a preliminary study, three scrub bower incubation mounds were also excavated (Fig. 1). Two disturbed mounds were excavated at Kumunkwi, one within a patch of monsoon vine-forest (Mound 1), the other some 80m outside the present forest boundary (Mound 2). A third mound was excavated at Kiina (Mound 3). Charcoal fragments were collected from the basal sides of excavation trenches and subsequently submitted for 14C dating. This charcoal is likely to have been incorporated within the mounds at about the time of their formation and thus resultant dates can provide a guide to maximum ages of these mounds.

Results

Pollen analysis of floodplain sediments

Fig. 2 summarises the results of pollen analyses conducted on floodplain sediments from Holes 3 and 4. Selected taxa are shown as relative frequencies on a total pollen sum. The first and final columns summarise stratigraphic data, and the relative proportions of mangrove, freshwater and mixed dry land/freshwater pollen taxa, respectively.

These pollen data are not detailed and require comment. Firstly, due to the difficulty of
discriminating absolutely between dry land and freshwater myrtaceous (eg. Eucalyptus and Melaleuca), and grass pollen taxa, these have been grouped as mixed taxa in the pollen diagrams. Secondly, while Pandanus is represented in the present day lowland flora by two taxa, Pandanus spiralis (essentially a dry land species) and P. aquatica (a species associated with freshwater communities) Pandanus-type pollen was found to occur mainly in association with freshwater pollen taxa. While open to other interpretation, the occurrence of this pollen type has accordingly been taken thereby as indicative of freshwater hydrological conditions. Thirdly, no pollen results are presented for samples above 60cm in Hole 3 due to evident stratigraphic disturbance of these sediments.

Analysis of the results presented as Fig. 2 suggests that, over a period spanning at least the last 6000 years, there have been four major phases of vegetation development associated with the evolution of the Kiuna floodplain. These phases are characterised as follows.

**Phase I.** This is characterised by the inclusion of very high concentrations of mangrove species pollen, especially Rhizophora, in grey clay sediments predominately, between the bottom sampling level at 4.2m through to 1.6m in Hole 3. Other identified mangrove pollen taxa comprise Bruguiera/Ceriops-type, Sonneratia alba, Avicennia, Lumnitzera racemosa, Cynometra sp., Xylocarpus, Excoecaria agallocha, Osborna ocuodonta, Aegiceras corniculata and Acanthus ilicifolius.

While the proportional representation of individual mangrove pollen taxa is relatively constant throughout, there is a slight trend of increasing frequencies of both myrtaceous, grass and cyperaceous pollen taxa in the closing stages of this phase. This is accompanied by the appearance of chenopod pollen in the sedimentary record, from 2.0m through to 1.6m. The closing stages of this phase are characterised also by a change in the sediments, at a depth of approximately 1.9m. Below this depth the sediments comprise grey clays containing large quantities of well-preserved mangrove wood and leaf fragments. Above this depth, to 1.3m, the clays are light in colour and contain abundant fine plant remains. The age of a mangrove root sample, from 2.9m depth, is 5990 ± 100 years B.P. (ANU 2988).

**Phase II.** In contrast to the earlier phase, this phase is characterised both by low concentrations of pollen and the absence of significant mangrove pollen representation in the sedimentary record, with the notable exception of Avicennia marina. While the frequencies of dry land or mixed taxa pollen types correspondingly increases, this is attributable mainly to the high frequencies of an unidentified legume species. Pollen are totally absent from the 1.0m sample in Hole 3. This phase is associated with light brown clay sediments, from 1.4m to 1.0m in the Hole 3 sequence, which are both conspicuously mottled and devoid of any evident organic remains.

**Phase III.** This phase is characterised by the inclusion of relatively high concentrations of aquatic, cyperaceous, grass, Pandanus-type and myrtaceous pollen taxa in black organic clay sediments between 0.95m and about 0.3m in the Hole 4 sequence. Whereas in Hole 3 there appears to be a clear transition between Phases II and III, in Hole 4 pollen analysis of the bottom-most sediment sample at 90cm indicates an admixture of mangrove and freshwater pollen taxa. A date of 1380 ± 100 years B.P. (ANU 2999), derived from fine organic remains at 0.75m, provides a minimum date, based on stratigraphic evidence, for the development of this vegetation.

**Phase IV.** This phase is representative of surficial mottled brown-grey clay floodplain sediments from Hole 4. Mangrove pollen taxa, especially Rhizophora, reappear in the sedimentary record. The proportional representation of freshwater pollen taxa is diminished relative to Phase III, while that of the mixed or dry land types remains relatively constant.

**Scrub fowl mounds**

The ages of charcoal from the excavated mounds are presented as Table 1.

**Discussion**

**Development of floodplain vegetation**

The results of the pollen analysis of floodplain sediments indicate that four major phases of vegetation development have been associated with the evolution of the Kiuna floodplain over the last 6000 years. It is suggested that these phases correspond with the development of the following types of vegetation.
Fig. 2. Pollen diagram from Kiina, South Alligator River, Northern Territory.

Phase I. The first phase corresponds with the development of dense mangrove vegetation. This is indicated by the presence of very high concentrations of mangrove species pollen, especially *Rhizophora*, as well as abundant well-preserved mangrove wood and leaf material, in these sediments. The preservation of these plant remains moreover, indicative of a reducing environment, clearly suggests that open estuarine conditions prevailed on the Kiina floodplain at this time, probably associated with daily tidal inundation. That the development of this mangrove vegetation corresponds with the last stages of the Holocene sea level rise is indicated by the age of a mangrove roof sample, from 2.9m in Hole 3, dated at 5990±100 years B.P. This data accords well with other evidence from northern Australia and elsewhere which indicates that the post-glacial rise in sea level terminated by about 6000 B.P. at a level slightly higher (ca. 1m) than present sea level (Chappell et al. 1982). Mangrove wood has been found also in estuarine sediments dated between 7000 and 6000 years B.P. in two other northern Australian studies: at Princess Charlotte Bay, north Queensland (J. Chappell pers. Comm.); and in the Fitzroy estuary, north-western Australia (Jennings 1975).
TABLE 1. The ages of scrub fowl mounds in the vicinity of Kiina.

<table>
<thead>
<tr>
<th>Mound</th>
<th>ANU sample No.</th>
<th>Locality (see Fig. 1)</th>
<th>Age (years BP)</th>
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<tbody>
<tr>
<td>1</td>
<td>3028</td>
<td>Kumunkuwi-inside monsoon forest</td>
<td>102 ± 3% (Modern)</td>
</tr>
<tr>
<td>2</td>
<td>3029</td>
<td>Kumunkuwi-outside monsoon forest</td>
<td>304 ± 140</td>
</tr>
<tr>
<td>3</td>
<td>3027</td>
<td>Kiina</td>
<td>102 ± 3% (Modern)</td>
</tr>
</tbody>
</table>

Phase II. The second phase is characterised by vegetation which appears to become increasingly open and sparse, such as one might expect with the development of an estuarine mud flat. Associated with both low concentrations of pollen, and the marked decline of mangrove pollen representation (with the exception of Avicennia marina), in the sediments representative of this phase, the conspicuous mottling and absence of evident organic remains in these light brown clay sediments indicates that the previous phase has been replaced here by conditions where soil forming processes become dominant. These various threads of evidence suggest that the floodplain at this time was probably an estuarine mud flat receiving irregular tidal inundation. The occurrence of Avicennia marina in similar habitats of the present day would support this interpretation (MacNae 1966; Wells 1982). The absence of pollen at 1.0m might be due to progressive development of a hypersaline environment inhospitable to plant growth but might imply also that environmental conditions were not conducive to pollen preservation. In either case it is likely that vegetation cover would have been minimal at this time. While this phase of vegetation development is undated, it accords, presumably, with the commencement of progressive sea level decline towards its present level (Chappell et al. 1982) and concomitant coastal progradation (Chappell 1982).

Phase III. This phase represents the development of freshwater wetland communities composed largely of aquatic, cyperaceous and grass species, such as those occurring over extensive areas of the Kiina floodplain at the present time (Fig. 1). The commencement of this phase of vegetation development is dated at 1380±70 years B.P. Whereas in Hole 3 there appears to be a clear transition between phases II and III, in Hole 4 pollen analysis of the bottom-most sediment sample at 0.9m indicates an admixture of mangrove and freshwater pollen taxa. While the occurrence of mangrove pollen taxa in this facies is enigmatic, the absence of mangrove pollen throughout Phase III as a whole indicates that freshwater hydrological conditions were predominant throughout this period. Although this study demonstrates that freshwater hydrological conditions suitable for the establishment and development of wetland plant communities were established around 1400 years B.P. at Kiina, it is to be expected that the development of similar wetland vegetation in other areas will have commenced at different times. Nearer the present coastline for example, the establishment of suitable conditions might be expected to occur later than that recorded here. At the present time no dates for other areas are available. Indirect archaeological evidence concerning changes in relative proportions of freshwater mussels (Velesunio ambiguus) with respect to estuarine and brackish water shellfish species in stratified midden deposits in the Cannon Hill area, some 40km from the present coastline, clearly suggests that there has been a recent change from estuarine to freshwater conditions (Kamminga & Allen 1973; Schrire 1982), probably within the
last thousand years (Allen 1977 and pers. comm.). Similarly, the basal age of a midden excavated at Kiina itself, and containing only the remains of freshwater shellfish species, has been dated at around 880 years B.P. (R. Jones pers. comm.). Thus, whilst the evidence available from archaeological studies and the palynological study reported here is clearly limited, taken together, these studies suggest nevertheless that the development of freshwater wetland ecosystems has occurred in the relatively recent geological past:

**Phase IV.** The fourth phase represents the development of extant saline grassland vegetation, dominated by *Sporobolus virginicus* and *Paspalum scrobiculatum* which occurs in situations localized to the vicinity of drainage depressions and channels (Fig. 3). Mangrove pollen taxa reappear in the sedimentary record, reflecting the reestablishment of tidal influences in the very recent, but as yet undated, past. The high concentration of rhizophoraceous pollen present in these sediments is interesting in that no stands of such species occur on the Kiina floodplain of the present day. Instead, young individuals of two other mangrove species, *Avicennia marina* and *Sonneratia caseolaris*, occur sporadically along most major tidal channels. While transport of rhizophoraceous pollen in tidal waters from downstream of Kiina cannot be discounted, this pollen is more likely to be derived from estuarine sediments underlying the Kiina floodplain which have been reworked through recent tidal channel incision. That tidal channels indeed have expanded over the floodplain in the very recent past is indicated by various lines of evidence; firstly, comparisons between 1950, 1964/5 and 1976 aerial photographic records; secondly first-hand accounts

Fig. 3. Saline grassland with extensive cover of *Sporobolus virginicus*. Note young *Sonneratia caseolaris* established along tidal channel.
Fig. 4. Excavated scrub fowl incubation mound in eucalypt-dominated woodland vegetation.

of aboriginal people (e.g. Minnie Anderson pers. comm.); and thirdly, the population structures of present day mangrove communities. Given the absence of supporting evidence for a recent rise in global sea level it is likely therefore that the expansion of tidal influence is attributable here to the impact of water buffaloes in effecting marked changes in wetlands vegetation and landform processes, as has been documented elsewhere (ANPWS 1980; Letts et al. 1979; Stocker 1970, 1971b, 1982). D. Lindner (pers. comm.) suggests that the dry season intrusion of tidal waters has been facilitated by the actions of buffalo in creating 'swim channels', some of which link tidal channels with relatively low-lying freshwater lagoons. The development of such channels is clearly portrayed in the aerial photographs noted above.

Elimination of monsoon vine-forest

A number of implications stem from the results of this preliminary study. Although scrub fowl no longer inhabit the small patches of monsoon vine-forest at Kumunkuwi, the recent age of a mound within the largest patch (ANU-3028) indicates that scrub fowl were active there until recently. This loss of a resident scrub fowl population is apparently
coincident with the total elimination of monsoon vine-forest from the headland at Kiina, given the recent age of that mound also (Fig. 4). These results clearly imply that marked vegetation and habitat change has occurred in the Kiina region within the last 100 years. The recent timing of this change suggests that reduction of monsoon vine-forest vegetation is here attributable to changes in ecological conditions associated with the arrival of Europeans.

Although the underlying cause of this reduction of monsoon vine-forest vegetation in the vicinity of Kiina is problematical, two factors stand out as having possible significance in this regard, namely, an increase in the severity of fire since the advent of Europeans, and the impact of feral animals, especially water buffalo.

While almost nothing is known of traditional aboriginal burning practices before or from the time of European contact, accounts of contemporary aboriginal practices in monsoonal areas of northern Australia indicate that fire is employed skilfully as a technique of resource management (e.g. Haynes 1978, 1985; Jones 1969, 1975, 1980). Haynes (1985), on the basis of observation and the results of a study in which country was burnt in mid-to-late dry season, indicates that burning is a complex activity which begins in the wet season and gradually picks up with the onset of the dry season. Although burning continues into the late dry season in certain communities (e.g. woodland), by the middle of the dry season a mosaic of burnt and unburnt country is created such that the risk of an intense wildfire spreading in the late dry season is minimised. This approach to burning differs quite markedly from current practices adopted in other parts of monsoonal northern Australia, especially pastoral regions, where extensive high-intensity mid-to-late dry season burns are undertaken frequently, often on an annual basis (e.g. J. House unpublished, summarised in Bell 1981).

In relation to patches of monsoon vine-forest vegetation, Haynes (1985) and Jones (1980) report that, in Arnhem Land, contemporary aboriginal burning practice requires that these be left unburnt, some even being afforded further protection by the burning of fire breaks. In this connection it is interesting to note that archaeological evidence from Kiina indicates that aboriginal people exploited freshwater wetland resources there from at least 880 B.P. (R. Jones pers. comm.); aboriginal occupancy may have been coincident therefore with monsoon vine-forest vegetation there over part, or all, of this time. However, the longevity of this former patch is not established beyond 100 years B.P.

That aboriginal burning practices may have been a significant factor in the demise of monsoon vine-forest in the Karajlaka Peninsula, Melville Island, however, is argued by Stocker (1968, 1971a). Stocker excavated five disused scrub fowl mounds in the vicinity of two small remnant patches of monsoon vine-forest, the ages of which ranged from 8200 ± 180 years B.P. to 1610 ± 80 years B.P. Stocker (1971a) suggested that gradual climatic deterioration or, alternatively, aboriginal burning pressure on the monsoon vine-forest margin, had resulted in a gradual reduction of this vegetation. That climatic deterioration may have been responsible for the diminution in area of this monsoon vine-forest patch, at least in part, could be argued given the suggestion that regional climates have been somewhat warmer and wetter between 7000 to 2500 years ago (Clarke et al. 1979; Kershaw 1975; Jennings 1975).

A second factor likely to have contributed to the reduction of monsoon vine-forest in the vicinity of Kiina within the last 100 years is structural damage due to water buffalo. While buffalo damage is often more conspicuous in moister types of monsoon vine-forest (Letts et al. 1979), or as browse lines in coastal forest (Stocker 1982), it is evident from studies currently in progress (Russell-Smith unpublished) that grazing and trampling pressures have inflicted a significant impact on the capacity of some types of monsoon vine forest to regenerate successfully.

Conclusions

This paper relates records of vegetation change pertaining to two different environmental situations in the vicinity of Kiina, near the South Alligator River. In the first study, pollen analysis of floodplain sediments indicates that four major phases of vegetation development have been associated with the evolution of the Kiina floodplain over the last 6000 years. These are:

i) Dense mangrove vegetation reflecting estuarine conditions associated with rising early to mid-Holocene sea levels.
ii) Sparse, open vegetation reflecting progressive development of a saline to hypersaline plain following sea level stabilization.

iii) The development of freshwater wetland vegetation around 1400 years B.P. associated with the establishment of freshwater hydrological conditions.

iv) Recent reversion to saline conditions attributable largely to the impact of feral water buffalo in this fragile ecosystem.

In the second study, the excavation and subsequent dating of scrub fowl incubation mounds indicates that marked reduction of monsoon vine-forest has occurred within the recent, historical past. It is suggested that the impacts of increased fire severity and/ or water buffalo may be responsible for this change.

These separate records demonstrate that there has been significant vegetation change that is associated in time with the advent of Europeans into this region. The nature of the vegetation change expressed in both records is one that reflects environmental deterioration: a reversion to saline conditions in the floodplain pollen record; and a reduction of monsoon vine-forest in the scrub fowl mound record. The results of these studies thus have clear implications for contemporary management and conservation practices in the region.

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THE STATUS OF MONSOON VINE-FORESTS IN THE
NORTHERN TERRITORY: A PERSPECTIVE.

Jeremy Russell-Smith and Clyde R. Dunlop
May, 1984

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World Wildlife Fund and Australian Conservation Foundation,
1.0 INTRODUCTION

This paper aims to provide an account of the ecology (so far as is known), the condition and the conservation status of monsoon vine-forests in the Northern Territory. Given the purposes of this paper it is pertinent to state at the outset that:

1. While increasing efforts have been made in recent years to document the diversity of higher plant taxa, and sufficient ecological study has been conducted to facilitate preliminary analyses of the biogeographical and ecological relationships of the vegetation, this work is still in its infancy. Large areas remain ecologically unexplored (e.g. most of eastern Arnhem Land and its offshore islands and inland regions), and much of the constituent flora (e.g. fungi and lichen) and fauna (e.g. most invertebrate groups) are unknown. Such information as is available however, reveals a vegetation which is diverse and highly fragmented, and highlights both the relative biotic and structural simplicity of these ecosystems and the wide ecological amplitudes and vagilities characteristic of many of the component species.

2. It is evident that the (often compounding) impacts of modern burning practices and feral animals, especially water buffalo and pigs, are affecting seriously the integrity of many monsoon vine-forest patches. Given that patch sizes are mostly small (mostly less than 5 ha), these ecosystems are particularly vulnerable in the face of continued disturbance. This is especially true for highly susceptible but ecologically very significant spring habitats associated with both the subcoastal lowlands and sandstone escarpments and their outliers.

3. A considerable proportion (see Fig. 4) of the Top End is given already to types of land tenure either actively sympathetic towards, or at least conducive for conservation interests (e.g. National Parks and Reserves, and Aboriginal Land respectively). Furthermore, with the likely declaration of further conservation areas to the south and in the vicinity of Darwin, nearly all major core areas of the coastal, subcoastal and escarpment forests will enjoy some form of legal protection. On the other hand, the lesser known hinterland lancewood (Acacia shirleyi) closed scrubs and scattered vine thickets, on rocky outcrops are virtually unrepresented in conservation areas.
The paper is divided into three main sections which, borrowing from the theme of the Symposium, cover broadly: the past history, the present expression, and future prospects of, monsoon vine-forests in the Northern Territory. In Section 2 (dealing with the past history), it has not been our purpose to attempt a reconstruction of past vegetations, nor have we considered in any detail biogeographical relationships both within the Northern Territory and between other Australian and extra-Australian regions. In the first instance, relevant palaeorecords such as exist for other Australian regions are simply not available. And in the second instance, such detailed treatment as required is both beyond the scope of the present paper, as well as being premature at the present time. Rather, on the basis of certain biogeographical and ecological characteristics of the extant regional flora (Sect. 2.1) and vegetation (Sect. 2.2), the approach we have adopted is to critically consider various historical influences which are likely to have contributed to the development and extant expression of regional vine-forest ecosystems (Sects. 2.3 - 2.6). In Section 2.7, the main points arising from this discussion are synthesised.

In Section 3, characteristics of the extant flora (Sect. 3.1), vegetation (Sect. 3.2) and fauna (Sect. 3.3) are described. In Section 4 the regional conservation status of vine-forest ecosystems is assessed.

2.0 HISTORICAL PERSPECTIVE

2.1 Biogeographical Overview

In 1838, a third attempt at the colonisation of northern Australia was made with the establishment of the settlement of Victoria, at Port Essington on the Cobourg Peninsula. Eleven years later the settlement was abandoned having failed the expectations originally held for it, the surviving remnants of the garrison despondent and wracked by malaria (see Spillett 1972). One hundred and forty five years later, only the more resilient constructions in stone and mortar and the failed wells remain as testament to this costly and miserable enterprise. Now occupying that area which was at one time the parade ground and adjacent vegetable garden however, is sprung up a well-developed, floristically-rich, semi-deciduous monsoon vine-forest (Plates 1, 2).
Plate 1: Victoria Settlement in the mid 1840's showing the parade ground and the vegetable garden (beyond the line of cottages in the centre of the illustration). The surrounding vegetation is evidently tall eucalypt forest dominated by *Eucalyptus miniata* and *E. tetrodonta*, such as occurs widely in the region at the present day. The building on the right is the Quartermaster's Store. From an original engraving by H.T. Melville, in Jukes (1847).

Plate 2: The surviving foundations of the Quartermaster's Store in 1982, encompassed by monsoon vine-forest vegetation. The mound against the foundations in the bottom right of the picture is half an incubation mound of the scrub fowl (*Megapodes freycinet*) - the other-half occurring on the other side of the wall.
This example is significant in so much as it illustrates firstly, the capability possessed by a great many monsoon vine-forest species to effectively exploit ecological opportunities as created through time. In this sense many of these species display the characteristics of nomads as described by van Steenis (1958).

Secondly, such establishment *de novo* of monsoon vine-forest vegetation has occurred in other situations, as evidenced by the occurrence of patches on or in association with landforms of demonstrably recent (mid to late Holocene) origin (e.g. coastal beach and chenier ridges and coastal and subcoastal floodplains, levees and margins). A characteristic feature of this vine-forest vegetation is, therefore, the capacity of many species to respond to environmental change. Indeed, 70% of the obligate monsoon vine-forest flora (Append.) has been found to occur on recent landforms; an observation which underlines the significance of dispersal in the flora as a whole.

This is not to say however, that all patches or tracts of vine-forest are recent in origin, nor that all species are highly vagile. In both cases, many clearly are not. A number of situations illustrate this. Many species and populations occupying rare spring habitats exhibit wide disjunctions in distribution both within the Northern Territory and with other regions, Cape York especially (e.g. *Elaeocarpus grandis*, *Horsfieldia australiana*, *Planchonella* sp. B2101*, *Ternstroemia* cherryl; see also Kikkawa et al.; 1981; Specht et al.; 1977). In another situation, a number of species, exemplified by capsular Myrtaceae in vine-forests of the western Arnhem Land escarpment (e.g. *Allosyncarpia ternata*, *Xanthostemon psidioides*, *X. umbrosus*), with limited capacity to disperse (see Sect. 2.5), exhibit highly disjunct distribution patterns in that local region (Plate 3). Major disjunctions between assemblages of populations also occur (e.g. Kikkawa et al. 1981). All these situations serve as illustration for a second characteristic feature of this vine-forest vegetation; namely, that it is highly fragmented.

The extant vine-forest vegetation of the Northern Territory may be considered to comprise, therefore, essentially two floristic elements. The larger of these elements comprises those taxa with a capacity to exploit new ecological opportunities. The other element comprises taxa which are confined to increasingly precarious refugia. On the basis of major disjunctions in the distributions of certain taxa in this latter element, one can be confident that vine-forest vegetation has been, at some time(s), more widespread across northern Australia than it is now.

Where given in the text, such labels refer to specimens lodged in the Darwin Herbarium (see notes to Append.).
Plate 3: An isolated and remnant patch of vine-forest, dominated by Allosyncarpia ternata, in exposed terrain on the western Arnhem Land escarpment.

Plate 4: Perigymnophyllum gallery associated with perennial spring, western Arnhem Land. Two species occurring here, Selendesmium obscurum and Taenites blechnoides, are each known from only a small number of localities in widely separated sandstone regions.
2.2 Extant Distribution Patterns

Monsoon vine-forests and thickets of the Northern Territory occur typically over a range extending from the islands to the north-west and north-east (11°S) to almost as far south, apparently, as Tennant Creek (Specht 1958:421-422). Within this range by far the greater proportion of patches, as well as the most structurally complex and floristically diverse vegetation, is confined to a narrow coastal/subcoastal belt, becoming increasingly scattered and attenuated further inland. In no region however, does monsoon vine-forest constitute more than a very small proportion of total vegetation, save on smaller islands where vine-forest may comprise almost the whole vegetation cover.

The broad region throughout which the Northern Territory monsoon vine-forests and thickets are distributed at the present day (i.e., north of 18°S) is characterised essentially by the following climatic features: marked seasonality in rainfall, rainfall gradients in rainfall distribution, and high year-round temperatures. Rainfall occurs almost exclusively in the summer months, typically from November through April, under the influence of a number of rain-producing systems (McAlpine 1969) of which the north-west monsoon and cycloidal disturbances are the best known. While the amount of annual rainfall in any one locality is variable, the occurrence of an annual wet season is highly predictable. Rainfall is highest in coastal regions of the north-west and north-east (Fig. 1), with average annual rainfalls generally of the order 1400-1600 mm; over 2000 mm being recorded annually at Garden Point, Melville Island. Away from these regions of slight increase in rainfall, the rainfall over most of the region is less than 1000 mm. The occurrence of a very dry season (i.e., winter) is highly predictable and rainfall is generally negligible, except in coastal and lowland areas where it may exceed 300 mm (McAlpine 1969).

Climate, therefore, has been attributed to a number of factors, namely: climatic sifting (Specht 1958:422), Aboriginal burning (Stocker and Mott 1981:435-7), climatic sifting in concert with Aboriginal burning (Gilligan 1983:184-5), and climatic sifting in concert with other environmental and biological factors which, collectively, have influenced the "mutability and stability of refugia" through time (Kikkawa et al. 1981:448, Webb and Tracey 1981). Beard (1976) suggests that vine-forest vegetation in the Kimberley region may derive from recent colonisation by the last (post-glacial) rise in sea level. In the following sections the available evidence is examined.
Figure 1: Annual Rainfall [mm] – 50 Percentile
NORTHERN TERRITORY
high rainfall, there is a relatively steep declining gradient in rainfall distribution, both towards central Arnhem Land in the north, and towards Tennant Creek in the south, the latter recording an average of less than 500 mm p.a. Temperatures are consistently high throughout the year in all areas with a mean annual temperature greater than 24°C, and the annual range in mean monthly maxima and minima being, respectively, greater than 35°C for October, and 9°C for July. Of critical significance for the vegetation therefore, is the coincidence of high temperatures (and incident radiation) with the end of a long rainless period.

The broad pattern of vine-forest distribution throughout the region corresponds closely with the present pattern of rainfall distribution; patches are most concentrated in high rainfall regions, becoming increasingly scattered and attenuated, both structurally and floristically, along gradients of declining rainfall. Such correspondence however, does not explain the manifest fragmentation of the vegetation.

The climatic history of monsoonal northern Australia is very poorly known. In the Barkly Tablelands region, the existence of fresh, late Tertiary limestones over a strongly laterised surface, sets an upper age limit to that surface (Williams 1969b:83), and suggests that a seasonal climatic regime was already well established by this time. Hays (1967) suggests that laterisation, under a tropical climate with heavy seasonal rainfall, may have occurred from the Cretaceous. Nin (1982) suggests that a megathermal climate probably prevailed throughout the Tertiary across northern Australia. Even for the late Pleistocene and Holocene, climatic reconstruction relies largely on studies of changes in sea levels and palaeoclimates from other Australian regions and elsewhere.

Such evidence as is available for these latter periods however, points to the likelihood that regional climates were substantially wetter at some period in the vicinity of, but previous to, 28,000 years BP (Jones and Bowler 1980; Bowler 1983). This has been determined on the basis of greatly expanded shorelines of Lakes Wood and Gregory, to the south of the region. Kershaw (1984) suggests, however, that these lakes were more likely to be full in the period 80,000 - 120,000 years BP, when sea level would have been sufficient to just cover the extensive northern continental shelf and thus provide higher levels of atmospheric moisture for monsoonal precipitation. Nevertheless, it would appear that at some period(s) since the last interglacial, effective precipitation probably has been sufficient to favour expansion of monsoon vine-forest vegetation. On the
assumption that rainfall distribution was still highly seasonal at this time however, an increase in rainfall may not necessarily have been associated with expansion of closed vine-forest vegetation. Subsequent to the period(s) of wetter conditions, it is likely that, at the height of the last glacial (18,000 ± 2,000 years BP), when sea level was around 150m lower than that at present (Chappell 1976), annual rainfall is likely to have declined considerably given that the continental shelf, as well as the Gulf of Carpentaria (Smart 1977), was exposed. Nix and Kalma (1972) suggest that closed forest formations would have been eliminated from all but the most favourable habitats in north-eastern Australia. Associated with the post-glacial rise in sea level there is the suggestion that regional climates were markedly wetter than that at present in the period 5,000-8,000 years BP (Clarke et al. 1979; Jenning 1975; Smart 1976), and that rainforests might be anticipated to have expanded at this time (Nix and Kalma 1972). By about 3,000 BP it is suggested that the present climatic pattern was established, and that closed forest formations would have begun to retreat to their present positions (Nix and Kalma 1972). Stocker (1971) attributes the retreat of a patch of monsoon vine-forest on Melville Island, in part, as a possible consequence of climatic attenuation in the mid to late Holocene.

Whilst it is evident from the foregoing discussion that the climatic history of this region is very poorly known, the vegetation history is even less so. With the single exception of rainforest macrofossils of possible Eocene age from Melville Island (White 1978), there is no fossil record to which one can refer. This assemblage is significant however in that most specimens, including a possible *Ceratopetalum* leaf, match with specimens in an Eocene assemblage for New South Wales, described by Ettinghausen (1888, in White 1978).

As poor as these palaeorecords clearly are, it is probable nevertheless, that general climatic deterioration through the Tertiary (Shackleton and Kennett 1975), and the climatic oscillations of the Quaternary (Shackleton and Opdyke 1973; van Andel et al. 1967), have had as profound an influence on the decimation of possible mesic rainforest archetypes in monsoonal northern Australia as is evident elsewhere (e.g. Kemp 1978, 1981; Kershaw 1981, 1986; Lange 1982; Martin 1978, 1981; Singh 1982; Truswell and Harris 1982). While the temporal span of seasonal water balance conditions before the late Tertiary is not known, climatic deterioration, and more recent oscillation, may be anticipated to have contributed directly to the extinction of mesic elements. The remnants of these today find refuge in rare pockets of perennial water availability, such as at springs, seepages.
and sheltered gorges. For taxa more tolerant of seasonally dry conditions however, fragmentation directly attributable to climatic deterioration is harder to sustain. Rather, one might assume that attendant with the progressive development of an erratic, deteriorating climate, would have emerged other potent selective pressures, not the least of which being the increased potential for fire, and increased competition from suites of taxa better suited to the changing conditions.

2.4 Landform Change

The distribution of monsoon vine-forest vegetation in the region can be shown to be influenced by landform change operating at essentially two scales of geological time. Over the greater part of the region landforms are deeply weathered, of low and rounded relief, broken only occasionally by sharp and jagged escarpments. For a general account of the geology of the region, with a description of Late Mesozoic and Cenozoic land surfaces and their associated weathering profiles, the reader is referred to Hays (1967). Soils, where present, are characteristically of low nutrient status (e.g. Aldrick 1976), being derived primarily from siliceous (e.g. sandstone) or acid igneous (e.g. granite) parent materials which, over vast areas, have undergone intense chemical weathering and laterization. While processes of erosion and soil development have been shown to be very active under present day climatic influences (Williams 1973, 1976, 1978), such environmental modification as results is relatively slow. By contrast, coastal and associated landforms have been subject to extreme episodic change throughout the Quaternary, primarily in response to glacio-eustatic sea level oscillations.

Fragmentation of extant sandstone floras throughout the Top End region can be traced from the Miocene at least when, as a result of slow uplift, the extensive, deeply weathered, lower Cretaceous sandstone surface began to be actively eroded (Noakes 1969; Williams 1969b). Prolonged differential erosion from Middle Tertiary times, dominated by scarp retreat and pediplanation, has largely destroyed this former land surface leaving scattered remnants, and exposing older sedimentary formations and igneous intrusions (e.g. Galloway 1976; Hays 1967; Williams 1969a,b; Wright 1963). Dissection of landforms in geological time may therefore help to account for the fragmentation and disjunction of monsoon vine-forest vegetation associated with sandstone formations through the Top End. For example, taxa such as *Ilex arnhemica*, *Polyscias australiana* and *Selenodesmum obscurum*, are known to occur only from widely separated sandstone regions.
Such fragmentation is a characteristic feature of the sandstone flora generally across the Top End.

A second, contrasting illustration of the influence of landform change is provided by the occurrence of isolated patches of monsoon vine-forest vegetation on landforms which are demonstrably Holocene in origin. Typical situations include sedimentary facies associated with prograding shorelines (e.g. chenier and beach ridges), actively slumping coastal cliffs and Holocene sediments and landforms of coastal and subcoastal riverine floodplains (Plate 5). As well, inferential evidence suggests that many vine-forest patches associated with the margins of these floodplains may likewise be Holocene in origin. In the western Arnhem Land region, for example, the riverine floodplains of the South Alligator River have been shown in recent studies (J. Chappell pers. comm.; Hope et al. in prep; Russell-Smith 1984), to be underlain by Holocene estuarine muds over a distance extending 80 km inland from the present coastline. Even to the present day the river is tidal almost throughout this range. Monsoon vine-forest patches occur only within the Holocene tidal range, distributed discontinuously along margins and on recently evolved landform features of the floodplain itself. With a couple of significant exceptions (such as certain lowland spring habitats which presumably represent more ancient refugia), the patches are composed of highly vagile and widespread species, many being typically maritime in distribution (e.g. Diospyros ferrea var. reticulata, Diospyros maritima, Ganophyllum falcatum, Pisonia aculeata).

Such observations suggest furthermore, that, in periods of falling sea level (i.e. marine regression), species with a demonstrated capacity to exploit maritime environments may actually prosper through the colonisation of freshly exposed and episodically created landforms at the periphery of the receding sea (Chappell and Thom 1977). These habitats are essentially ephemeral in geological time. Webb and Tracey (1981a) describe such habitats as a form of refugium.

Attendant with the last post-glacial rise in sea level, it is probable also that regional seasonal water balance improved in the Holocene, relative to the last glacial period at least, on two counts. Firstly, regional climates probably have been wetter, possibly markedly so for the period 5,000-8,000 years BP (Clarke et al. 1979; Jennings 1975; Nix and Kalma 1972; Smart 1976; Stocker 1971; Webster and Stretten 1972), although such evidence is suggestive only (Schrire 1981:8). And secondly, regional water tables would have risen, especially in
Plate 5: Monsoon vine-forest occurring on coastal beach ridge sediments with mangrove vegetation at the left of the picture (Photo: Ian Morris).

Plate 6: Regeneration of vine-forest species from coppice following a late dry season fire, South Alligator River floodplain margin.
coastal/subcoastal regions, in sympathy with the rising sea level. While such improvement in water balance conditions might also be expected to favour expansion of monsoon vine-forest vegetation, there is no direct evidence to indicate whether this vegetation has been significantly more, or less, extensive in the late Pleistocene and early Holocene than it is now. In certain localised coastal situations, and along the margins of tidal rivers, however, the occurrence of disused incubation mounds of the scrub fowl, *Megalopodius freycinet*, in sites currently occupied by eucalypt-dominated vegetation, indicates that for some unspecified past period, monsoon vine-forest vegetation previously occupied these sites (Russell-Smith 1984; Stocker 1971). Radiocarbon dating of charcoal and shell fragments incorporated within the fabric of a number of mounds, has yielded estimates of maximum mound ages which all fall within the Holocene (ibid.). Thus, while the occurrence of such mounds in eucalypt-dominated vegetation provides clear evidence for localised contraction (even elimination e.g. Russell-Smith 1984), of certain patches during the Holocene, a greater antiquity for these patches is not yet established.

2 5  Fire

On the basis of observations made from an ecological survey of over 200 patches of monsoon vine-forest vegetation in the north-west sector of the Top End by one of the authors (Russell-Smith unpub. data) it is evident that fire is a major ecological determinant in the localised distribution and boundary characteristics of vine-forest patches at the present day. In western Arnhem Land, for example, the boundaries of patches associated with certain estuarine springs, swamps, and sandstone pavements, are being eroded actively by fire at the present time, as evidenced by the burnt out shells and standing remnants of monsoon vine-forest species in many, sometimes extensive situations, marginal to extant patches. In coastal and subcoastal lowland situations the detrimental effects of modern dry season burning practices frequently are exacerbated by the impacts of feral animals, water buffalo especially (Braithwaite et al. in press[a]; Letts et al. 1979).

While the impact of fire at the present day is evident, the impact of fire over the longer span of geological time, and the influence of Aboriginal burning practices from the late Pleistocene, is not clear for the simple reason that palaeorecords such as exist for elsewhere in Australia (e.g. Singh et al. 1981) are not available. This notwithstanding, it is likely, given the probable existence of seasonal climatic conditions from the mid to late Tertiary at least, that fire has been a potent
factor in monsoonal northern Australia throughout this period (see Galloway and Kemp 1981, Kemp 1981b). While Aboriginal burning practices and their influence on monsoon vine-forest vegetation are discussed later in this section, it is necessary to consider at this point the responses and tolerances of individual species and diverse types of monsoon vine-forest vegetation, in relation to different fire regimes.

While it is often tacitly assumed that rainforest and monsoon vine-forest species are relatively fire sensitive, many species exhibit a broad tolerance to isolated, even frequent burning. This is evidenced by those species which characteristically occupy the exposed margins and ecotones of vine-forest patches and which regenerate vegetatively following fire (Plate 6). The monsoon vine-forest flora of the Top End comprises many such species, represented by nomadic and opportunistic shrubs, trees, vines and geophytes: *Antidesma caesembila*, *Brennia cernua*, *Bridelia tomentosa*, *Glochidion spp.*, *Macaranga spp.*, *Mallotus spp.*, *Phyllanthus spp.*, *Securinega melanthesoides* (Euphorb.); *Clerodendrum spp.*, *Premna spp.*, *Vitex spp.* (Verben.); *Alstonia actingophylla*, *Alyxia spp.*, *Ervatamia spp.*, *Ichnocarpus frutescens*, *Wrightia spp.* (Apoc.); *Ampelocissus spp.*, *Cayratia spp.*, *Cissus spp.* (Vit.); *Dioscorea spp.*, *Dioscor.); and a great many more. In a similar vein one can erect other categories of relative susceptibility, ending finally with that category comprising totally fire intolerant species (e.g. many ferns, mosses, mesophytic herbs).

When considered in this way, it emerges that only in the most sheltered and moist habitats is it likely that isolated fires would have catastrophic consequences; at the same time, such habitats are the least likely to be burnt.

With increased frequency of fire, or its increased intensity, many species otherwise relatively tolerant become increasingly susceptible. A salient example of this is provided by the myrtaceous tree *Allosyncarpia ternata*, which is restricted to the western Arnhem Land escarpment. This species is ecologically significant moreover, in that it is often the sole canopy species present in many local patches, and thus exerts a controlling influence on the subcanopy microclimate. *Allosyncarpia* is relatively tolerant of occasional fires given that, as a mature or immature tree, or as a sapling, it coppices readily. With increased fire severity however, saplings become susceptible given that regenerative tissues are held at, or just beneath, the soil surface. Mature trees also become more susceptible in that they typically are "piped", and once fire enters through fire scars or other deformities are liable to smoulder for weeks or more. When
individuals at the patch margin are killed in these manners, the surviving understorey and regeneration is exposed both to the full intensity of dry season conditions, as well as to competition from invading grasses (e.g. Triodia spp., Plectrachne spp.) and other opportunistic species (e.g. Acacia spp.). Under such a fire regime therefore, the retreat of patch boundaries may proceed rapidly.

With release from fire pressure on the other hand, the patch margin responds relatively slowly. In a typical Allosyncarpia forest situation, patch boundaries are sharp with only a narrow ecotone, and saplings and seedlings seldom occur beyond the limit of the forest canopy. This is because the dry, gravity-dispersed seeds of Allosyncarpia are seldom disseminated beyond the extent of the parent canopy (except where transported by water), and seedlings are highly intolerant of fully exposed conditions. Thus advancement of the patch boundary can occur essentially only through extension of the boundary canopy. Thus the rate at which a patch boundary can expand initially is dependant on the time taken for recruitment at the margin to attain sexual maturity; this is unlikely to be less than 20 years in a natural situation. While this example is exceptional in that it describes the fate of patch boundaries dependant largely on the adaptive traits of only one species, it serves as an illustration for the principle that different fire regimes affect patch margins differentially.

The vulnerability of patches is related, in the first instance, to the degree of protection afforded them by the habitats they occupy. Many extant patches, for example, occupy relatively protected situations, such as rock outcrops, screes and gorges. Others however, occupy relatively vulnerable open situations, such as sandplains, floodplain margins, lowland springs and coastal dunes (see Sect. 3.2). In these latter situations, the vulnerability of patches is very much dependant on the fuel characteristics of surrounding vegetation types, especially understoreys, since crown fires are virtually unknown. The vulnerability of patches is influenced also by the relative vigours of component species in different habitat types. Taking raw seedling survivorship as a measure of vigour, it is observed that, in perennially wet habitats, the density of seedlings surviving at the end of the dry season, is often as high as 200 seedlings per m$^2$ in localised situations; whereas, in harsh conditions, as on rock outcrops, seedling survivorship is as low as one seedling per 20m$^2$ (Russell-Smith unpub. data). Given the low level of effective recruitment which probably exists in many seasonally dry habitats, especially in inland regions, the frequency of fire in such situations is likely to be a critical ecological factor for the continued persistence of local populations and patches.
Where habitat conditions are more favourable for recruitment, the vigour of regeneration may be such as to effect the 'escape' of occasional cohorts from destruction by burning, even where fires occur relatively frequently.

With these considerations in mind, it is evident that historical and prehistorical fire regimes are likely to have affected different types of monsoon vine-forest vegetation, and different species, in a highly differential manner.

Aboriginal burning

Human occupation of the Top End is proven to extend beyond 20,000 years BP, based on the archaeological excavation of occupation sites in western Arnhem Land by Kamminga and Allen (1973), Schrire (1982) and Rhys Jones and others (pers. comms.). While a marked change is evident in stone tool technologies and subsistence patterns in the early to mid-Holocene, certain occupation sites excavated by Kamminga and Allen (1973) and Jones (pers. comm.) indicate that human occupation of this particular region has been more or less continuous through time. Human populations however are likely to have increased dramatically through the mid to late Holocene in response to the formation of extensive freshwater wetland ecosystems (Allen 1977; Hope et al. in prep; Jones and others pers. comms; Kamminga and Allen 1973; Schrire 1982).

Lewis (1982) suggests that Aboriginal burning practices in northern Australia have differed significantly from that which may be termed the natural system in four key ways: the seasonality of burning, the frequency with which fires are set, the intensity of fires and the human selection of sites for burning.

In the absence of human intervention, the main fire period in the Top End occurs at the end of the dry season, at the time Gunwinngu speaking people for northwest Arnhem Land call gunumeleng, the 'first-storm time' (Figure 2). Gunumeleng is the time of the pre-monsoon build-up, with its fierce electrical storms and localised gusty conditions. Although Stocker and Mott (1981:435-6) suggest that fires initiated by lightning strike are virtually unknown in the wetter forests and woodlands of the coastal belt, such observations apply mostly to the common situation where dry season burning-off is undertaken frequently, often annually; consequently, by gunumeleng, fuel loads are patchy and light. In situations where burning-off of large tracts of country is not undertaken at the present time, such as much of the Arnhem Land escarpment and in the Murganella region of northwest Arnhem Land, fires initiated by lightning strike are reported frequently.
Figure 2: Seasonal calendar for Western Arnhem Land Region in Gundjeidmi (Majiti) and Gunwinngu languages showing main burning periods. (Adapted from 'Seasonal calendar of Kakadu Region'; Alderson, Gangalf and Haynes, 1970)
By contrast, traditional Aboriginal 'cleaning up' of the country commences in the late wet season, at banggerreng, the 'knock 'em down storm' time, and continues unabated until gurrunng, the 'hot sand time'; that is, typically from April through November. While burning is undertaken also in gurrunng through gunumeleng, and even into the wet season proper, in western and north central Arnhem Land at least, restrictions are imposed on uncontrolled burning-off in the late dry season given the potential fire danger of this period, and the catastrophic effect such would have on game resources through destruction of feeding habitat (N. Kapirigi pers. comm.). A first difference between Aboriginal and natural fire regimes therefore, is the timing of the fire period.

A second difference concerns the frequency of burning. At the Blythe River in north central Arnhem Land, Jones (1975) records that, in each year, about half the clan estate was burnt, including all habitats with the singular exception of small patches of monsoon vine-forest, almost nowhere escaping the firesick over a three to four year period. While other estimates are lacking, such anthropogenic fire frequency is probably typical of other indigeniously populated areas. The frequency of lightning-set fires, while unreported in the literature, is certainly far less than that for anthropogenic fire given the shorter ignition season and the requirement for a sustaining fuel. Haynes (1982) suggests that the periodicity of lightning-set fires in open forests, woodlands and floodplains is unlikely to be less than five years. Hooper (1974) on the other hand suggests a frequency of two years. The intensity of fires under a natural fire regime however is likely to have been far greater than that under Aboriginal burning practices. In the latter instance, regular burning not only reduces fuel loads but, as well, creates mosaics of burnt and unburnt patches which would assist in checking the advance of an inadvertent late dry season conflagration (Haynes 1983). In this connection, for example, it is plausible that the present erosion of Allosyncarpia forest patch boundaries in the western Arnhem Land escarpment, may be the result of cessation of widespread Aboriginal burning-off in recent times. Such cessation has encouraged the development of highly flammable flash-fuels, especially the spinifex grasses, Tridria spp. and Plectachne spp. Haynes (1978) discusses the catastrophic effect of cessation of Aboriginal burning practice on plantations of the relatively fire-sensitive species, Callitris intratropica, at Maningrida.

The fourth way in which natural and Aboriginal fire regimes differ concerns the human selection of sites for burning. While the incidence of lightning strikes in different terrain types is not known, it presumably is concentrated in certain
situations (e.g. coastal regions, topographic high points). Aboriginal burning, on the other hand, is likely to have been concentrated in areas receiving the greatest utilisation (i.e. radiating from camp sites occupied through the seasonal cycle). Within this context furthermore, habitats are likely to have been burned preferentially (Haynes 1983). In north central Arnhem Land, for example, Haynes (1982) and Jones (1975) both report that small and evidently rare patches of monsoon vine-forest are left unburnt for spiritual and economic reasons. Some are even afforded protection through fire-breaks, by back-burning. In western Arnhem Land and the Cobourg Peninsula however, such prohibitions did not apply (N. Kapirigi, I. Morris pers. comms.). In these regions, "cleaning up" of patches was pursued actively, especially in the vicinity of camp sites, for the stated purposes of eliminating snakes and encouraging the regeneration of important yams, particularly Amorphophallus spp. and Dioscorea spp. It is evident, therefore, that burning practices are also likely to have differed culturally between regions.

Aboriginal occupancy of these monsoonal regions is likely, therefore, to have been accompanied by major changes to the prehuman fire regime. The influence of changed time of burning alone, is likely to have affected the reproductive and regenerative capacities of many populations, possibly even at the level of communities. These features notwithstanding, there is little evidence to indicate what impact Aboriginal burning practices have had on the regional distribution of monsoon vine-forest vegetation. It is improbable however, that such burning has contributed significantly to the fragmentation of populations associated with spring habitats, these distributions being better attributed to the scarcity of suitable habitat (Sects. 3.2.1, 3.2.2). It is even possible, furthermore, that much coastal and subcoastal vine-forest vegetation may not have been affected until the very late Pleistocene, and through the Holocene, given that such vegetation may not have been even present at this time (see Sect. 2.4). Thus, in the absence of any definitive evidence, the impact of Aboriginal burning on the regional distribution of this vine-forest vegetation is unknown.

That such burning practices have influenced the expression of vine-forest vegetation at least locally however, is illustrated by a number of situations. The most direct evidence for this concerns the occurrence of old campsites in...

As Haynes (1982) indicates, such "reasons" do not convey the full cultural significance of burning; it being an activity which is as much a (pleasurable) part of everyday living, as it is often utilitarian.
extensive clearings, within certain patches associated with riverine floodplain margins in western Arnhem Land. This is supported by oral evidence from elderly Aboriginal people who indicate that 'cleaning up' of such camp sites was undertaken regularly (B. Neiiji, L.D. Yarnmalu pers. comm.). As well, the sharp delineation of patch boundaries in situations where there is no evident change in edaphic conditions, provides for a less direct example. This is illustrated by the sharp boundary of a lowland patch of tall Allosyncarpia forest on deep moist gradational sands, where trees 25m tall and 1.5m DBH, give way abruptly to a shrubland of native weedy species (e.g. Acacia difficilis, Grevillea pteridifolia, Hibiscus arnhemensis, Triumfetta rhomboidea). While organic horizons are deeper under the closed canopy Allosyncarpia forest, this is an expression of the vegetation itself (e.g. Aldrick 1976:82; Markham and Babbedge 1979; Tinley 1982:178), and is not a determining factor. This boundary is likely therefore to be determined by fire, and given the proximity of this forest to a major floodplain camping area of pre-European times, is likely also to be a legacy of Aboriginal occupancy. In western Arnhem Land at least, such situations are common. Similarly, examination of the ethnographic record led Stocker (1968, 1971) to suggest that the reduction of a patch of monsoon vine-forest on the Karslake Peninsula, Melville Island, may have been attributable, at least in part, to fires lit for the purposes of driving game. In certain coastal and subcoastal situations furthermore, it is evident that, with the cessation of regular burning in the recent past, some patches are expanding at the present time. Near Cape Don, on the Cobourg Peninsula, for example, vine-forest vegetation is colonising recently abandoned camp sites on coastal dunes; such expansion being facilitated perhaps by the absence of thick and highly flammable grass understoreys.

While the impact of Aboriginal burning practices over a span of time encompassing more than 20,000 years, an ice age, and subsequent climatic amelioration and landform change is clearly difficult to assess, it is possible to make three broad generalisations. First, it is evident that traditional Aboriginal burning practices are likely to have significantly altered the fire regime operating prior to Man's arrival. Second, it is evident that Aboriginal burning practices are likely to have differed culturally, between regions and through time. And third, the impact of such practices is likely to have affected monsoon vine-forest vegetation differentially, depending both on the proximity of patches to areas of concentrated resource utilisation and occupation, and as well, on those factors which influence the relative susceptibility of different vegetation types, and the degree of protection afforded patches by different habitats.
2.6 Biological Responses and Interactions

In preceding sections we have considered environmental influences which have helped shape the evolutionary development of regional vine-forest vegetation and which find their expression in extant patterns of distribution. Whereas discussion of these influences has not been exhaustive (e.g. edaphic conditions, described in Section 3.2), so too is it evident that biological responses are expressed in ways other than distribution. Thus, for example, the flora is characterised both by its relative impoverishment and by the wide ecological amplitudes of many component species. While these and other attributes of the flora, and vegetation, are described in more detail in following sections, the biogeographical significance of dispersal is such as to warrant preliminary treatment here.

That the capacity to disperse effectively is an important characteristic of the extant flora, is demonstrated by the observation that over 70% of the flowering plant species so far recorded, have been found to occur on landforms of demonstrably recent origin (see Append.). Such observations demonstrate also a capacity for genetic exchange between specific populations, at least locally, and a qualified suggestion that such exchange may be exhibited more widely in the vegetation as a whole.

A second illustration of dispersal in action is provided by very small escarpment spring and seepage habitats where patch sizes may be as small as 0.01 ha, and yet where as many as 40 monsoon vine-forest species may be present. Population sizes are thus characteristically small. However, while woody species may be represented by from one to a small number of mature individuals, a census of seedlings and saplings frequently reveals the occurrence of other species, often in large number, for which no mature individuals are present. In Table 1, for example, is presented data from a census of woody species in a relatively isolated spring habitat in the western Arnhem Land escarpment of 0.025 ha extent. It may be observed from this Table that of the 18 species whose mature growth form is that of a small or large tree, 10 are represented only by sexually immature seedlings and saplings. That recruitment of such species is attributable, at least in part, to dispersal from other populations, is demonstrated by the variety of seeds, including Calophyllum sil and Canarium australianum, which have been collected in seed traps suspended above-ground in this and other small spring habitats (Russell-Smith unpub. data; see also Begg & Dunlop 1980). Dispersal agencies are discussed in Sect. 3.1.3.
This demonstrated capacity of many species to disperse widely from the parent plant has three important implications. The first is that, while individual patches may be relatively isolated spatially many specific populations may not be isolated genetically. Secondly, the persistence of species in individual patches may not be so much dependent on the maintenance of viable population structures and sizes in each patch in isolation, as on the collective population scattered through a number of local patches. And thirdly, such capacity for dispersal demonstrates that a characteristic feature of this flora is the ability possessed by a majority of species to take advantage of new ecological opportunities as these are created through time.
**TABLE 1** Census of Plants at a small perennial spring, western Arnhem Land escarpment (July 1982). Area of monsoon vine-forest patch 0.025 ha.

<table>
<thead>
<tr>
<th>Species</th>
<th>Seedlings</th>
<th>Saplings</th>
<th>Mature Trees</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;1m ht</td>
<td>&gt;1m ht, 3-10cm</td>
<td>10cm DBH</td>
</tr>
<tr>
<td></td>
<td>&lt;3cm DBH</td>
<td></td>
<td>DBH</td>
</tr>
</tbody>
</table>

1. **Trees**

- *Syzygium angophoroides* (Myrt.) 21
- *Xanthostemon eucalyptoides* (Myrt.) 3
- *Rapanea benthamiana* (Myrsin.) 165
- *Illex arnhemica* (Aquifol.) 8
- *Elaeocarpus arnhemica* (Elaeocarp.) 10
- *Lophostemon lactifluus* (Myrt.) 4
- *Helicia australasica* (Prot.) 12
- *Acacia aulacocarpa* (Mimos.) 12
- *Carallia brachiata* (Rhizophor.) 4
- *Calophyllum sil* (Clus.) 61
- *Diospyros calycantha* (Eben.) 10
- *Drypetes lasiogyna* (Euphorb.) 8
- *Canarium australianum* (Burser.) 2
- *Maytenus ferdinandi* (Celastr.) 1
- *Maranthes corymbosa* (Chrysobalan.) 8
- *Pouteria sericea* (Sapot.) 3
- *Buchanania obovata* (Anacard.) 1
- *Ixora tomentosa* (Rub.) 1
- *Memecylon pauciflorum* (Melastom.) 1

2. **Shrubs**

- *Melastoma malabathricum* (Melastom.) 86
- *Coelospermum reticulatum* (Rub.) 2
- *Boronia lanceolata* (Rut.) 2
- *Alyxia ruscifolia* (Apocyn.) 2
- *Bridelia tomentosa* (Euphorb.) 1

**Other Species:**
- Lianes: *Flagellaria indica, Smilax australis, aff. Coelospermum B1523.*
- Ferns: *Nephrolepis biserata, Lindsaea ensifolia, Schizaea dichotoma, Drynaria quercifolia, Stenochlaena palustris, Dicranopteris linearis, Taenites blechnoides.*
For less vagile species however, or for species whose habitat or microhabitat requirements are such that ecological opportunities are scarce, persistence is dependant on the maintenance of viable populations in each isolated patch, concomitant with the preservation through time of sufficiently large and stable areas of habitat refugia.

Furthermore, given that many species are evidently highly vagile, and given that many of the same species are tolerant of a wide range of environmental situations (see Sect. 3.2), it would thus appear that monsoon vine-forest vegetation presently occupies but a fraction of its potential ecological domain. While in previous discussion we have considered largely the selective agencies of various environmental determinants, a further factor likely to have contributed to this is the influence of increasing competition from species generally better suited to mid to late Tertiary and Pleistocene environmental conditions, including fire. That such competition may be a very significant factor is suggested by the apparent difficulty which monsoon vine-forest species typically have in establishing in essentially undisturbed eucalypt forest or woodland situations. On certain offshore islands which are seldom burnt, for example, monsoon vine-forest species have had little success in surplanting eucalypt-dominated vegetation, despite the availability of seed sources at these islands' peripheries, and despite the availability of suitable conditions for establishment. In these same situations however, where habitats have been disturbed sufficiently through high energy events, such as the deposition of coastal sands over lateritic profiles or where new habitats have been made available through processes of coastal progradation and other agencies, monsoon vine-forest species have responded vigorously.

As well, while such competition as these examples suggest may be attributable, in part, to direct competition for resources, and indirectly through the influence of other vegetation components on fire behaviour, it is possible also that sclerophyll vegetation (e.g. Eucalyptus spp.) may exclude vine-forest species allelopathically. While this has not yet been tested rigorously, an exploratory pottrial experiment undertaken by Stocker (1968:105-112) is at least suggestive. Information regarding other biotic interactions (e.g. termites) is not available.
2.7 Synthesis

Such information as is available indicates that the extant expression of this vine-forest vegetation is likely to have been derived holocenotically (Sarmiento and Monasterio 1975), reflecting the interaction and concurrence of a variety of factors and processes through time.

3. BIOTA
3.1 Flora
3.1.1 Introduction

At the outset we suggested that detailed biogeographical comparisons were somewhat premature and in any case were beyond the scope of this paper. However, as a contribution towards future comparative studies of vine-forest floras in the Australian region, we have listed all known species, in their community types (see Sect. 3.2), in the Appendix. Moss and lichen records are as yet incomplete and have therefore had to be omitted. Also absent are a small number of flowering plants, collected in a sterile state, which could not be placed with certainty in a family.

For the most part there has been little difficulty in deciding whether or not a species is a genuine inhabitant of monsoon vine-forest. In general we omitted those species which, although occasionally found along the boundary or caught in an expanding thicket (e.g. Lophostemon lactifluus, Erythrophleum chlorostachys), do not regenerate successfully in closed canopy vine-forest.
The authors are indebted to the report of Webb and Tracey (1979) from which floristic data have been freely used.

To date, 358 species in 250 genera in 95 families have been recorded. Thus the flora shows a high diversity at the higher taxonomic levels, a feature noted for the Queensland rainforest flora by Johnson (1984).

It is not certain how many species are endemic to the region but at the generic level these are relatively few: e.g. Allosyncarpia, Carpentaria, aff. Coelospermum B1523. A few more extra-Australian taxa are represented in Australia in this region only: Peitophorum, Lophopetalum, Seregada. In general however, the taxa are widespread (see Specht 1958b:420; Taylor and Dunlop 1984) and there is very little evidence that regional influences have led to any degree of speciation.

3.1.2 Life Forms

An analysis of life forms from the Appendix reveals the following percentages of species in each category:

- trees 47
- geophytes 4
- graminoids 2
- shrubs 10
- climbers 21
- epiphytes 2
- herbs 10
- palms 2
- scandent shrubs 2

Of particular note is the low figure for epiphytes (2%) which is undoubtedly a direct result of the long dry season with its attendant low humidities. For the same reason the number of ferns is low (31 spp.), only one of which is a filmy fern (Selenodesmum, family Hymenophyllaceae) restricted to ever-humid Sandstone Spring habitats.

The degree of deciduousness in the flora is relatively high in all community types though less marked in the Sandstone Spring forests (see Taylor and Dunlop 1984). The ability to remain leafless for an extended period is perhaps the most critical criterion for survival in seasonally extreme sites. In vine thickets on coastal dunes for example, over 90% of the canopy species present may be deciduous. An interesting parallel adaptation is the retention of the foliage in a wilted state, a feature exhibited by a small number of species, e.g. Micromelum minutum, Murraya exotica, Glycosmis pentaphylla (Rutac.) and Aglaia eleagnoides (Melia).
Elsewhere in the paper we have indicated (see Sect. 3.2) that a large proportion of the monsoon vine-forest species of the Top End region are vagile; i.e., they occur frequently over a wide geographic range, often on relatively recently evolved landforms such as stabilised beach dunes and riverine floodplains. By definition therefore, a vagile species is one which can both disperse and establish effectively.

We have recognised 10 categories of propagule (Appendix) for the flora and listed their frequency of occurrence in each community type in Table 2. The categories are self-explanatory with perhaps "presented" and "bouyant" requiring an added note. The "presented" type includes dry seeds or seeds with an insignificant sarcotesta which are held in the open fruit on the plant. The group corresponds closely with the Mimesis dispersal class of van der Pijl (1969) and includes highly coloured seeds (e.g. Glochidion xerocarpum), bicoloured seeds (e.g. Abrus precatorius), bicolour fruit-seed combinations (e.g. Sterculia quadrifida), glistening black seeds (e.g. Euodia ellervana) and dull, apparently unattractive seeds (e.g. Homalanthus navo-guneensis). "Bouyant", although it is a dispersal mechanism as opposed to a propagule type, is a convenient category to describe those propagules for which water is known to be the major (if not the only) dispersal agent. Inedible and dry fruits (e.g. Cathormium umbellatum) and the large (>2.5cm) fleshy fruits of riparian species such as Syzygium forte belong to this group though we have omitted many other possible contenders (e.g. plumed seeds of family Asclepiadaceae) which are not necessarily dependent on water transport explicitly. The fruit of Syzygium forte is too large for bird-dispersal but floats well.

Species with bird-dispersed propagules (fleshy fruit, arillate and funiculate, presented) are clearly the most numerous in all community types (Table 2). Webb and Tracey (1981a) had a similar result for north Queensland rainforests. A variety of birds have been observed feeding on fleshy fruits (Table 3) but we regard the Torresian Imperial Pigeon (Ducula epilophos) as the most significant dispersal vector for this group. It is significant by virtue of the following characteristics: (i) migratory habit, (ii) occurrence in large numbers during the fruiting period, (iii) large size, enabling it to eat all but a few of the larger fruits. Frith (1982, and references therein) provides details on all aspects of the bird's biology, including diet and dispersal ability in coastal Queensland. In suburban Darwin Ducula is conspicuous from the later Dry season through to the
end of the Wet feeding on cultivated *Carpentaria acuminata* and many other species. They are also plentiful at this time in the monsoon vine-forest patches across the region, ranging as far inland as the Katherine district. Although systematic observations on their role as vectors have not been undertaken in the Top End, it would be fair to assume that they are the major carriers of seed along the riparian strips and between monsoon vine-forest patches. From Frith's notes (op. cit.) on the Rose-crowned Fruit Dove (*Philinopus regina*) it may be inferred that this species is an equally important dispersal agent. It has perhaps a broader dietary spectrum than *Ducula* since it is resident throughout the year. The Banded Fruit-Dove (*Philinopus alligator*) similarly plays an important role in linking the Sandstone Springs and Dry Sandstone patches in the Alligator Rivers region (see Frith, op. cit.).

A number of other frugivorous birds which typically frequent the open forest are listed in Table 4. These birds are occasional visitors to the monsoon forest and are local dispersers of fleshy and mimetic propagules.

From the literature it appears that the importance of fruit bats (*Pteropus* spp.) in dispersing fleshy fruits is inconclusive though they are undoubtedly vectors of pollen (Leen 1969) and Figs. Myrtaceous trees (*Syzygium* spp., *Kapokstemon* spp.), which are heavy producers of nectar, would undoubtedly benefit from cross pollination by fruit bats travelling between patches and along riparian strips. Those figs which are large-fruited and cauliflorous (e.g. *Ficus racemosa*, *F. congesta*) and therefore not generally accessible to birds are reliant to some degree on dispersal by bats. For example, in germination studies on droppings from a fruit bat colony in Kakadu National Park (Russell-Smith, unpub. data), *Ficus racemosa* was the most common germinant; other species recorded were *Morinda citrifolia*, *Passiflora foetida*, and *Ficus hispida*.

An interesting distributor of fleshy fruit is the feral pig (*Sus scrofa*). We have recorded seed and seedlings of *Carpentaria acuminata* in pig dung in Sandstone Spring forests in the Arnhem Land escarpment and seed of *Tamarindus indica* in dung in coastal forests at the Daly River mouth. As pigs forage over large areas it is probable they are effective local dispersers of fleshy fruits.

Species with wind dispersed propagules which are winged or plumed (e.g. *Bombax*, Asclepiadaceae) favour the dry habitat types (Table 2); conversely, species with spores or dust-like seeds (ferns, orchids) which are also wind dispersed, favour the perennially wet communities.
J.1.4 **Intersperse species**

The interspersion of monsoon vine-forest related species through the open, eucalypt-dominated communities has been noted by several authors (e.g. Gardener 1942, Walter 1971, Webb and Tracey 1981b). Although more obvious in the monsoon tropics, the phenomenon is nevertheless quite widespread (Beadle 1981). In the monsoon tropics the intersperses are widespread in a variety of community types though they are most conspicuous in the eucalypt open forest and woodland savannas. Here the broad, horizontally held leaves and dense canopy of such species as *Terminalia ferdinandiana* and *T. lolipes* is in marked contrast to the thin-taliaged dominant eucalypts. Many species are completely leafless during the dry season though a number are evergreen (e.g. *Buchanania obovata*, *Erythrophleum chlorostachys*). Similarly, the intersperses of the sandstone and sandstone-derived soils consist of deciduous (e.g. *Cochlospermum fraseri*, *C. gillivraei*, *C. gregorii*) and evergreen species (e.g. *Owenia vernicosa*, *Blepharocarya depauperata*).

Life forms of the intersperses are invariably perennial. The majority are trees (e.g. *Gardenia* spp., *Brachychiton* spp.) with a lesser proportion of shrubs (e.g. *Carissa lanceolata*, *Coelospermum reticulatum*) and geophytic vines (e.g. *Cynanchum* spp., *Marsdenia* spp., *Tylophora* spp., all Asclepiadaceae). Added to these is a sprinkling of other, more specialised life forms such as stem parasites (e.g. *Cassytha* spp.) and epiphytes (*Cymbidium-canaliculatum*).

Propagule types are mainly of two categories: fleshy fruits (e.g. *Terminalia* spp.) and winged/plumed (e.g. *Terminalia platyptera* for winged, *Cochlospermum* spp. for plumed). Species with dry, dehiscent fruits (e.g. *Croton arnhemicus*) are few.

Further to the above, the intersperses of the monsoon tropics are characterised by:

1. A close genetic affinity with vine-forest taxa. Many have congeners in the vine forest (e.g. *Buchanania*, *Capparis*, *Ficus*, *Livistona*, *Planchonella*, *Stenocarpus*, *Syzygium*).

2. The capacity to establish in open savanna conditions. Such conditions include not only the exigencies of a seasonally harsh physical environment, but competition from graminoid components as well.
A tolerance of frequent low-intensity fires: a feature shared with many
vine-forest taxa (see Section 2.5). On the basis of casual observations it
would appear that the great majority of woody interspersive taxa readily
regenerate from coppice following burning. Resilience is afforded
gephytes through their seasonal growth habit.

Low competitive vigour under closed canopy vine-forest conditions. While
interspersives may occur occasionally under closed canopies, such
individuals typically are suppressed or exist only as seedlings.

The production of flowers and new vegetative growth in the late dry
season. While such a phenology is shared also by many monsoon vine-
forest taxa, as well as being a feature of tropical floras in seasonal
climates generally (see Janzen 1967, Walter 1971), it is in contrast to the
dominant eucalypts which, with the exception of the paper-fruited
bloodwoods (subgenus Blakelea [Pryor and Johnson 1975]), flower at
different times through the year.

Thus, while interspersive and vine-forest taxa share a common genetic heritage,
the former are distinguished ecologically by their tolerance of savanna conditions
and their intolerance of closed canopy situations. Such distinctions suggest that
interspersive species are unlikely to be remnants of a former, more widespread
vine-forest vegetation.
TABLE 2 Frequency of occurrence of propagule/dispersal type within each community type.

<table>
<thead>
<tr>
<th>Propagule/Dispersal Type</th>
<th>Subcoastal</th>
<th>Coastal</th>
<th>Lowland Spring</th>
<th>Sandstone Spring</th>
<th>Dry Sandstone</th>
<th>Rock Outcrop</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fleshy fruit &gt;2.5cm wide</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Fleshy fruit &lt;2.5cm wide</td>
<td>52</td>
<td>54</td>
<td>52</td>
<td>49</td>
<td>54</td>
<td>37</td>
</tr>
<tr>
<td>Arillate, funiculate</td>
<td>3</td>
<td>2</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Presented</td>
<td>9</td>
<td>8</td>
<td>6</td>
<td>6</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>Dry. - explosive, gravity</td>
<td>10</td>
<td>9</td>
<td>9</td>
<td>7</td>
<td>12</td>
<td>11</td>
</tr>
<tr>
<td>Spores, dust like</td>
<td>5</td>
<td>4</td>
<td>14</td>
<td>24</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Winged, plumed</td>
<td>10</td>
<td>10</td>
<td>4</td>
<td>2</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>Burred, sticky</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Bulbils</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Bouyant</td>
<td>4</td>
<td>6</td>
<td>5</td>
<td>4</td>
<td>–</td>
<td>1</td>
</tr>
</tbody>
</table>
TABLE 3 Birds in the Northern Territory for which monsoon vine-forest is the preferred or obligate habitat (data supplied by J. McKean, C.C.N.T.)

| Pacific Baza (Aviceda subcristata) |
| Grey Goshawk (Accipiter novaehollandiae) |
| Orange-footed Scrub Fowl (Megapodus freycinet) |
| Band-tailed Scrub Fowl (Megapodus freycinet) |
| Grey Goshawk (Accipiter novaehollandiae) |
| Rose-crowned Fruit-Dove (Ptilinopus regina) |
| Torresian Imperial Pigeon (Ducula spilorrhoa) |
| Bar-shouldered Dove (Geopelia humeralis) |
| Emerald Dove (Chalcophaps indica) |
| Bush Cuckoo (Cuculus variolosus) |
| Little Bronze Cuckoo (Chrysooceyx minitillus) |
| Rufous Owl (Ninox rufa) |
| Little Kingfisher (Ceyx pusillus) |
| Rainbow Pitta (Pitta iris) |
| Cicadabird (Coracina tenirostris) |
| Varied Triller (Lalage leucomea) |
| Mangrove Golden Whistler (Pachycephala melanura) |
| Grey Whistler (Pachycephala simplex) |
| Little Shrike-Thrush (Colluricinclat megarrhyncha) |
| Broad-billed Flycatcher (Myiagra ruficollis) |
| Shining Flycatcher (Monarcha alecto) |
| Rufous Fantail (Rhipidura rufifrons) |
| Large-billed Gerygone (Gerygone magnirostris) |
| Green-backed Gerygone (Gerygone chloronota) |
| Helmeted Friarbird (Philomachus pectoralis) |
| White-lined Honeyeater (Meliphaga albilineata) |
| White-faced Honeyeater (Lichenostomus unicolor) |
| Red-headed Honeyeater (Myzomela erythrocephala) |

# Obligate frugivores
* Opportunistic frugivores
+ Obligate inhabitants
TABLE 4 Fruit-eating Northern Territory birds which occasionally visit monsoon vine-forest. None are obligate frugivores.

<table>
<thead>
<tr>
<th>Bird Name</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-bellied Cuckoo-shrike</td>
<td>Coracina novaehollandiae</td>
</tr>
<tr>
<td>Common Koel</td>
<td>Eudynamys scolopacea</td>
</tr>
<tr>
<td>Channel-billed Cuckoo</td>
<td>Scythrops novaehollandiae</td>
</tr>
<tr>
<td>Silver-crowned Friarbird</td>
<td>Philemon argenticeps</td>
</tr>
<tr>
<td>Blue-faced Honeyeater</td>
<td>Entomyzon cyanotis</td>
</tr>
<tr>
<td>Mistletoe Bird</td>
<td>Dicaeum hirundinaceum</td>
</tr>
<tr>
<td>Yellow Oriole</td>
<td>Oriolus flavocinctus</td>
</tr>
<tr>
<td>Olive-backed Oriole</td>
<td>Oriolus sagittatus</td>
</tr>
<tr>
<td>Figbird</td>
<td>Sphecotheres flaviventris</td>
</tr>
<tr>
<td>Great Bowerbird</td>
<td>Chlamydera nuchalis</td>
</tr>
</tbody>
</table>
3.2 Vegetation Habitat Types

Descriptions of Northern Territory monsoon vine-forest vegetation, especially at the narrow regional level, are provided by Burgman (1980), Chippendale (1974), Christian and Aldrick (1977), Christian and Stewart (1953), Kikkawa et al. (1981), Langcamp et al. (1981), Schodde and Martensz (1973), Specht (1958a), Speck (1965), Stocker (1968), Storey (1969, 1973, 1976, 1982), Taylor and Dunlop (1984) and Webb and Tracey (1979). For the purposes of this paper however, the vegetation is described with reference to six broad habitat types: lowland springs, sandstone springs, seasonally dry escarpment situations, coastal landforms, subcoastal landforms and rock outcrops.

These habitat types are useful in so much as they provide a framework for assessing the condition and, in Section 4, the conservation status, of diverse elements which constitute this vegetation. As well, these habitat types, whilst derived subjectively are supportable floristically. In Table 5a, derived from data presented in the Appendix, the number of flowering species occurring in each broad habitat type, and shared with other habitat types, is indicated. Thus, for example, it may be observed that 140 species are shared between coastal and subcoastal seasonally dry habitats, representing 70% of the coastal and 88% of the subcoastal habitat floras. In a sense, therefore, the subcoastal flora may be considered a subset of the coastal type, the latter being distinctive however, in that 34 species occur exclusively in coastal situations. Similarly, we have found it useful to distinguish between spring habitats associated with the coastal/subcoastal lowlands, and those associated with sandstone formations. Thus, while 83 species are shared between these similar habitat types, representing 73% and 56% of the sandstone and lowland spring floras respectively, 13 species are known to occur only in sandstone situations and 20 species in lowland spring situations. Such a dichotomy is reinforced with reference to similar data for the distribution of fern species in these two habitat types (Table 5b). However, given that there is a certain degree of floristic overlap evident between each pair of habitat types, and that at least 33 flowering plant species are shared in common between all habitat types (from Appendix), these broad categories may best be considered as representing various nodal conditions of the environmental mosaic.
TABLE 5  Number of Species Known to Occur in, and Shared Between, Habitat Types

Numbers in round brackets refer to species known to occur on Holocene landforms.
Numbers in square brackets refer to species found exclusively in one habitat type.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Subcoastal</th>
<th>Coastal</th>
<th>Lowland Springs</th>
<th>Sandstone Springs</th>
<th>Dry Sandstone</th>
<th>Rock Outcrops</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Flowering Plants</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coastal</td>
<td>199[35]</td>
<td>87</td>
<td>53</td>
<td>90</td>
<td></td>
<td>110</td>
</tr>
<tr>
<td>Lowland Springs</td>
<td>147[20]</td>
<td>83</td>
<td>60</td>
<td>63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandstone Springs</td>
<td>113[13]</td>
<td>56</td>
<td></td>
<td>42</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry Sandstone</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock Outcrops</td>
<td>144[28]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>125[2]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b) Ferns</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subcoastal</td>
<td>7</td>
<td>1</td>
<td>7</td>
<td>5</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Coastal</td>
<td>2[1]</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Lowland Springs</td>
<td>17[2]</td>
<td>13</td>
<td>4</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandstone Springs</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry Sandstone</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Rock Outcrops</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3</td>
</tr>
</tbody>
</table>
In presenting this account, we must ask the reader to excuse a number of manifest deficiencies. We have as yet, little data regarding vine-forest vegetation in eastern Arnhem Land, and for inland regions. In the former case, with the exception of seasonally dry sandstone escarpment habitats, it is likely that vine-forest vegetation is similar to that as described here for western coastal and subcoastal regions. Floristic similarities with Cape York are likely to be greater. However, for inland regions, the absence of sufficient data is more critical. In these regions vine-forest vegetation is known to occur on rock outcrops, on deep loams (often in association with Lancewood, Acacia shirleyi, thickets), and as riparian strips. At the present time, the extent of these communities, their composition and their condition, is too little known to warrant their inclusion here. Riparian vine-forest vegetation associated with both subcoastal tidal and freshwater watercourses however, is described under seasonally dry subcoastal landforms.

A schematic representation of the habitat types of monsoon vine-forest described in this paper is presented as Figure 3.

3.2.1 Lowland Springs

The optimal expression of vine-forest vegetation in the Top End occurs as Complex Notophyll Vine Forest (CNVF)*, in rare perennial spring and seepage habitats. In low-lying coastal and subcoastal regions, such habitats are associated both with the sources of small streams (Plate 7), as well as with the margins of riverine floodplains or prograding estuarine landforms, where terrigenous freshwater seepages are impounded. In these latter situations, Notophyll Evergreen Vine Forest, with palms, (NEVF) is also associated with springs or seepages which intrude Holocene sediments such as occurs on the Adelaide River floodplain, on Koolpinyah Station near Darwin. Soils are characteristically waterlogged, with shallow (20-50cm) organic-rich loams through loamy sands, overlaying deep gleyed clays. Such soils are readily eroded, and the nutrient status depleted, under the impact of feral animals, especially water buffalo.

Patches range in size from less than 1 ha to more than 100 ha in extent, their boundaries frequently protected by only narrow ecotones. In many, but not all boundary situations, burning, in combination with feral animal impact, is exacting severe damage at the present day. This is especially true for smaller patches associated with the sources of streams.

* Structural terminology where used, as per Webb (1978).
Figure 3: Schematic representation of vine-forest habitat types

LEGEND

OOO monsoon vine-forest  ○ eucalypt woodland

OOO mangroves  :: floodplain

HABITAT TYPES:
5. Dry Sandstone  6. Rock Outcrop
Plate 7: A small discrete patch of lowland Notophyll Vine Forest associated with widespread seepage in gently undulating terrain, Melville Island. In the absence of other constraints this boundary probably reflects the influence of fire.

Plate 8: Evergreen Notophyll Vine Forest associated with a perennial spring in dissected sandstone terrain, western Arnhem Land. The palm is Carpentaria acuminata and is endemic to the Top End.
Under optimal conditions, canopy height is seldom greater than 25 m, the upper canopy dominated by evergreen trees (e.g., *Acacia auriculiformis*, *Buchanania arborescens*, *Endospermum medullosum*, *Horsfieldia australiana*, *Syzygium operculatum*), and palms (*Carpentaria acuminata*, *Livistona benthamii*), with a smaller number of deciduous elements (e.g., *Gmelina dalrympleana*, *Nauclea orientalis*, *Terminalia sericocarpa*, *Vavsea australiana*). Buttressing is common. Understoreys are composed of small evergreen trees and tall shrub species, a number of which respond vigorously to canopy gaps created through localised disturbance (e.g., *Alphitonia excelsa*, *Hibiscus tiliaceus*, *Homolanthus novoguineensis*, *Macaranga involucrata*, *M. tanarius*). Groundcover is usually sparse but in certain situations ferns may be abundant (e.g., *Acrostichum aureum*, *Blechnum indicum*, *B. orientale*, *Microsorum* sp. aff. *coleopendria*, *Lindsaea ensifolia* sp. *ensifolia*). Lianes are common, and seldom thicker than 5 cm in diameter. Epiphytic (and ground) orchids are uncommon, and epiphytic ferns are mostly absent.

In situations where perennial streams/seepages abut riverine floodplains over black (organic) clays, species richness declines considerably. The canopy is dominated by deciduous species and myrtaceous sclerophylls (*Melaleuca cajuputi*, *M. leucadendron*). As well, a number of other species more tolerant of floodplain (wet-dry) conditions are often present (e.g., *Barringtonia acutangula*, *Cathormion umbellatum*).

### 3.2.2 Sandstone Springs

Evergreen vine-forest vegetation, comprising a number of structural types, occurs also in ever-wet situations associated with sandstone formations. Three types of habitat may be distinguished: seepages from undulating slopes of sandstone plateaux; sand-sheet springs; and springs and seepages in dissected sandstone terrain. In many respects, the habitats provided by the former two situations are homologous with those described for lowland springs under optimal conditions; their margins are unprotected topographically, and soils exhibit similar characteristics to those described previously. As such, the influences of fire and buffalo impact apply here equally.

On the Tolmer Tableland (to the south of Darwin) and on Melville Island, very rare patches of CNVF, from 5 to 100 ha in extent, are associated with extensive seepages from the sides of sandstone plateaux. In these situations, shallow
organic loams over sandstone debris give way, towards the bottom of the slopes, to deep saturated podzols with humic horizons up to 50 cm deep. Canopy height is around 30 m, dominated by evergreen trees (e.g. *Elaeocarpus grandis*, *Horsfieldia australiana*, *Planchonella* sp. B2101, *Syzygium angophoroides*, *S. minutuliflorum*, and the palm, *Carpentaria acuminata*). Characteristic dominant lowland spring species such as *Livistona benthamii*, *Nauclea orientalis* and *Syzygium operculatum* are absent. Smaller trees, ground ferns, and sedges are abundant. Slender lianas are common. Structurally, and to a large degree floristically, therefore, this vegetation is similar to that of lowland springs under optimal conditions.

The second habitat type concerns the association of NVF with small springs in gently undulating sandstone terrain with deep sandy mantles. Soils comprise saturated organic loams through loamy sands overlaying deep gleyed clays. Patch boundaries are sharp, partly reflecting the localised occurrence of spring conditions and partly reflecting the influence of recurrent fires in trimming margins. Patches range in size from less than 1 ha to 2 ha, often as narrow strips 10-20 m wide along stream channels. The impact of buffalos in such situations as we have observed is devastating.

Canopy height seldom attains 20 m since, in most situations, the canopy is composed largely of regenerating immature trees through which protrude fire-killed stags. Canopy species include *Euodia elleryana*, *Ilex arnhemicus*, *Planchonella* sp. B2101, *Syzygium angophoroides*, *S. minutuliflorum* and *Xanthoslemon eucalyptoides*. Smaller trees and shrubs are occasional, and ground ferns are abundant. Vines are uncommon.

The third habitat type concerns the association of CNVF through ENVF (with feather palms), with springs, seepages and riparian situations in dissected sandstone terrain (Plate 8). While such vegetation probably occurs in all sandstone regions, its best expression is known to occur on Melville Island and in western Arnhem Land. In the former locality, CNVF is associated with shallow stream gullies incised into fine-grained sandstones. Landform relief, however, is subdued. In western Arnhem Land, ENVF is associated with springs and seepages in deep sheltered gorges. Given the highly protected nature of these habitats, fires are infrequent, their restricted occurrence dependent largely on lightning strike. Soils are characteristically shallow to deep organic sands, overlaying, or interspersed with, sandstone stones and boulders. Properties of drainage and soil aeration in these coarse textured soils are likely to differ significantly therefore, from those in other spring habitat types with ever-wet fine-textured soils.
On Melville Island, canopy top height is around 20-25 m; the upper canopy dominated by evergreen tree species such as Acmena hemilampra, Acmena claviflorum, Elaeocarpus culminicola, E. grandis, Endop tertum medullosum, Planchonella sp. B2101. Smaller trees, vines and ground/rock ferns are common.

In western Arnhem Land, canopy top height is similar although, in situations where deep gradational sands have accrued in relatively wide gorges, canopy height may be as much as 35 m; but comprising only one species (Allosyncarpia ternata).

These forests are structurally and floristically simple, being dominated by a relatively small number of evergreen species (typically Allosyncarpia ternata, Buchanania arborescens, Calophyllum his, Carpentaria acuminata, Horsfieldia australiana, Planchonella sp. B2101, Syzygium anogrophoroides, S. forte, S. minutuliflorum, Xanthostemon eucalyptoides), with few shrubs, lianas, other smaller trees, and only a scatter of ground ferns. On rockwall seepages however, ferns (e.g. Blechnum indicum, Dicranopteris linearis, Drynaria quercifolia (common on dry rock faces), Nephrolepis biserrata, N. oblitterata, Stenochlaena palustris, Taenites blechnoides), and mosses, are common.

Patches range in size from very small pockets in the vicinity of seepages, often much less than 0.1 ha, through narrow strips along sheltered gorges up to 1-2 ha in extent, to extensive but rare riparian types up to 10 km long and 50 m wide (50 ha) along more open Arnhem Land escarpment valleys, and the creeks of Melville Island. The riparian types of western Arnhem Land are characteristically intermixed with sclerophyll species (e.g. Acacia spp., Lophostemon lactiflussy, Melaleuca spp.). In this latter situation moreover, fast-moving seasonal floodwaters up to 5 m depth are an annual source of disturbance (Plate 9).

3.2.3 Seasonal Escarpment Habitats

As with vine-forest vegetation associated with springs in dissected escarpment terrain, patches of vine-forest occupying escarpment habitats which are markedly seasonal with respect to water balance conditions probably exist in all regions. The best expression of this vegetation however, is found in western Arnhem Land (Plate 10). Essentially two structural types occur: Simple Notophyll Semi-Evergreen Vine Forest (SNEVF), dominated monotypically by Allosyncarpia ternata; and Semi-Deciduous Notophyll Vine Forest (SDNVF) where Allosyncarpia is absent. This second type however, is composed essentially of the same species which occur with Allosyncarpia forests with, in some instances, another myrtaceous sclerophyll assuming dominance (i.e. Xanthostemon psidioides, X. umbrosus).
Plate 9: Riparian vine-forest interspersed with paperbarks (Melaleuca leucadendron) following annual wet-season flooding, upper Magela Creek, western Arnhem Land.

Plate 10: Simple Notophyll semi-Evergreen Vine Forest, dominated by Allosyncarpia ternata, on sandstone scree, western Arnhem Land.
In earlier discussion (Sect. 2.5), the ecological significance of *Allosyncarpia* to the well-being of seasonal escarpment vine-forests was described, the distribution of that vegetation very much being tied to that of *Allosyncarpia*. *Allosyncarpia* occurs over a wide range of conditions, from perennially wet sheltered situations through deep inert colluvial sands, steep rocky scree, exposed gulches and bare sandstone pavements. Thus, as well as enjoying sites of optimal regional conditions, *Allosyncarpia* is also tolerant of harsh xeric and infertile sites. *Allosyncarpia* is relatively susceptible however to fires under certain interactive conditions as described previously (Sect. 2.5). Fire is thus likely to have contributed significantly to its present patterns of distribution within the Alligator Rivers region.

Patches range in size from 0.1 ha on isolated topographic refugia through to extensive, more-or-less continuous tracts hundreds of hectares in extent. These latter forests are restricted to very dissected broken country at the edge of the escarpment. Canopy height ranges from 35 m in perennially wet sites as described earlier, through 25 m on certain protected scree, to less than 10 m on bare pavements. Over this range growth form changes from a forest tree through to a short-trunked woodland form.

Through this range, understoreys vary from being relatively open and sparse at either end of the moisture continuum, to dense tangles of tall shrubs and scramblers in many intermediate situations. Vines, especially geophytic species, may be common, but ferns, except for *Drynaria quercifolia*, and other life forms, are not so.

### 3.2.4 Seasonal Coastal Habitats

Vine-forest vegetation is distributed discontinuously along all mainland and island coastlines, on a variety of landform types. Seasonal coastal habitats include calcareous and siliceous dunes, actively slumping coastal cliffs, and a variety of lateritic landform types immediately adjacent to modern coastlines and Holocene sedimentary facies. While edaphic conditions are likely to be highly variable with respect to both seasonal water balance and nutrient status, in common all these situations have been affected to some greater or lesser extent by recent sea level and attendant climatic influences. Furthermore, on the basis of a limited number of observations (17) extending over a wide region, from Port Keats (250 km south of Darwin) through to the Cobourg Peninsula (200 km to the east), there is some
suggestion that this vegetation is relatively homogeneous floristically. This is not
to say however, that there is no biogeographical differentiation between regions,
not that individual species display little preference for habitat conditions; in both
cases, such conditions apply. In the first instance, for example, a number of taxa
are recorded only from coastal habitats in the Cobourg Peninsula region (e.g.
*Berrya cordifolia*, *Harpullia leichhardtii*, *Paramignya trimera*, *Pisonia grandis*,
*Salacia chinensis*). And in the second instance, many species do indeed exhibit
habitat preferences, as exemplified by those species which occupy littoral fringes
(e.g. *Caesalpinia bonduc*, *Dodonaea platyptera*, *Guettarda speciosa*, *Ipomoea spp.*, *Peltophorum pterocarpum*, *Pongamia pinnata*), and those species which evidently
prefer habitats of favourable soil water balance (e.g. *Buchanania arborescens*,
*Cryptocarya cunninghamii*, *Dyssoxylum oppositifolium*, *Ficus virens*, *Hibiscus
tiliaceus*, *Maranthes corymbosa*, and many others). In the main however, this
coastal habitat flora is composed largely of widespread and/or ecologically
tolerant species. That many of these species also have the capacity to disperse
with effect at least locally, is indicated by the observation that 182 of the 199
(91%) flowering plant species recorded in these coastal situations have been found
to occur on landforms of demonstrable Holocene origin (Appendix ). Thus, in any
one local region, scattered populations of many species are unlikely to be
genetically isolated.

Patch sizes range from scattered clumps on coastal dunes through to extremely
large and continuous tracts over 1000 ha in extent. At Cape Van Diemen, Melville
Island, one patch, occurring over a variety of sandy and lateritic substrates,
extends continuously behind the beach for 16 km, often up to 1 km inland. Such
large patches are rare however, most being only a few hectares, or less, in extent.

A number of structural types occur. Evergreen Notophyll Vine Forest (ENVF) with
or without palms (*Carpentaria acuminata*, *Livistona benthamii*), occurs in a
number of restricted situations both on calcareous dunes, and lateritic "islands"
within mangrove vegetation, where soil water is evidently available year round
(Plate 11). Structurally and floristically, this vine-forest vegetation resembles
closely the vegetation of lowland springs, from which it is ostensibly derived.

On coastal siliceous and calcareous sediments, vine-forest vegetation grades from
Semi-Deciduous Notophyll Vine Forest (SDNVF) through to Deciduous Vine Thicket
(DVT), essentially along a gradient of declining seasonal moisture availability. On
deep chenier ridges, beach dunes, and wind blown siliceous sands, SDNVF occurs
Plate 11: A small patch of Evergreen Notophyll Vine Forest surrounded by mangrove vegetation, Bathurst Island.

Plate 12: Semi-Deciduous Notophyll Vine Forest occurring on deep sandy loam laterised colluvia adjacent to the East Alligator River floodplain. The sharpness of the boundary is intriguing since the terrain is essentially level, there is little surrounding flammable fuel, and the soil profiles under the forest and in the foreground are very similar. While the local area was a favoured camping site for Aboriginal people within living memory and may have been partially cleared, other boundaries of this same patch are expanding actively at the present time. The status of this boundary thus poses an enigma.
with deciduous emergents to 22m over canopies as much as 16m in height. Canopy tree species are mostly deciduous (e.g. Antiaris toxicaria, Bombax ceiba, Canarium australianum, Grewia breviflora, Pongamia pinnata, Popowia australis, Sterculia quadrifida, Terminalia sericeocarpa, Zanthoxylum parviflorum), although tall evergreen species are often present (e.g. Maranthes corymbosa, Tamarindus indica, Mimusops elengii). On shallow facies, even within the same general patch, canopy height may drop to as low as 5 m, the small trees and scrubs smothered with vines (e.g. Cansjera leptostachya, Grewia sp. 06477, Malaisia scandens, Pachygone ovata, Pisonia aculeata, Secamone elliptica).

On lateritic landforms, SDNVF occurs typically on flat to gently sloping terrain behind coastal cliffs, or where lowland plains abut prograding coastline facies. In the former case, red to brown-red loam surface horizons, over massive or concretionary laterite, are often shallow or skeletal. In the latter case, loamy to sandy loam colluvial soils are frequently deep (02 m). In situations where the rooting zone is deep, or where substrate moisture is more readily available (see Aldrick 1976:79-81; Specht et al. 1977), canopy species may be as tall as 26m, the canopy dominated equally by evergreen tree species (e.g. Acacia auriculiformis, Alstonia pseudophylla, Buchanania arborescens, Carallia brachiata, Canophyllum falcatum, Maranthes corymbosa) and deciduous species (e.g. Canarium australianum, Ficus virens, and others cited previously). The palm Carpentaria acuminata may be common. Understoreys are frequently open, containing a variety of small tree, shrub and vine species. Ferns are absent.

With less favourable substrate water balance conditions, canopy height declines, deciduous elements feature more prominently (often as emergents), and understoreys become increasingly a tangle of shrubs and vines. On relatively harsh sites, such as on skeletal massive laterite, or on slumping coastal cliffs, vine-forest vegetation is expressed characteristically as Deciduous Vine Thicket (DVT). Canopy height may be as low as 2-3m with few emergents. Such thickets are often impenetrable, the canopy a blanket of vines.

That mature canopy height in these lateritic situations is essentially an expression of water balance conditions is illustrated by a patch of vine-forest vegetation occurring on a rocky (lateritic) moderate slope (ca. 6°), at Black Point, Cobourg Peninsula. At the bottom of the slope, a perennial pond is impounded by coastal dunes, the adjacent SDNVF vegetation comprising emergents to 20m in height over a general canopy to 16 m. Away from these relatively favourable water
balance conditions (i.e. effectively upslope), canopy height declines to as little as 4m; the vegetation here being of a DVT type. DVT structure is attributable also to wind-shearing in some exposed situations, as described by Story (1982).

Given the absence of thick grass understoreys adjacent to many of these coastal habitats, especially on coarse-grained sediments, fires, except where set deliberately, are unlikely to be of major significance. Exceptions to this however, concern patches associated with relatively shallow lateritic loams, where thick grass understoreys (e.g. Heteropogon spp., Sorghum spp.) provide readily combustible fuels. The impact of buffalo (and banteng cattle on the Cobourg Peninsula) is also reduced given the absence of available surface water, and other conditions suitable for wallowing. In some areas however, coastal vine-forest vegetation affords a favoured resting habitat, especially where adjacent to floodplains (Braithwaite et al., in press[a]). Cyclonic, or other high energy disturbance, is a recurrent, if occasional, influence (see Stocker 1976).

3.2.5 Seasonal Subcoastal Habitats

This broad category essentially comprises two main habitat types: the levee margins of both freshwater and tidally influenced watercourses; and lateritic landforms associated with the margins of subcoastal riverine floodplains. Vine-forest vegetation associated with rock outcrops is considered in the next Section.

Vine-forest vegetation associated with subcoastal lateritic landforms occurs typically as SDNVF, and is both structurally and floristically very similar to that described previously for more coastal situations (Plate 12). Landform relief is very subdued and lateritic profiles range from those with shallow loams over massive laterite, through to deep sandy loam colluvia with or without the inclusion of lateritic pisoliths. In many low-lying situations such profiles may be overlain by a veneer of fine-grained organic floodplain sediments. The expression of vine-forest vegetation is thus variable, but reflecting largely, the influence of substrate water balance conditions, as with coastal situations. DVT vegetation however, is uncommon.

Patches range in size from less than 1 ha through to large tracts several kilometres long and some hundreds of metres wide. These larger patches are characteristic of lower tidal reaches where they are commonly contiguous with coastal vine-forest vegetation. Buffalo impact however, is more severe in patches adjacent to freshwater floodplains, as opposed to estuarine situations. The impact of fires is essentially that as discussed for coastal lateritic landforms.
Plate 13: Semi-Deciduous Notophyll Vine Forest occurring along drainage channels of the East Alligator River floodplain (Photo: Ian Morris).

Plate 14: Deciduous Vine Thicket on granitic rock flow surrounded by eucalypts over dense grasses, Goodparla Station.
Before leaving subcoastal lateritic landforms, a second situation, whilst rare, warrants mention. This concerns the very restricted occurrence of patches on deep sandy loams in subcoastal lowland regions which are not immediately adjacent to riverine floodplains. We are aware of two such occurrences on the mainland. Both comprise SDNVF vegetation composed of widespread species under tall (to 20 m) eucalypt (E. miniata, E. tetrodonta) and ironwood (Erythrophleum chlorostachys) overstores; the individual patches constituting scattered clumps which total less than 0.5 ha in extent. Inside these clumps eucalypt regeneration is absent. There are no scrub fowl mounds. The history of these patches is thus enigmatic. Whereas in certain other situations similar SDNVF vegetation is evidently regenerating, or establishing de novo, in areas where land has been cleared for grazing or other purposes, on some of the larger coastal islands similar relatively isolated patches, without sclerophyll emergents, are known to occur (e.g. Langcamp et al. 1981). Without other evidence, it is impossible to say at the present time whether such occurrences represent remnants of SDNVF vegetation more widespread in late Quaternary time (cf. Stocker and Mott 1981); remnants of vegetation which expanded early in the Holocene and which has since contracted through the impacts of burning and other agencies (see Section 2); or de novo establishment within the recent past. Given examples presented in Section 2 however, it is highly probable that each of these scenarios may apply in different individual situations.

SDNVF vegetation occurs also as gallery forest on levee banks of tidal rivers and on other elevated floodplain landforms (e.g. levees of former river channels) (Plate 13). In lower tidal reaches such vegetation frequently intergrades with mangrove species on fine or coarse grained sediments; vine-forest species (e.g. Bombax ceiba, Celtis philippensis, Cordia dichotoma, Diospyros ferrera var. reticulata) generally being restricted to situations above the range of dry season spring tides.

In upper reaches, where the dry season influence of saline tidal waters is much diminished, extensive gallery forests, to 25m in height, may occur. Species composition resembles that occurring on relatively moist substrates in other coastal and subcoastal situations (e.g. Hibiscus tiliaceus, Livistona benthamii, Nauclea orientalis, Terminalia sericeocarpa); although sclerophyll emergents (and recruitment in open situations) such as Lophostemon lactiflues, Melaleuca argentea and M. leucadendron are commonly conspicuous. As well, a number of species more characteristic of freshwater riparian situations are frequently
present (e.g. Bambusa arnhemica, Ficus racemosa). Such levees, whilst underlain by fine-grained Holocene estuarine sediments, are commonly capped by more sandy facies; conditions favouring dry season gas exchange of roots at the soil surface. In the wet season however, these levees are covered by floodwaters up to 3m in depth and often for periods up to 2 months.

Beyond the limits of dry season tidal waters, gallery forest vegetation threads its way discontinuously along narrow corridors of both perennial and seasonal watercourses, well inland. Vegetation structure and floristic composition is locally highly variable, reflecting different interacting geomorphological situations and seasonal conditions. In sandy situations where water is readily available throughout the dry season, for example, canopy height may be as much as 25m; the vegetation often dominated by sclerophylls (e.g. Melaleuca spp.) over mixtures of typical vine-forest species (e.g. Bambusa arnhemica, Carallia brachiata, Ficus racemosa, Maranthes corymbosa, Myristica insipida, Nauclea orientalis, Syzygium armstrongii). Along smaller creeks with fine textured alluvia, where moisture availability through the dry season is more restricted, vine-forest vegetation may be represented by only scattered low clumps or individuals, and species which are evidently tolerant of such conditions (e.g. Bambusa arnhemica, Ficus scobina, Litsea glutinosa, Strychos lucida). However, all these situations are open to episodic disturbance through flooding and burning. The impacts of buffalo and cattle are likely to be considerable in many situations.

Little is known of the actual extent and composition of vine-forest vegetation associated with lowland riparian habitats. On the basis of a limited number of observations however, gallery forest vegetation appears to occur discontinuously, in association with all major river and creek systems. Taken as a whole therefore, the extent of this vegetation, as well as its significance as a major gene pool for many species, is considerable. In a regional vine-forest vegetation furthermore, which is characterised by its fragmentation, the discontinuous distribution of populations along these reticulated corridors probably provides a significant opportunity for genetic interconnections.
3.2.6 Rock Outcrops

Rock outcrop habitats comprise small outcropping landforms, from hills through to boulders, composed of a variety of igneous, sedimentary and metamorphic rock types, as well as lateritic landforms. While opportunities for root exploration at depth may occur along cracks and fissures, soils where present are typically skeletal. With the probable exception of lateritic substrates, the status of nutrient availability is likely to be relatively favourable given both the inherent nutrient status of certain parent materials (e.g. limestone, dolerite), as well as the continuous availability of nutrients through rock weathering (e.g. Eiten 1982; Tinley 1982; Webb 1968).

In coastal and adjacent subcoastal regions, vine-forest vegetation associated with low rock outcrops occurs typically as SDNVF, with deciduous and occasional evergreen emergents to 16 m, over a general canopy up to 12 m in height. Away from these relatively high rainfall regions, or in coastal/subcoastal situations where substrate moisture availability is seasonally scarce (i.e. excessively drained, topographically high situations), canopy height declines, and structure is expressed characteristically as a DVT type. Within the one climatic region however, the influence of different parent materials on the expression of vine-forest vegetation may be marked. In the Pine Creek region (150 km SE of Darwin), for example, scattered patches of DVT vegetation occur mainly on doleritic and granitic outcrops (Plate 14). DVT vegetation associated with fine-textured doleritic parent materials tends to be more dense, and floristically distinct from that occurring on granitic substrates. While this may be attributable, in part, to the higher nutrient status of dolerite parent materials, measurement of pre-dawn xylem pressure potential (see Ritchie and Hinckley 1975), comparing a number of vine-forest taxa shared between dolerite and granite outcrops, indicates that the dolerite also provides for a more favourable substrate with respect to seasonal water balance conditions (Russell-Smith unpub. data). Using the same technique, it is observed that, relative to seasonal water balance conditions pertaining at the bases of these respective outcrops (supporting eucalypt savanna vegetation), substrate moisture availability on the outcrops themselves (supporting vine-forest vegetation) is seasonally unfavourable. In the absence of limiting nutrient or moisture conditions therefore, the containment of DVT vegetation in rock outcrop habitats is probably due to of the influence of fire (e.g. Webb and Tracey 1981a). As well, such occurrences demonstrate also the capacity of many, vine-forest species to colonise and occupy bare rocky substrates (e.g. see Beard 1976; Eiten 1982; Story 1976; Tinley 1982).
While the flora associated with rock outcrops, especially in inland regions, is poorly known, such information as is available indicates that it essentially comprises species otherwise found to occur in other seasonal habitat types, especially coastal and subcoastal situations (see Table 5). That many of these species, given the availability of dispersal vectors (e.g. frugivorous birds), are potentially vagile is indicated by the occurrence of 117 species from a total of 125 species recorded from rock outcrops, on coastal Holocene landforms (Appendix). This flora is therefore composed largely of nomadic species with wide ecological amplitudes. In inland regions however, where individual populations may be widely separated, the potential for genetic exchange may be rare to nonexistent. As Kikkawa et al. (1981) and Webb and Tracey (1979, 1981a) suggest, many of these populations and assemblages of populations may therefore be relictual. Some opportunity for genetic exchange may exist however, where patches are in close proximity to vine-forest vegetation occurring along watercourses.

Patches range in size from highly fragmented tracts over 100 ha in extent in rare coastal/subcoastal situations, typically through isolated patches less than 1 ha to 2 ha in extent, to a scatter of individuals associated with outcropping boulders. While the impact of fire on extant patch boundaries appears to be a recurrent factor in all but the most topographically protected situations, buffalo impact is limited to occasional low outcrop habitats in coastal and subcoastal floodplain situations.

3.3 Native Fauna

Descriptions of vertebrate faunas at the narrow regional level are provided in CSIRO (1973), Frith and Calaby (1974) and Specht (1964). As well, a further faunal ecological study, in the western Arnhem Land region, is nearing completion (R. Braithwaite pers. comm.). These studies reveal that, with the exception of a number of bird species (Table 3), the vertebrate fauna obligately dependent on monsoon vine-forest habitats is singularly depauperate (see also Kikkawa et al. 1981). Of the mammals, only three species are regular users of vine-forest habitats: Melomys burtoni, Pseudocheirus dahlia, and Zyzomys woodwardi, (R. Braithwaite pers. comm). In their study of the diet of Zyzomys woodwardi, Begg and Dunlop (in press) discuss the dependence of this species on fruits of monsoon vine-forest species, especially in the late dry/early wet season. Only one other vertebrate, a microhylid frog, Sphenophryne robusta, is considered to be a regular
user of monsoon vine-forest habitats (Braithwaite *et al.* in press [b]; Cogger and Lindner 1974); although a second, undescribed species of *Sphenophryne* is known from a lowland spring monsoon vine-forest habitat on Croker Island (I. Morris pers. comm.).

The invertebrate fauna is poorly known, and only one survey, in the western Arnhem Land region, has been undertaken (Kikkawa and Monteith 1980). This survey comprised the seasonal collection of 4,500 arachnids and 5,500 insects in a number of escarpment and lowland monsoon vine-forest habitats. These authors note that in contrast to tropical closed vine-forest habitats developed under optimal conditions, animals in these monsoon vine-forest habitats are characterised by a tendency of normally non-social insects to aggregate (e.g. Diptera, Lepidoptera and Hemiptera); and that monsoon vine-forest habitats are used as ecological refugia during the dry season. A further intriguing aspect of their study was the observation that lowland and escarpment vine-forest habitats share obligate species, but differ in those species which are more widely distributed through other lowland and escarpment habitats, respectively. Given that a number of their lowland sampling sites are clearly Holocene in origin, this suggests that many obligate invertebrate species may be similarly vagile as with other floristic and vertebrate components. While it is not possible at the present time to pursue this matter further, it is pertinent to note that in their discussion of the biogeographical relationship of the amphibians and terrestrial reptiles of the Cobourg Peninsula, Cogger and Lindner (1974:104) state that:

"What we wish to imply is simply that the reptiles and frogs of Arnhem Land, north-western Australia, southern Papua and north-eastern Australia have many common elements which not only indicate recent faunal exchanges between each of these areas but, because of the present habitat differences between each area, also indicate a high degree of ecological vagility among the component species. These observations do not deny the presence of older endemic elements in each of these areas, nor some degree of differentiation within these areas since they were last isolated from one another".

Clearly, the long-term status of faunal components associated with these monsoon vine-forest habitats requires further examination.
4. CONSERVATION STATUS

Land tenure in the Northern Territory's Top End (Figure 4) falls into three main categories: leasehold (mainly grazing leases), Aboriginal land and National Parks and reserves. The amount of land held under freehold title is quite minor and will not be considered here. Before discussing the relationship between land tenure and the conservation of monsoon vine-forests, Figure 4 requires some explanation. Firstly, the point must be made that land tenure is changing rapidly at the present time. Much of the land mapped as leasehold is under Aboriginal land claim and so in future may be Aboriginal land. There is also an Aboriginal land claim on the Katherine Gorge National Park and on some small conservation reserves held by the Conservation Commission of the Northern Territory. Kakadu National Park is also expanding and will in the near future encompass the two leasehold blocks on its southern boundary and thus will virtually abut the borders of Katherine Gorge National Park.

Secondly, Kakadu National Park and Cobourg National Park have, for convenience been mapped simply as National Parks. They are in fact under Aboriginal ownership; Kakadu has been leased by Australian National Parks and Wildlife Service and Cobourg is jointly managed by the traditional Aboriginal owners and the Conservation Commission of the Northern Territory.

From Figure 4 it is clear that the largest tracts of land are either leasehold or under Aboriginal ownership. Aboriginal land for the most part is not intensively developed for agriculture or pastoral pursuits and so must be regarded as affording a reasonable level of protection for the monsoon vine-forests.

On the basis of the six habitat types, the best conserved are the Dry Sandstone and Sandstone Spring forests. These are well represented in Arnhem Land, Kakadu National Park and Melville Island. There are also good, well-protected representatives of this type under private ownership on the Mt. Tolmer escarpment south-west of Darwin. The coastal, sub-coastal and lowland spring habitats are reasonably well represented in reserves though a couple of outstanding examples of Lowland Spring forest in the Darwin-Daly region are in urgent need of effective conservation management. On the other hand, very few of the Rock Outcrop habitats and the hinterland Acacia shirleyi-type thickets enjoy legal protection, though many of these situations are to a large degree protected topographically.
Figure 4: Land Tenure of the Top End
For future acquisition of monsoon vine-forest for conservation purposes, attention is drawn to the necessity for appreciating that patches and populations do not necessarily exist in isolation. The long term viability of these patches may well be dependant on conserving the diffuse genetic connections between them (e.g. riparian habitats). For rational assessment of future conservation requirements, an ecological survey of inland vine-forests is urgently needed.

While much vine-forest habitat is already, or likely to be protected by forms of land tenure which are conducive for conservation, the small size of most patches means that they are vulnerable to certain types of continued disturbance. For the most part, vine-forests in the Northern Territory have been little affected by the direct impact of settlement. In contrast to eastern Australia, such clearance of patches, and logging, which has occurred, has been both highly localised and relatively insignificant. It is improbable that such activities have affected the status of any taxon, plant or animal. The most serious threat to the integrity of patches concerns their utilisation as favoured resting habitats by feral and domestic ungulates (Plate 15), especially the introduced water buffalo, \textit{(Bubalus bubalis)}, and through the rooting up of regeneration by pigs. With respect to ungulates, such utilisation leads to the creation of both woody fuels (through habitat destruction) and fine fuels (through promoting the spread of native and exotic weedy species). Such a situation, in combination with the widespread practice of frequent late dry season burning, can lead to rapid retreat of patch boundaries. Braithwaite \textit{et al.} (in press [a]) also discuss the affect of buffalos on moisture characteristics of surface soils through impaction.

While uncontrolled feral and domestic ungulate numbers are likely to be greatly reduced under Government policy aimed at eradicating \textit{brucellosis and tuberculosis} by 1992 (Calley 1982), it is questionable whether this will significantly release pressure from monsoon vine-forests in many situations. Such pessimism is based both on the geographical scale of the problem as well as on the observations that: in the event of shooting or catching activities, buffalo often seek refuge in vine-forest habitats; and even small numbers of animals can occasion severe damage, especially in fragile spring habitats. Thus, despite the relative degree of legislated protection which monsoon vine-forests in the Northern Territory enjoy, many threatened and significant
Plate 15: 'Buffalo camp' in the middle of vine-forest, western Arnhem Land. The lack of regeneration and promotion of fire is evident.
patches are presently, and for the foreseeable future, beyond the means of effective conservation.

Outside urban areas, exotic weeds are not a serious problem at the present time. While *Hyptis suaveolens* and *Passiflora foetida* are now so widespread as to be considered naturalised, only one species, *Lantana camara*, currently restricted to the Darwin region, presents a potential threat given its highly aggressive habit. More ominous, especially to vine-forest invertebrates, is the recent arrival of the cane toad (*Bufo marinus*) at the Queensland-Northern Territory border.

5. CONCLUSION

In this paper we have presented a regional perspective of the status of monsoon vine-forests in the Northern Territory. By way of conclusion we would summarise the main points arising from preceding discussion as follows:

1. The extant vine-forest vegetation may be considered to comprise essentially two floristic elements. On the one hand, the occurrence of a great majority of the known taxa on Holocene landforms indicates many species possess the capacity to respond to environmental change. On the other hand, a lesser number of taxa are restricted in their distributions to often widely disjunct refugia. On the basis of such disjunctions in the latter element, it is evident that vine-forest vegetation has been more widespread across northern Australia than it is now.

2. The patchy distribution of vine-forest vegetation, and the fragmentation of its constituent flora, is likely to have been derived Holocenotically, i.e., reflecting the interaction and concurrence of a variety of factors and processes through time. In earlier discussion we have identified the following minimum set of historical factors and processes as being contributive: long-term climatic deterioration and more recent oscillation; landscape fragmentation through deep weathering; episodic coastal/subcoastal landform evolution primarily in response to global sea-level changes; fire,
including Aboriginal burning (and occupation) in localised situations; and competition from other sclerophyll and graminoid floristic elements. To these may be added the adaptive responses of vine-forest taxa themselves (e.g. the high vagility of many species) in meeting such challenges.

3. Extant patches are confined to the northern sector of the Northern Territory which receives an annually reliable, but highly seasonal rainfall greater than 500 mm approximately. Annual temperatures throughout this region are consistently high, with the mean everywhere exceeding 26°C. Patches are most concentrated in high rainfall regions, becoming increasingly scattered and attenuated, both structurally and floristically, along gradients of declining rainfall.

4. Patch sizes are typically small (mostly less than a few hectares), ranging from a scatter of individuals or clumps on rocky scree or along watercourses, through to tracts over 1,000 ha in occasional coastal situations.

5. Patch boundaries are mostly sharply defined, reflecting principally, but not exclusively, the influence of fire.

6. For convenience, we have described vine-forest vegetation with reference to six habitat types. These are: lowland springs, sandstone springs, seasonally dry sandstone habitats, seasonally dry coastal habitats, seasonally dry subcoastal habitats, and rock outcrops. Given the lack of information available for inland regions, especially vine-forest vegetation associated with closed scrubs dominated by Acacia spp., these were not considered in any detail.

7. Structural types range from Complex Notophyll Vine Forest associated with rare perennial spring habitats, through Evergreen Notophyll Vine Forest associated with sandstone terrain, to Semi-Deciduous Notophyll Vine Forest and Deciduous Vine Thicket types associated with seasonally dry habitats.

8. The vine-forest flora, comprising largely woody species, is impoverished relative to homologous vegetation in north-eastern Australia. The flora comprises somewhere in the vicinity of 400 species. There are few endemics.

9. Many vine-forest plant taxa exhibit broad ecological tolerances, occurring through a range of different habitat types. Taxa exhibiting relatively narrow ecological tolerances are associated...
mostly with perennally wet habitats. As well, seasonally dry coastal and sandstone landforms support relatively large numbers of taxa which are exclusive to each of these habitat types.

10. As evidenced by the wide occurrence of plant taxa on Holocene landforms, and demographic data from small spring habitats, the flora as a whole is characterised by high vagility. From propagule/dispersal-type data presented in Table 2 it is evident that a majority of plants rely principally upon animals, especially birds, for dispersal beyond the parent canopy. By habitat type, this reliance ranges from 62% of plant taxa with propagules adapted for animal transport in sandstone springs, to 74% on rock outcrops.

11. The vine-forest fauna is depauperate relative to homologous habitats in Cape York. While only three vertebrate species, all of them birds, are obligately dependant on vine-forest habitats, many vertebrate species use vine-forests as refugia during the dry season.

12. Much vine-forest is already, or likely to be afforded protection by types of land tenure which are conducive for conservation. Significant exceptions to this, however, concern: scattered vine thickets on rock outcrops, especially in inland regions; hinterland closed scrubs dominated by Acacia spp.; discontinuous and elongate patches associated with riparian habitats; and certain lowland spring habitats of high biogeographical significance in the Darwin-Baly region. As noted previously, the genetic significance of riparian vine-forests warrants special consideration.

13. For rational assessment of future conservation requirements, an ecological survey of inland vine-forests is urgently required.

14. Despite relatively insignificant direct impact of European settlement, and despite the relative degree of legislated protection afforded much vine-forest in the Northern Territory, feral animals, especially water buffalo and pigs, are affecting seriously the integrity of many patches at the present time. This is especially true for vulnerable but ecologically very significant lowland and sandstone spring habitats. In the absence of realistic (economically prohibitive?) measures being taken to exclude feral animals from such habitats, many significant patches will remain beyond the means of effective conservation.
That the scattered vine-forest patches of the Northern Territory are deserving of the highest conservation priority is indicated in two studies commissioned by the Australian National Parks and Wildlife Service, and undertaken by Webb and Tracey (1979) and Kikkawa and Monteith (1980), concerning vine-forest vegetation and fauna, respectively. Both studies conclude that the biogeographical significance of these ecosystems is of international stature.
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Deep weathering and erosion surfaces in the Daly River basin,
APPENDIX

Checklist of monsoon vine-forest species recorded in the Top End of the Northern Territory. Descriptions of habitat types may be found in the text.

Unnamed taxa are followed by a herbarium number (DNA) or a collector's initial and collecting number which refer to a specimen in the Darwin Herbarium of the Conservation Commission of the Northern Territory. Collectors are as follows:-


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<th>Spring</th>
<th>Sandstone</th>
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- *Cayratia trifolia*
- *Cayratia sp. W248*
- *Cissus adnata*
- *Cissus repens*
- *Cissus sp. J1534*

### ZINGIBERACEAE
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### SUMMARY

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THE STATUS AND CONDITION OF
MONSOON VINE-FORESTS IN THE KAKADU REGION:
A MANAGEMENT REPORT

Jeremy Russell-Smith
September, 1984

Unpublished report to the Australian National Parks
and Wildlife Service, Canberra.
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* Only references not given in the first part of this Report are listed here.
Appendices

2. Higher plant species occurring at survey sites in the Kakadu region.

3. Occurrences of rare vine-forest taxa in the Kakadu region.

4. Aboriginal plant names and uses in Kakadu National Park: Listings in Mayiali/Kun jeyhmi and Gunwinngu languages.

5. Plants used traditionally as foods and in material culture in the Kakadu region.

There are 11 Figures, 5 Tables, and 30 Plates.
1.0 INTRODUCTION

The Report presented here forms the second part of the Final Report of the Consultancy Project entitled "The Biogeography, Ecology and Ethnobotany of the Monsoon Vine-Forests of Kakadu National Park". Whereas Part 1 provided a regional perspective of the status and ecology of monsoon vine-forests in the Northern Territory, the present Report focuses exclusively on Kakadu National Park. As well, the present Report addresses much more closely issues of relevance to Management. Since much of the material covered in Part 1 is not repeated here, it is suggested that the reader consult Part 1 before proceeding with the present document. An amended version of Part 1 is submitted with this Report.

As outlined in the "Consultancy Agreement", the Consultant is required to provide:

(a) a detailed description of the ecology of monsoon vine-forests and the identification of vegetation types or individual patches of special conservation significance;

(b) an historical perspective of the use of fire by Aboriginal people as seen through its impact on monsoon vine-forests;

(c) a preliminary analysis of the impact of fire regimes on monsoon vine-forest boundaries;

(d) an assessment of the impact of feral animal damage to monsoon vine-forests;

(e) an assessment of the status of the scrub fowl (Megapodes freycinet) in the region; and

(f) documented reports.

In fulfilling these requirements this Report is arranged as follows. In Section 2 the monsoon vine-forests of Kakadu National Park are described and attention is given both to the condition, and biogeographical significance, of different vegetation types and individual patches. In discussion, the status of scrub fowl in the region is also considered. In Section 3 the role of fire as an ecological factor is assessed in relation to other determinants (e.g. soil conditions), and the current influence of fire on monsoon vine-forest boundaries is discussed. In Section 4 ethnobotanical aspects are considered and in Section 5, the recommendations which flow from preceding discussion are outlined.
A final note is required concerning the regional scale of the present Report. "Kakadu National Park" as used here refers to that region which covers broadly Stages 1 and 2, as well as Goodparla and Gimbat pastoral leases. In describing the monsoon vine-forests of Kakadu, a number of Survey Sites adjoining Kakadu have been considered also.
2.0 DESCRIPTION OF THE MONSOON VINE-FORESTS OF KAKADU NATIONAL PARK

In Part 1 of this Report the vine-forest vegetation of the Northern Territory is described with reference to six major habitat types. These are: perennial springs associated with sandstone terrain, springs of the lateritic lowlands, seasonally dry sandstone, coastal and subcoastal habitats, and rock outcrops. Each of these habitat types is represented in Kakadu.

For the purposes of the present report, however, escarpment and lowland vine-forests are considered separately, and the condition of vine-forests in the region is assessed with reference to nine habitat types.

2.1 Data Base

The description which follows is based on survey data collected from 127 sample sites in the Kakadu region. A further 76 sites were sampled in other regions, principally to the north and east, but are not considered here. For a description of vine-forest vegetation in the Top End generally, which is based on the total data set, the reader is referred to Part 1 of this report (Section 3.2).

As a guiding principle for this survey, the prime consideration was to sample as many vine-forest patches in as many ecological situations and areas as constraints of time and accessibility would permit. While maps and aerial photographic records were consulted in site selection as a matter of course, practical considerations concerning accessibility were largely determinant. In this latter respect, I was greatly assisted by many people who gave of their time and local knowledge in either directing me, or taking me to areas with which they were familiar. To gain access to certain outstanding patches in deeply dissected escarpment terrain, limited use was made of a helicopter. Of the 127 sites sampled, 89 were associated with sandstone terrain. Such a concentrated sampling effort reflects both the proportional representation of vine-forest vegetation associated with sandstone landforms vis-a-vis other landform types in the region and, as well, the greater diversity of such vegetation.
Sampling of individual sites was conducted with reference to a standard proforma comprising essentially two parts. In the first part the environmental characteristics of each site were recorded. Such characteristics included the physiographic setting, geology, soils, evidence for fire, and feral animal impact. In the second part the characteristics of the vegetation were recorded. Such characteristics included structural parameters, physiognomy, and a complete species list. Population sizes of individual species were estimated using a 5 point Abundance Scale. The essential feature of this Scale (see Appendix 2) is that it employs categories designed to record very small population sizes, with 4 categories covering the range from 1 up to 50 individuals. As indicated in both parts of this report, a characteristic feature of many vine-forest patches is the very small population sizes of many, if not most, component species.

With experience, sampling of a patch 1-2 ha in extent could be completed within 3 hours. For larger patches a whole day might be required and even then only a representative section might be sampled effectively. Sampling was undertaken without resort to defined plots of fixed dimension. Rather, the whole patch was sampled as a single entity. However, where a patch might comprise more than one ecologically distinguishable facet (e.g. in gorges where vegetation associated with watercourses is clearly floristically and structurally distinct from that occurring away from the stream), these were sampled separately. Similarly, care was taken to distinguish between edge communities (ecotones) and the internal patch vegetation.

2.2 Data Presentation

The geographic location of the 127 sample sites is given in Appendix 1. In Appendix 2 is provided a list of species encountered in the survey. Species are listed in generic alphabetical order. Site occurrence data for each species, including a measure of each population's abundance, is also provided in this Appendix.

Given the large quantity of data which is collected in surveys of this type, it has been necessary to be highly selective as regards the information presented for discussion. Data summarising the key attributes of each site are presented in Table 2. The construction of this Table is rather complex and requires detailed comment.

1. Firstly, the ordering of sites has been undertaken by habitat type. It is to be noted that not all the habitat types employed here are equivalent to those in Part 1.
As well, the Table is presented in two parts. Sites associated with sandstone terrain, and those in lowland types, are listed in Tables 2(a) and 2(b) respectively.

2. Patch sizes as given refer to the size of the area actually sampled. Where the extent of the patch is greater than the area sampled this is denoted by a 'greater than' (>) sign. For some situations, especially the extensive tracts of evergreen vine-forest in rugged and dissected escarpment terrain, only a very small proportion of the whole patch was sampled.

3. The number of species occurring at each site is to be taken as a minimum number. While many sites were sampled at least twice, once in the dry season and again in the wet, many occurrences will have remained unrecorded. This relates especially to plants with seasonal growth habits (e.g. geophytes). A second contributing factor concerns the highly occasional occurrence of many taxa in Top End vine-forests. As indicated in this Table the population sizes of many species at any one site are often very small. Finally, it is to be noted that the number of species recorded includes taxa which are not strictly components of vine-forests as defined in Part 1 (Section 3.1, and Appendix). Such species include sclerophyll types (e.g. eucalypts and grasses) where these were encountered in sampling. Their inclusion in this Table (and Appendix 2) is warranted, however, in that they provide insights into the condition and dynamic status of patches.

4. Estimates of the reproductive population sizes of species occurring at each site are provided in two columns. These columns relate to the proportion of species of the total number recorded which have populations less than 50 mature individuals, and 7 individuals, respectively. These are derived from data presented in Appendix 2.

5. Aspects of the long-term stability and present condition of individual sites are considered in 6 columns. The aspects considered comprise: the geomorphic stability of the habitat in time; the current influence of fire; the impacts of buffalos and pigs; and the occurrence of exotic weeds. This information is presented in the form of numerically scaled indices. The respective indices are described in Table 1.

6. The observed occurrence of scrub fowls at each site is given in column 12 employing a similarly scaled index. It is to be noted that no specific study of scrub fowl populations was undertaken. Rather, the information given here is
TABLE 1:
Key for Scaled Indices used in Tables 2(a) and 2(b)

Column 6: Geomorphic Habitat Stability (1-5 Scale)
1. habitat virtually never prone to widespread geomorphic disturbance within the Quaternary - highly stable habitats.
2. habitat substrate largely older than 10^4 years (i.e., largely pre-Holocene), but markedly affected by Holocene geomorphic conditions (e.g., lateritic landforms at the edge of Holocene floodplains).
3. habitat substrate of Holocene origin.
4. habitat severely disturbed by episodic flooding or cyclonic events on a time scale of around once every 10^4 to 10^2 years.
5. habitat severely disturbed by episodic flooding etc. on a time scale of around once every 10^0 to 10^1 years.

Column 7: Fire Severity (0-4 Scale)
0. absent.
1. localised fire due to lightning strike.
2. limited impact on exposed patch boundaries only.
3. severe impact on exposed patch boundaries with little affect on internal vegetation.
4. severe impact on patch boundaries and internal vegetation.

Column 8: Fire Frequency (0-3 Scale)
0. absent/virtually never.
1. evidence for occasional fires but apparently not within the past 10 years.
2. within the past 2-3 years; evidently frequent.

Columns 9 and 10: Buffalo Impact and Pig Impact (0-3 Scale)
0. absent.
1. widespread/localised but not significant.
2. localised and severe.
3. widespread and severe.

Column 11: Exotic Weed Species (0-3 Scale)
0. absent.
1. uncommon or rare, widespread/localised.
2. abundant, localised.
3. abundant, widespread.

Column 12: Scrub Fowl Occurrence (0-5 Scale)
0. no evidence of occurrence.
1. sitings of birds (aural or visual), no mounds.
2. mound(s) present, no evidence of recent usage or occurrence of birds.
TABLE 1 Continued.

3. from 1 to a few mounds present, evidence of recent usage.
4. many mounds, no evidence of recent usage.
5. many mounds, evidence of recent usage.

Column 13: Conservation Priority (1-5 Scale)
1. site of limited biogeographical significance, not requiring management attention.
2. site of outstanding biogeographical significance, not requiring management attention.
3. site of limited significance, requiring management attention.
4. site of outstanding significance, requiring management attention.
5. site of exceptional significance, requiring urgent attention.

* site outside Park boundaries.
based largely on the occurrence of incubation mounds and whether these were currently in use.

The biogeographical significance of each site is indicated in column 13 using a scaled index. This index also indicates whether management attention is required at the present time. Where such attention is required the nature of the problem is also given. It is to be noted that the scale value of 5 indicates that the vine-forest patch is of exceptional significance and is seriously threatened. This is indicated in only 2 instances; both warrant immediate attention.

Finally, the locations of sampling sites for each habitat type are given in Figures 1-5. A distribution map of Kakadu vine-forests is not presented with this Report.

2.3 Ecological Description and Condition of Vine-Forests in Kakadu

2.3.1 Vine-forests associated with sandstone terrain

For the purposes of this report five habitat types are recognised:

(i) topographically protected perennial spring/streamline habitats;
(ii) topographically exposed perennial spring/streamline habitats;
(iii) evergreen vine-forests associated with seasonally dry escarpment streamlines;
(iv) evergreen vine-forests not associated with springs and watercourses;
(v) semi-deciduous vine-forests.

(i) **Topographically protected perennial springs/streamline habitats**

The habitats range from rock seepages, through springs in steep-sided gorges, to riparian types along escarpment watercourses. These habitats all occur as topographically sheltered and protected situations and as such are distinguished here from other escarpment springs (see Section 2.3.1 (ii)). While patch sizes are typically very small (often much less than 1 ha), such vegetation frequently occurs in association with other vine-forest which occupies the upper slopes and surrounding dissected terrain. Vine-forest vegetation associated with seepage habitats often abuts directly with other sandstone vegetation types. The most extensive patches are the riparian types (e.g. sites 183, 188). As with perennial spring habitats in general, topographically protected escarpment...
## Key Site Attributes for Vine-Forest Habitat Types Associated with Sandstone Terrain

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#### 3 Evergreen Vine-Forest Associated with Seasonally Dry Escarpment Streamlines

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5 Semi-Deciduous Vine-Forests

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types are very uncommon, often separated from each other by distances of 5 km or more.

The canopy may be as tall as 25m, and comprising a relatively small number of evergreen tree species: typically Allosyncarpia ternata, Buchanania arborescens, Calophyllum sil, Carpentaria acuminata, Euodia elleryana, Horsfieldia australiana, Planchonella sp. B2110, Syzygium angophoroides, S. forte, S. minutuliflorum, Xanthostemon eucalyptoides. Smaller trees, shrubs, vines and ground ferns are uncommon; those occurring being mostly widespread in other seasonally drier habitats. Exceptions are Ternstroemia cherryi and Polyscias australianum. Both these tree species are of highly restricted occurrence in the Kakadu region and are widely separated from other populations in northern Australia. Ferns and mosses are common on rockwall seepages. Of the former group at least four taxa are highly restricted in their occurrences (Histiopteris incisa, Nephrolepis oblitterata, Selenodesmium obscurum, and Taenites blechnoides). The total known populations of Histiopteris and Selenodesmium in the region stand at 3 individuals each, at sites 99 and 187, respectively.

While the small population sizes cited above are extreme, it is a characteristic feature of vine-forests associated with springs (indeed as it is for Top End vine-forests generally) that a significant number of the species occurring in any one patch are often represented by a small number of mature individuals. In Table 2-(a) it may be observed that, for the springs under discussion, the proportion of species with populations less than 50 mature individuals range between 100% and 5%; the latter value concerning a riparian patch over 15 ha in extent, occurring along the upper Magela below the falls (Site 188). Furthermore, the proportion of species represented by 6 or less individuals may be seen to range as high as 64% (Site 9). At face value such figures might be taken to suggest that many populations are well below critically viable levels and, as such, are in imminent danger of local extinction. However, as discussed in Part 1 of this Report (Section 2.6), it is evident that many taxa are highly vagile, i.e., they are readily capable of dispersing and establishing effectively. Thus, while such figures probably do not represent genetically critical levels for the majority of populations, it follows that the regional viability of many taxa may be dependent on the maintenance and conservation of small populations scattered through a number of patches. In this regard it is noted that suitable escarpment spring habitats are often separated by distances of 5 km or more. Spring habitats thus warrant a high conservation priority.

Given the topographic protection afforded the spring vine-forests under discussion, they are little affected by fire and feral animals, and free of exotic weeds (Table 2-(a)). Moreover, as indicated in this Table, such habitats are not necessarily fragile - at least to the extent that they can withstand certain types of disturbance. Sites 30, 31, 63 and 188 for example, are all riparian forests which are affected frequently (annually?) by deep and fast-flowing floodwaters. As well, Sites 6, 15, 177, 178, 181 and 183 all exhibit structural evidence which indicates that these
Figure 1: Perennial spring/streamline vine-forest sampling sites in sandstone terrain.
too are similarly, if more occasionally, prone to such disturbance. Ian Morris tells me that following atypical torrential rain, whole forests have been swept from the bottom of gorges in north-western Arnhemland.

(ii) Topographically exposed perennial springs/streamline habitats

Whereas the spring habitats considered previously occur in topographically protected situations, those described here are not protected topographically, and are exposed to disturbance on at least one margin. As such they are more vulnerable to fire and feral animal impact. While some of the habitats are essentially analogous to the topographically protected types (e.g. gorge springs and seepages), three further types occur. The first type concerns springs which arise either at the base of the escarpment and its outliers, or in isolated drainage depressions in gently undulating plateau terrain (Sites 52, 53, 55, 64, 67, 68, 128, 130, 131, 185 and 186). The second type concerns riparian patches which are essentially extensions of topographically protected springs, where the patch has left the relative safety of dissected gorge terrain (e.g. Sites 13, 29, 40, 58, 65, 72 and 163). The third type concerns riparian strips along major watercourses (such as the South Alligator River, Site 135), where these are in close proximity to the escarpment (also Sites 33 and 91).

Of these various habitat sub-types, vine-forests associated with springs at the base of the escarpment, and in undulating plateau terrain, warrant special comment. The occurrence of evergreen vine-forest patches associated with such situations is rare. Of the eleven patches sampled, three occur at the base of the southern face of the Mt. Brockman outliers (Sites 52, 53 and 55), the remainder occurring in the southern region. Of these, two occur in the Jim Jim Falls region (Sites 185 and 186) on the Goodparla 'jumpup' (Sites 65, 67, 68 and 128), and two on Gimbat (Sites 130 and 131). The floristic composition of the vegetation, similar to that associated with protected escarpment springs described previously, is highly variable from patch to patch. Population sizes of many species present are small. The biogeographical significance of these habitats therefore, is outstanding. One patch (Site 185), of 1.2 ha in extent, contains the only known N.T. population of the terrestrial orchid, Dendrobium lobii, as well as a number of other biogeographic oddities. At the present time, however, buffalos, pigs, and fire are having a serious impact on these vine-forests. Given that the surface soils comprise waterlogged organic loams or sands, they are readily eroded and their nutrient status depleted by the wallowing and rooting activities of feral animals. Physical destruction of the vegetation has permitted the penetration of fire. Riparian patches which are essentially extensions of escarpment springs (e.g. at Radon Gorge, Baroalba Springs), are being affected similarly, if less severely.
(iii) *Evergreen vine-forests associated with seasonally dry escarpment streamlines*

The habitats comprise boulder-strewn seasonal watercourses mostly in steep escarpment terrain. Evergreen vine-forest vegetation occurs in association with these watercourses as narrow strips, with woody species rooted between boulders. Patch sizes are small, and of the 12 sites sampled 11 are 1 ha or less in extent. The vegetation comprises mainly widespread species which are often associated with perennial springs, as well as more hardy types common in other seasonally dry escarpment vine-forests. Characteristic tree species include *Allosyncarpia ternata*, *Buchanania arborescens*, *Calophyllum sil*, *Carpentaria auminata*, *Myristica insipida*, *Polyalthia holtzeana*, *Syzygium angophoroides*, *S. forte* and *Xanthostemon psidioides*. Other growth forms are uncommon.

As indicated previously for Top End vine-forests in general, the population sizes of many species occurring in these particular habitats are small. While a few species have propagules which are essentially gravity dispersed (e.g. *Allosyncarpia tenata*, *Xanthostemon* spp.), the great majority of at least the woody taxa are fleshy fruited and readily dispersed by birds. The populations of these latter species may thus be considered to be genetically connected with other populations. For less readily dispersed taxa the continued persistence of local populations is dependent on the maintenance of viable population sizes in each isolated patch. In this respect it is to be noted that where *Allosyncarpia* or *Xanthostemon* spp. are associated with these seasonal watercourses, they occur mostly in situations where larger populations occupy drier habitats in the surrounding terrain.

Given the relative protection afforded these seasonal watercourse habitats by both the steepness and rockiness of the terrain, neither fire nor feral animals appear to be incurring any significant impact at the present time (see Table 2(a)).

(iv) *Evergreen vine-forests not associated with watercourses*

By far the largest extent of escarpment vine-forest occurs as structurally simple forests, dominated almost monotypically by the local endemic species, *Allosyncarpia ternata*. Extensive tracts of such forest occur in deeply dissected terrain at the edge of the escarpment, mostly north of Deaf Adder Gorge and on the Mt. Brockman outlier. To the east, and to the south of Deaf Adder Gorge, patches of such forest become increasingly scattered and much smaller in size. They range, however, as far south as Katherine Gorge. In the northern region individual, more-or-less continuous tracts may extend over 1,000 ha or more.

As described in Part 1 of this report (Sections 2.5 and 3.2.3), the geographical distribution of this evergreen vine-forest vegetation very much reflects the distribution and ecological characteristics of
Figure 2: Evergreen vine-forest sampling sites in sandstone terrain.
Allosyncarpia ternata. This species occurs over a wide range of conditions, from perennially moist and sheltered situations in deep escarpment gorges, through to rocky screes and bare sandstone pavements. Along this declining gradient in seasonal moisture availability, canopy height declines from over 35 m to less than 10 m, and the growth form of Allosyncarpia changes from a forest tree through to that of a short-trunked woodland form.

The flora associated with these Allosyncarpia-dominated forests can be considered to comprise three elements. The first and largest element concerns species which are widespread in other seasonally dry vine-forest habitats, associated both with the sandstone and with coastal and subcoastal landforms. The second element concerns ca. 30 taxa which, if not restricted to the Arnhem Land escarpment, only occur in the Northern Territory associated with widely scattered sandstone surfaces. The great majority of these occur in north-eastern Queensland as well. In the Arnhem Land escarpment region a relatively small number of taxa are known from only one to a few localities (See Figure 6). The third element comprising these evergreen vine-forests concerns taxa more widespread in other sandstone vegetation types, but which are occasional inclusions (e.g. Phyllanthus spp., Terminalia carpentariae, Biepharocarya depauperata) or fire-weeds (e.g. Hibiscus spp., Triumfetta spp.).

Where these evergreen vine-forests are not protected topographically, they are prone to recurrent burning. In all situations examined where patch boundaries are exposed (i.e. abutting directly with other sandstone vegetation types), the structural expression of the vine-forest at the boundary clearly reflected the influence of fire. While the influence of fire in these situations will be considered in detail in Section 3, it is pertinent to note here that in no situation examined was there any structural evidence to indicate recent patch expansion. Rather, where patch boundaries could be shown to have "moved" in recent time, this had involved contraction. The impact of feral animals is of no significance in these evergreen vine-forests.

(v) Semi-deciduous vine-forests

In situations where Allosyncarpia is absent, small patches of vine-forest occur comprising a relatively high proportion of semi-evergreen or semi-deciduous canopy elements. Canopy height is often less than 10 m. Such vegetation may occur in fissures and small gullies in the sandstone, or associated with talus slopes at the base of escarpment cliffs. In the latter situation, such vegetation may be diffusely scattered along the slope intermixed with sclerophyll taxa (e.g. Eucalyptus, spinifex grasses).
Figure 3: Semi-deciduous vine-forest sampling sites in sandstone terrain.
Patch sizes are characteristically very small, often comprising but a handful of individuals in any one locale. Site 164, for example, concerns deeply fissured terrain in the escarpment to the south of East Alligator Ranger Station. Vine-forest taxa occur in many of the fissures in small numbers, with discrete patches separated from each other by rock pavement supporting sandstone heath species. In the same general region other semi-deciduous patches occur associated with the lower talus slopes of the escarpment (e.g. Site 93). Such 'patches' comprise vine-forest ecotone species in various regenerative phases under diffuse eucalypt canopies. The influence of fire is clearly indicated here (See Section 3).

The floristic composition of these semi-deciduous vine-forests is very similar to that of the evergreen forests dominated by Allosyncarpia ternata, commonly with another Myrtaceous species assuming canopy dominance (e.g. Xanthostemon psidioides, x. umbrosus). Given the small sizes of the patches it is not surprising that population numbers are small. As with other vegetation types a majority of the species rely on birds for dispersal. While feral animals incur insignificant impact in these situations, fire is a recurrent factor in all but the most topographically protected situations.

2.3.2 Vine-forests of the lateritic lowlands and related landforms

Four habitat types are recognised:

(i) seasonally dry coastal habitats;
(ii) seasonally dry subcoastal habitats;
(iii) lowland springs;
(iv) rock outcrops.

(i) Seasonally dry coastal habitats

Vine-forests associated with seasonally dry coastal habitats have been described in detail in Section 3.2.4 (First Report). Only two patches in the Kakadu region were sampled, one on calcareous beach sediments at Point Stuart (Site 116), and the other, an incipient patch on sandy deposits over laterite on Field Island (Site 3). Webb and Tracey (1979) sampled two further patches as part of their survey, near the mouth of the West Alligator River.

As has been discussed at length in the first part of this Report, many coastal and subcoastal patches are relatively recent in origin, occurring as they do on Holocene landforms. Such observations underline the high vagilities of many N.T. vine-forest taxa, i.e., they demonstrate a ready capacity to exploit new ecological opportunities as these arise in time.
TABLE 2(b):
Key Site Attributes for Vine-Forest
Associated with Lowland Habitats.

<table>
<thead>
<tr>
<th>Site no.</th>
<th>Patch Size</th>
<th>Species No.</th>
<th>50 Indiv. (%)</th>
<th>1 Indiv. (%)</th>
<th>Habitat Stability</th>
<th>Fire Severity</th>
<th>Fire Frequency</th>
<th>Buffalos</th>
<th>Pigs</th>
<th>Exotics</th>
<th>Scrub Fowl</th>
<th>Conservation Priority</th>
</tr>
</thead>
</table>

1. **Seasonally Dry Coastal Habitats**

| 3 | 0.6 | 58 | 66 | 21 | 3 | 2 | 1 | 0 | 0 | 2 |
| 116 | >25 | 109 | 31 | 7 | 3 | 0 | 0 | 2 | 1 | 5 | 2* |

2. **Seasonally Dry Subcoastal Habitats**

| 8 | >2 | 43 | 30 | 15 | 3 | 2 | 2 | 2 | 1 | 0 | 2 |
| 10 | 5 | 46 | 9 | 9 | 4 | 2 | 3 | 2 | 2 | 1 | 3 | 2 |
| 11 | >3 | 63 | 22 | 9 | 2 | 3 | 2 | 1 | 1 | 4 | 3 | 2 |
| 12 | >3 | 62 | 48 | 0 | 2 | 3 | 2 | 0 | 0 | 1 | 0 | 2 |
| 17 | 1.4 | 46 | 67 | 15 | 2 | 3 | 3 | 3 | 2 | 4 | 4 |
| 18 | >2 | 43 | 86 | 23 | 2 | 4 | 3 | 1 | 0 | 3 | 2 | 1 |
| 22 | 1.5 | 67 | 85 | 22 | 2 | 4 | 3 | 2 | 0 | 3 | 2 | 3 |
| 23 | >1.5 | 35 | 77 | 11 | 2 | 2 | 3 | 3 | 3 | 1 | 4 | 4 |
| 39 | >1.5 | 49 | 29 | 4 | 2 | 3 | 3 | 1 | 0 | 3 | 2 | 1 |
| 42 | 3 | 51 | 86 | 29 | 2 | 2 | 3 | 1 | 0 | 3 | 2 | 1 |
| 43 | 0.3 | 26 | 77 | 27 | 3 | 2 | 3 | 2 | 1 | 4 | 3 | 2 |
| 44 | 1.5 | 38 | 76 | 13 | 3 | 3 | 3 | 3 | 3 | 2 | 3 |
| 45 | 2 | 45 | 80 | 24 | 2 | 3 | 3 | 1 | 0 | 3 | 2 | 1 |
| 46 | 0.6 | 35 | 77 | 29 | 3 | 2 | 3 | 3 | 3 | 3 | 0 | 1 |
| 49 | 3 | 71 | 71 | 6 | 2 | 3 | 3 | 3 | 3 | 3 | 5 | 4 |
| 50 | 2 | 42 | 74 | 7 | 2 | 3 | 3 | 3 | 2 | 3 | 5 | 4 |
| 70 | >3 | 87 | 85 | 16 | 3 | 2 | 3 | 3 | 1 | 2 | 4 |
| 74 | 2 | 36 | 92 | 25 | 2 | 3 | 3 | 1 | 0 | 3 | 2 | 1 |
| 101 | 5 | 86 | 58 | 13 | 3 | 2 | 3 | 3 | 2 | 5 | 4 |
| 104 | >1 | 54 | 91 | 35 | 1 | 3 | 3 | 2 | 2 | 2 | 0 | 2* |
| 105 | 7 | 72 | 68 | 7 | 3 | 2 | 2 | 3 | 3 | 3 | 2 | 4 |
| 106 | 2 | 101 | 80 | 26 | 2 | 2 | 2 | 3 | 3 | 3 | 5 | 4 |
| 161 | 0.6 | 46 | 61 | 7 | 1 | 4 | 3 | 2 | 3 | 0 | 4 |
| 167 | 4 | 91 | 45 | 12 | 2 | 3 | 3 | 2 | 2 | 2 | 4 | 2 |
| 168 | 1.2 | 68 | 49 | 15 | 2 | 2 | 3 | 2 | 1 | 3 | 0 | 3 |
| 170 | >1.6 | 77 | 65 | 22 | 3 | 2 | 3 | 3 | 3 | 2 | 3 |

- buffalo, pigs, fire
- buffalo, fire
- buffalo, pigs
- buffalo, pigs
- buffalo, pigs
- buffalo, pigs
- weeds, pigs
- buffalo, pigs, weeds
- fire, vandalism
- buffalo, weeds
- buffalo, pigs, weeds
TABLE 2(b) Continued

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<th>.7 indivs. (%)</th>
<th>Habitat Stability</th>
<th>Fire Severity</th>
<th>Fire Frequency</th>
<th>Buffalo</th>
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<th>Exotics</th>
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3. Rock Outcrops

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</table>

4. Lowland Springs

| 2          | 43         | 79          |                |                |                |               |              |         |      |        |            |                       |
| 2          | 43         | 79          |                |                |                |               |              |         |      |        |            |                       |
| 2          | 43         | 79          |                |                |                |               |              |         |      |        |            |                       |
| 2          | 43         | 79          |                |                |                |               |              |         |      |        |            |                       |

50 indivs. (%)空白处应填写50个体的百分比。
The patch sampled on Field Island warrants special mention here. Empirical evidence indicates that the vegetation of this island is seldom burnt (at least in modern times) and, given that the island is devoid of feral animals, provides a very useful ecological benchmark in the region. While not visited, the vegetation of Baron Island presumably reflects the same situation. On Field Island, vine-forest occurs on beach ridge fascies, and over a lateritic profile behind the beach on the eastern side of the island. In this latter situation (Site 3), a small, incipient patch of semi-deciduous forest is developing at the present time. This is indicated by: the entrapment of mature eucalypts within vine-forest vegetation; the absence of scrubfowl incubation mounds which are otherwise common in vine-forest associated with beach ridges on the island; and the population structures of many of the species present (e.g. a single mature individual of the palm, *Carpentaria acuminata*, directly beneath a single mature individual of the evergreen tree, *Maranthes corymbosa*). While certain other vine-forests associated with subcoastal landforms can likewise be shown to be expanding at the present time, this particular patch provides outstanding potential for monitoring developmental processes given its undisturbed state.

(ii) Seasonally dry subcoastal habitats

Extensive patches of semi-deciduous vine-forest occur in the Kakadu region associated with the lateritic margins of riverine floodplains. These are best developed towards the coast. As described in detail in the first part of this report, the vine-forest vegetation associated with floodplain margins is essentially continuous with that occurring on coastal landforms. However, whereas the floristic composition of coastal and subcoastal types is very similar, the coastal vine-forests contain ca. 40 taxa which are not known to occur further inland (see Table 5, first report). As argued in that report, many of the subcoastal vine-forest patches occurring within the tidal range of the South, East, and West Alligator Rivers, and the Wildman, are most probably Holocene in origin (i.e. they have developed within the last 10,000 years).

While much subcoastal (and coastal) vine-forest does not therefore conform to the relict status usually accorded vine-forest vegetation, such patches do provide a very significant genetic reservoir for many taxa. At the present time many patches are being battered by feral animals, especially buffalo. Associated with the use of these patches by buffalo as resting habitat, and as a food resource by pigs, exotic weeds have become widespread (e.g. *Hypistis suaveolens*, *Cassia spp.*). Destructive fires, which at one time may have been confined to boundary situations, have been able to penetrate deep within certain patches; such penetration being facilitated by the creation of woody fuels (through physical destruction) and fine fuels (weeds). Braithwaite et al. (in press) suggest that, apart from physical damage caused by buffalo through rubbing and trampling activities, buffalo activity also causes tree death through impacting surface soils and thereby altering the moisture relations of the substrate. Such impact probably also has a severe impact on fine root systems since these are most concentrated near the soil surface.
Figure 4: Semi-deciduous vine-forest sampling sites in coastal/subcoastal lowlands.
Whereas in lower tidal reaches (i.e. near the coast) vine-forest vegetation occurs as long strips associated with lateritic floodplain margins, in upper tidal reaches extant patches are small (mostly less than 1-2 hectares) and more widely scattered. That vine-forest vegetation has been locally more abundant in these regions is indicated by the occurrence of scrub fowl incubation mounds in situations currently occupied by eucalypt-dominated vegetation. While the occurrences of such mounds are very localised, it does indicate that vine-forests in these regions have been in decline (see Russell-Smith 1984). The specific locations of areas where vine-forests have been more abundant, on the basis of scrub fowl remains, are indicated in Figure 5.

Beyond the limits of the upper tidal range, vine-forest vegetation threads its way discontinuously through the lateritic lowlands along narrow corridors of both perennial and seasonal watercourses, well inland. While such habitats were little sampled in the present study, they doubtlessly represent significant genetic reservoirs for many taxa, as well as providing corridors for genetic communication between isolated patches. They are thus likely to be of considerable biogeographical and ecological significance. In the Kakadu region, such habitats occur extensively on Goodparla-station. The species composition of these vine-forests comprises widespread types (e.g. Site 104).

(iii) Rock outcrops

Five patches of semi-deciduous vine-forest associated with rock outcrops were sampled in the Kakadu region. Three of these concerned granitic and doleritic intrusions on the edges of riverine floodplains (Sites 47, 48 and 165). The floristic compositions of these resemble closely that of semi-deciduous vine-forests in other seasonally dry subcoastal and coastal habitat types. Each of these patches is very seriously disturbed by buffalo and/or pig activity, is smothered in exotic and native weedy species, and is being affected severely by fire at the present time.

The two other rock outcrop patches sampled occur on Goodparla, and near Moline, north of Pine Creek. Both occupy topographically protected situations and are removed from the influence of fire. The patch on Goodparla (Site 129) occurs on a granitic boulder flow surrounded by dense perennial grass cover. It appears to be very isolated from other vine-forest vegetation (ca. 5 km) and 36 out of the 37 species recorded there exist as populations of much less than 50 individuals. One species present, Embelia sp. W306, is otherwise known to occur only in coastal and subcoastal patches, especially springs. The other patch sampled (Site 60), occurring at the site of the abandoned Evelyn mine, comprises mainly typical coastal/subcoastal species. There is some indication that this patch is not particularly isolated genetically, given its close proximity (ca. 1 km) to a small creek with vine-forest vegetation of similar species composition. For example, the introduced custard apple (Annona reticulata) is very common on the rock outcrop, and seedlings of Annona are found along the creek.
(iv) Lowland springs

As far as is known, the occurrence of floristically rich lowland spring habitats, such as those in the Darwin region, is very restricted in Kakadu. Lowland spring habitats supporting geographically widespread species are known from a few areas, mostly on the margins of the riverine floodplains (e.g. Sites 4, 75 and 160). In all three sites, buffalo and pig impact is severe. A patch of considerable biogeographical significance is Ballyongady Spring on Munmarlary (Sites 73 and 169). This spring is dominated by tree species which are generally restricted to escarpment springs (e.g. *Ilex arnhemica*, *Planchnonella xerocarpa*, *Syzygium angophoroides*, *S. minutuliflora*), as well as others of more widespread distribution. The occurrence of such taxa in this situation is not problematic, however, given the widespread sandstone lithology of the area. This patch is being severely affected by feral animal impact and warrants urgent management attention.

In considering lowland springs it is interesting to observe that many typical floristic elements common in the Darwin region evidently do not range as far as Kakadu. For example, tree species such as *Artocarpus glaucus*, *Calophyllum soulattri*, *Endospermum medullosum*, *Schefflera actinophylla* and *Vavaea australiana*, which are common in spring vine-forests to the west, do not reach Kakadu. The most easterly occurrence of such vegetation is so far known from Wildman Station. They probably occur in wetter regions to the north and north-east, however (e.g. Coburg Peninsula).

Another spring vine-forest, not sampled in this survey, is known to occur on Goodparla. It goes colloquially by the name of 'Black Jungle', and is said to be severely affected by buffalos (George Mingam pers. comm.).

2.4 Discussion

2.4.1 Biogeographical significance

The Kakadu vine-forest flora is composed very largely of taxa which occur elsewhere in northern Australia, both within the N.T., and in other regions. A great majority of the known flora is shared with homologous habitats in northern Queensland (e.g. Kikkawa et al. 1981, Specht 1958; Webb and Tracey 1979, 1981a, 1981b). There are few endemics.

While a biogeographical analysis of the N.T. vine-forest vegetation is premature at the present time given that many areas (e.g. most of Arnhem Land) are yet to be explored botanically, it may be stated confidently that the vine-forests in Kakadu of greatest biogeographical significance are those associated with sandstone habitat types. Thus, whereas taxa comprising lowland habitat types are generally widespread and/or well represented in other areas, escarpment vine-forests contain as well many taxa of very restricted distribution. For example, associated with escarpment spring habitats are taxa otherwise unrecorded from the N.T.
rock outcrops
conservation priority of value 4 or 5 (see Table 1)
scrub fowl incubation mounds in eucalypt dominated savanna

Figure 5: Vine-forest sampling sites associated with lowland springs and rock outcrops.
(e.g. Dendrobium lobii, Ternstroemia cherryi), or which are known only from a small number of widely separated localities (e.g. Neprolepis obliterata, Ophioglossum intermedium, Polyscias australinum, Selenodesmium obscurum, Taenites blechnoides). The seasonally dry escarpment vine-forests are distinguished both by the singular dominance of the local endemic, Allosyncarpia ternata, as well as the occurrences of at three other myrtaceous taxa widely disjunct with other sandstone regions (i.e. Xanthostemon eucalyptoides, X. psidioides, X. umbrosus). To these may be added taxa not known to occur elsewhere in the N.T., or those restricted largely to this particular region. The occurrence of rare taxa is indicated in Figure 6. The taxa are listed in Appendix 3.

It must be stressed, however, that, in the absence of any definitive genetically-based taxonomic studies, the genetic status of many N.T. populations is uncertain. This would apply especially for taxa restricted to isolated habitats such as certain springs, sandstone habitats, and inland rock outcrops. Such populations are likely to have been isolated genetically, at least from east coast populations, for considerable spans of time. For taxa widespread in coastal/subcoastal lowland situations however, with a demonstrated capacity to disperse effectively, genetic exchanges between regional and extra-regional populations are likely to have occurred regularly, albeit occasionally, as a consequence of oscillating Pleistocene sea-levels (see Chappell and Thom, 1977; Sect. 2.3, first Report).

2.4.2 Condition of vine-forests in Kakadu

(1) Feral animal impact

Of the vine-forests associated with sandstone terrain only those associated with topographically exposed spring or streamline habitats are being affected seriously by buffalo at the present time (see Table 2(a)). Every site sampled in this category exhibited signs of being disturbed to some greater or lesser extent by buffalo. Of particular concern are the perennial spring vine-forests associated with sand sheets and/or undulating terrain (Sites 52, 53, 64, 67, 68, 128, 131, 185 and 186). As described in Section 2.3.1(ii), these vine-forests are of outstanding biogeographical significance, with Site 186 being exceptional. In the absence of these vine-forest patches being afforded protection from buffalos, and to a lesser extent pigs, their long-term viability is seriously in doubt.

The general pattern of impact in these situations is that buffalo wallow extensively around the margins, and at the heads of springs especially. In time this totally destroys the integrity of margin vegetation as well as causing severe erosion of the ever-wet organic top soils. Such activities lead to tree death and, as a consequence, the impact of fire is exacerbated.

For other habitat types associated with sandstone terrain, buffalo impact is either insignificant or absent. This is evidently an expression
Figure 6: Site occurrences of rare taxa in the Kakadu region. See Appendix 5 for a listing of rare species.
both of the intractability of such terrain and/or, the absence of free
water. Outside the exposed springs considered previously, pigs are nowhere
causing severe disturbance.

Feral animal impact is widespread in lowland habitat types. In
seasonally dry habitats such impact is an outcome both of their being
used as favoured resting habitat by buffalos, as well as a source of yams,
shoots, etc., for pigs. Lowland springs are affected similarly as for
the escarpment springs described above. This is particularly serious
in the case of Ballyangardy Spring (Site 169) since this patch is of
exceptional biogeographical significance (see Section 2.3.2(iv)).

As described by Braithwaite et al. (in press) the most obvious
impact of buffalo in these situations is the elimination of lower strata
and, at a higher level of impact, the death of canopy trees. Such impact
opens the way for weed invasion in gaps, and promotes the impact of fire.
It is to be noted, however, that within the one patch such disturbance
is often localised to the vicinity of favoured camp sites and tracks.
Pigs can occasion severe impact on recruitment similarly, by methodically
working over extensive areas of the forest floor, even in rocky situations
(e.g. Sites 47, 48 and 160).

That such impact is widespread in lowland vine-forests is indicated
in Table 2(b). Only four sites sampled were free of feral animals (Sites
3, 12, 61 and 129). Of these, three occur in situations which are either
topographically inaccessible (Sites 61 and 129) or where feral animals
are absent (i.e. Field Island, Site 3). The remaining site was at
Nourlangie Camp, close to habitation (Site 12). That the potential for
effective regeneration still exists in even severely affected situations,
however, as long as the canopy is maintained, is indicated in Table 3.
This Table compares understory structures on two severely disturbed plots
(at North Point, Kapalga, and Bindjil Bindjil, north of Cannon Hill) with
those on two undisturbed plots (at Nourlangie Camp and Field Island).
It may be observed from this Table that although understory components
are less abundant on the disturbed plots, considerable potential for
regeneration still exists. These data are presented here as a form of
encouragement. For those with a perverse interest in seeing what unchecked
feral animal impact can occasion, a visit to the forests fringing the Mary
River floodplain is essential.

(ii) Fire

While the role of fire is considered in some detail in Sections 3
and 4, it is pertinent to note here that its impact in any one situation is
dependent, in the first instance, on factors such as the degree of
topographic protection afforded different habitats, the fuel
characteristics of surrounding vegetations, and the tolerances of
individual species to different fire regimes. As such it may be
appreciated that fire is likely to affect the boundaries of different types
of vine-forest in a highly differential manner (see Section 2.5, first
Report). This notwithstanding, it is noted that fire is exerting
considerable pressure on many vine-forest patches in Kakadu at the present
time.
TABLE 3:
Effect of Feral Animals on Recruitment in Seasonally Dry Lowland Vine-Forests

Notes: The data presented here were collected in June 1983. On each plot, understorey data were obtained using 20 quadrats, with dimensions 2x2m². Quadrats were located at a set interval along two parallel transects enclosed within the circular plot. Where given, 95% confidence limits are based on the t-distribution. Each plot is located in closed canopy vine-forest. Numbers in square brackets refer to the number of tree species occurring on each plot of 20m radius.

Regeneration Size Classes (individuals per quadrant)

<table>
<thead>
<tr>
<th>Severeley disturbed plots</th>
<th>No. Species</th>
<th>1. per quadrant (20cm tall)</th>
<th>2. 20cm - 2m tall</th>
<th>3. &gt;2m tall</th>
<th>&lt;5cm DBH*</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Point (Kapalga) [20]</td>
<td>x</td>
<td>5.4</td>
<td>9.9</td>
<td>0.6</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>±</td>
<td>1.5</td>
<td>3.3</td>
<td>0.4</td>
<td>0.02</td>
</tr>
<tr>
<td>Bindjil Bindjil [16]</td>
<td>x</td>
<td>5.2</td>
<td>6.6</td>
<td>2.6</td>
<td>0.3</td>
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<td></td>
<td>±</td>
<td>1.2</td>
<td>2.0</td>
<td>1.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Undisturbed plots</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Neurlangie Camp [14]</td>
<td>x</td>
<td>8.0</td>
<td>84.0</td>
<td>5.2</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>±</td>
<td>1.1</td>
<td>41.0</td>
<td>1.4</td>
<td>0.3</td>
</tr>
<tr>
<td>Field Island [10]</td>
<td>x</td>
<td>7.1</td>
<td>19.5</td>
<td>3.8</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td>±</td>
<td>2.2</td>
<td>16.0</td>
<td>2.9</td>
<td>1.4</td>
</tr>
</tbody>
</table>

1. Severeley disturbed is defined here as where over 75% of the plot has been either trampled or worked over.

* DBH diameter at breast height.
Here I will consider only the situation where fire impact is promoted by feral animals, buffalo especially. This is exemplified by two vine-forest patches occurring on low rock outcrops at Couramoul, just to the south of the South Alligator River bridge (Sites 47 and 48). In these instances, fire has severely eroded the margins, penetrating deep within the patches themselves. As may be observed when walking through these patches, such penetration of 'fire tongues' occurs commonly in association with buffalo thoroughfares. Not only is woody vegetation immediately adjacent these thoroughfares physically destroyed (thus creating woody fuels) but, with the opening of the canopy, light-demanding weed species are able to establish as well. In the Couramoul situation, such weeds are extremely vigorous and provide a very substantial fuel when cured in the dry season. The activities of buffalo in such situations can, thus be seen to contribute significantly to the promotion of fire impact.

(iii) Exotic weeds

The occurrence of exotic weed species in Kakadu vine-forests is restricted very largely to situations where there is significant feral animal impact. Of the sandstone vine-forests, only those associated with accessible spring/streamline habitats are significantly infested, especially in southern regions. In these situations Hystis suaveolens is often widespread on patch margins. By contrast, nearly all lowland vine-forests are infested to some greater or lesser extent. The main exotic weed species comprise Cassia obtusifolia, Cassia occidentalis, Hystis suaveolens, Malachra fasciata, Physalis minima and Sida acuta. As well, the exotic passionfruit (Passiflora foetida) is now so widespread as to be considered naturalised. To these exotic weeds may be added native species which have responded similarly to such disturbance (e.g. various Acacia spp., Hibiscus meranikensis, Triumfetta rhomboidea and Waltheria indica).

In passing, it is interesting to note that exotics which have established successfully belong to the same genetic groups which commonly comprise the native weedy types. In this connection the planting of species such as Lantana camara (as at Cooinda) is not to be encouraged given the problems they potentially pose.

2.4.3 Status of scrub fowl

As indicated previously, no systematic study of scrub fowl populations was undertaken in this survey. Rather, the observations presented here are based largely on the occurrences of incubation mounds and whether these were in use. As indicated in Tables 2(a) and (b) the occurrence of scrub fowl mounds in sandstone habitats is very restricted. Isolated mounds are known to occur only as far south as the Deaf Adder Gorge area. In no region of the escarpment however, are mounds common;
i.e. they occur only occasionally in larger patches or tracts of evergreen vine-forest, and even then mostly at densities of one to a few mounds per patch (see Table 2(a)).

Incubation mounds are very common; however, in many patches associated with seasonally dry coastal and subcoastal landforms. At the present time scrub fowl populations occur almost exclusively in northern coastal and subcoastal areas. It is in this region that the largest expanses of lowland vine-forest habitat occur. Furthermore, given that much coastal and subcoastal vine-forest is likely to derive from the Holocene (see Sect. 2.4, first Report) it is equally likely that regional scrub fowl populations have actually expanded during this epoch. That this species is highly mobile, moreover, is indicated by the occurrence of large numbers of mounds on Holocene substrates (e.g. Site 116).

That suitable habitats have contracted in localised situations, however, is indicated by the occurrence of disused incubation mounds in extant eucalypt-dominated vegetation. In Kakadu such occurrences are uncommon and are located mostly along floodplain margins in the upper tidal reaches of the South Alligator River (see Fig. 5). In the Ginja area a number of mounds have been excavated and charcoal submitted for radiocarbon dating (see Russell-Smith 1984). The resulting dates confirm that not only were scrub fowl active in this area within the last century at least, but as well that vine-forest vegetation was at the same time locally more abundant.

While it is not known whether such habitat reduction has occurred likewise in other localised situations within the historical past, the coincidence of the reduction of vine-forest at Ginja with the advent of Europeans is striking. In this respect, moreover, a number of isolated mounds in the Cannon Hill area are of interest. Bill Neilji indicates that in his youth these mounds were enclosed in vine-forest such as occurs at the base of Hawk Dreaming at the present day (Site 167). He attributes the removal of vine-forest cover primarily to buffalo impact.

Whatever the cause(s), it is unlikely that this localised reduction of habitat would have affected significantly the status of the scrub fowl in the region. The impact of shooting, removal of eggs, etc., however, is unknown.

2.4.4 Conservation priorities and management prescriptions

In preceding discussion the condition of the various habitat types of vine-forest vegetation occurring in Kakadu has been described. Vine-forests associated with exposed escarpment springs; lowland springs, and seasonally dry coastal and subcoastal habitats have all been identified as being severely affected by feral animals, especially buffalo, at the present time. While many of these same patches are also being affected by fire, and invaded by exotic weeds, it has been argued here that such impacts arise largely in response to disturbances induced by buffalo.
activity. If this proposition is accepted, it follows that, in order to rehabilitate such affected patches, the elimination of feral animals is a fundamental priority.

Whilst the eradication of feral buffalo is pursued actively in many areas of Kakadu, many significant patches continue to be threatened. There are a number of reasons for this. Firstly, even very small buffalo numbers may occasion severe impact in fragile habitats, such as springs. Secondly, in the event of shooting or catching activities buffalo often 'lie low' in vine-forest refuges. Thirdly, given the intractability of much of the terrain, and the isolation of many affected patches, it is hardly surprising that local populations of buffalo often are able to wreak destruction with impunity. And fourthly, it is hardly to be expected that constant attention be given to the protection of individual patches, even where the need for this is recognized. Faced with these realities, and accepting that the problem of feral animals is unlikely to vanish overnight, it is recommended that serious consideration should be given to fencing biogeographically significant patches where these are threatened.

In Tables 2(a) and (b), patches requiring management attention have been identified in the column entitled, 'conservation priority'. Such patches are ranked as either 4 or 5. The rank of 5 designates that the patch is of exceptional biogeographic significance and warrants immediate attention. Two patches have been ascribed this value. The first of these (Site 169) is Ballyangardy Spring on Mummalary. The second (Site 185) concerns an isolated and exposed sandplain spring in the Jim Jim Falls area. Consideration should be given to fencing these springs as a matter of urgency. It is accepted, however, that the isolated location of the second patch would entail very considerable logistic costs.

At a second level of priority (ranking of 4) are 32 biogeographically outstanding patches distributed in various habitat types as follows: 2 protected escarpment springs; 15 exposed escarpment springs; 9 subcoastal patches; 3 rock outcrop patches; and 3 lowland springs. Of these, moreover, special consideration should be given to protecting spring habitats wherever economically and logistically feasible.

Further to the above, a number of other considerations are relevant here. Firstly, 3 patches have been designated a value of 4 (i.e. requiring management attention) on the basis of their sensitivity to either actual or potential visitor usage. These concern the small seepage near the Nourlangie Rock gallery (Site 9), Radon Springs (Site 15), and the Moline rock-hole on Goodparla (Sites 64and 65). Toprotect the Nourlangie Rock seepage with its associated specialised flora, there would appear no option other than to fence it off (i.e. wooden railings). Consideration should be given to providing walkways in the Radon Springs forest, especially in sections where ground seepage occurs. Adequately protected this patch would provide an excellent interpretative destination. Whilst currently outside the southern boundary of Kakadu, the Moline rock-hole
is a popular camping area. Considerable damage has occurred in various places below the falls. If when this area is included within Kakadu, appropriate management will be required. As well as these situations, a number of subcoastal lowland patches are being affected by human usage or vandalism at the present time (e.g. around the South Alligator Motor Inn, and Site 161 on Mummalary).

Secondly, until such time as the buffalo research programme on Kapalga is concluded, consideration should be given to assisting CSIRO in protecting vine-forest patches. The destruction of these vine-forests is senseless as it serves no useful function. Whilst much of the northern part of Kapalga was not surveyed in the present study, such vine-forests as visited were found to be incurring severe impact at the present time (e.g. North Point, Site 106).

Thirdly, it is accepted that fencing of individual patches is likely to be considered economically viable only in exceptional cases. Given this, an alternative solution might be to consider the fencing-off of relatively large areas followed by destocking. Many situations in the escarpment, for example, would lend themselves readily to this approach (e.g. Deaf Adder Gorge). In this respect also, the biogeographical significance of vine-forests (Sites 130 and 133) and other vegetation types in the vicinity of the source of the South Alligator River, Gimbat, is such as to warrant this whole area being fenced. This area is, as well, scenically outstanding.

And finally, it is necessary to indicate that other outstanding and threatened patches undoubtedly exist besides those considered here. On the basis of the work undertaken, however, it is probable that most of these occur in association with topographically exposed sandstone springs. Their occurrence warrants investigation.

The recommendations which flow from this discussion are itemised in Section 5.
Plate 1: Topographically protected evergreen vine-forest at the base of Magela Falls.

Plate 2: Regenerating vine-forest associated with an exposed sand-plain spring, Jim Jim falls region.
Plate 3: The escarpment and the lowlands. The dark canopies in chasms and gorges in the foreground belong to *Allosyncarpia ternata*.

Plate 4: A closer view of *Allosyncarpia* forest occupying rugged and dissected terrain.
Plate 5: Zonation of coastal vegetation, Bathurst Island. The dark band adjacent the sea is mangrove vegetation. Semi-deciduous vine-forest occurs next as a more-or-less continuous strip behind the mangroves. The vegetation to the right is open eucalypt forest.

Plate 6: Semi-deciduous vine-forest (gallery forest) on recent floodplain sediments, Ubirr.
Plate 7: Spring forest margin in the Jim Jim falls area (Site 185). This small patch is of outstanding biogeographical significance. Note however, the extent of recent tree death. Buffalos are also incurring severe impact.

Plate 8: Death of a spring forest (Site 128). The photo is taken at the head of the spring, in the zone of seepage. The vine-forest has been replaced totally by paperbarks and Pandanus. Buffalo impact is savage.
Plate 9: Margin of Ballyangardy Spring (Site 169), showing occasional tree death and absence of regeneration.

Plate 10: Buffalo impact in the same patch. This very significant spring forest is seriously affected by buffalo.
Plate 11: The beginnings of the end for a patch of spring forest, Daly River area.

Plate 12: Margin of a floodplain forest which is retreating rapidly under buffalo impact.
Plate 13: A small spring forest at the base of the Mt. Broekman outlier (Site 52); retreating rapidly under buffalo and fire impact. In the absence of any management attention this forest will undoubtedly vanish.

Plate 14: Vine-forest vines and shrubs occurring on an escarpment talus slope under a eucalypt canopy. This situation is clearly maintained by recurrent fires.
Plate 15: Fine crop of native weeds (Triumfetta rhomboidea) which have penetrated semi-deciduous vine-forest largely as an effect of buffalo activity, Couramoul (Site 47).

Plate 16: Weeds (mainly the native, Cleome viscosa) where vine-forest once stood, Couramoul. Such growth provides a good light fuel. Vine-forest trees can be observed in the background.
Plate 17: Dense growth of the exotic weed 'Hyptis suaveolens' at the rapidly retreating margin of a small patch of semi-deciduous vine-forest, Kumunkuwi (Site 17).

Plate 18: The logical outcome of buffalo impact, weeds, and late dry season burning, Couramoul, (Site 48).
Plate 19: Exposed scrub-fowl incubation mound, Cannon Hill. The retreat of vine-forest is evident.

Plate 20: A similar situation, but on the margins of the South Alligator River floodplain, Kumunkuwi. Vine-forest vegetation occurs in the background. The retreat of this patch has occurred in the very recent past (see text).
3.0  FIRE IN THE PRESENT DAY

3.1  Introduction

That fire is exerting considerable pressure on many vine-forest margins at the present time is indicated in Tables 2(a) and (b). While this is commonly associated with disturbance induced by feral animals (e.g. exposed springs, seasonally dry lowland habitats); fire is also exerting pressure on many exposed patch boundaries in escarpment vine-forests, in the absence of other disturbance. While the evidence for this is considered in Section 3.3, it is useful first to put fire in ecological perspective by considering other determinants which affect the distribution of vine-forest.

3.2  The role of fire in relation to other ecological determinants

In Section 2 of the first part of this Report, it is concluded that the patchy distribution of vine-forest vegetation throughout the Top End, and the fragmentation of its constituent flora, is derived holocenotically, i.e. reflecting the interaction and concurrence of a variety of factors and processes through time. The following minimum set of historical factors and processes were identified as being contributive: long-term climatic deterioration and more recent oscillation; landscape fragmentation through deep weathering; episodic coastal/subcoastal landform evolution primarily in response to global sea-level changes; fire, including Aboriginal burning in localised situations; competition from other sclerophyll and graminoid floristic elements; and the adaptive responses of vine-forest taxa themselves (e.g. the high vagility of many species) in meeting such challenges. In the very recent past factors such as feral animals, exotic weeds and modern burning regimes (often in combination) have been contributive also. As such, fire is but one significant factor of a multi-factorial array.

While these factors will not be considered further here since they have been discussed at length elsewhere in this Report, it is necessary to pay brief attention to the properties of soils and substrates (i.e. edaphic conditions) on which regional vine-forests occur.

3.2.1  Edaphic conditions

(i)  Water balance

While it is commonplace to suggest that vine-forest vegetation attains its optimal expression in situations with a year-round water supply (e.g. springs), it does not necessarily follow that all vine-forest species require such conditions for growth, nor that the occurrence of vine-forest vegetation necessarily denotes the ready availability of water even at depth. Indeed, as indicated in Section 3.2 (first Report), many species and patches occur in situations where substrate water balance conditions are seasonally harsh.
To examine this, a study was conducted in which the internal water status of vine-forest plants was monitored through the 1983 dry season. Using a device known as a "pressure bomb", the internal water status may be measured by excising a leaf (or small leafy twig) and inserting it into a pressure chamber, leaving the cut end protruding from the chamber. With the application of pressure (from an attached nitrogen gas cylinder) at a slow and steady rate, an equilibrium is attained, where the internal pressure potential of water held in the xylem conduits of the leaf is said to equal that of the pressure chamber. At such an equilibrium, xylem water is extruded from the cut surface protruding from the chamber, and the equilibrium pressure is read off from a dial. This equilibrium pressure is known as the 'xylem pressure potential'.

The pressure bomb technique has a variety of applications in ecological investigation (see Ritchie and Hinckley 1975). For the purposes of the present study the pressure bomb was used mostly as an indirect means to assess the status of substrate moisture; in other words, to assess the availability of ground-water supply as plants themselves "see" it. Given that water is required by plants only during daylight hours for photosynthetic and transpirational purposes, it follows that, at night-time, the internal water status of plants should assume an equilibrium with that of the soil or substrate (i.e. the plant is not drawing on the soil). By measuring the xylem pressure potential (XPP) of plants before dawn, therefore, after they have had many hours to attain equilibrium with the substrate, it is assumed that the measurements so obtained provide a realistic expression of the status of substrate water availability.

Before considering some of the results of this study, one further point requires mention. In Figures 7, 8 and 9, it will be observed that XPP is given in units of - bars. The measurement of XPP as a negative pressure simply reflects that water held in xylem conduits of plants exists under tension or "suction", as opposed to an applied pressure (i.e. + bars).

In Figure 7, data are presented for the internal water status of two evergreen species over the course of a single day, at the height of the dry season. These species were sampled at two locations each, within a large patch of semi-deciduous vine-forest occurring on shelly beach sediments at Point Stuart. The first location concerned tall forest to 18 m, over relatively deep sediments. The second location concerned an almost completely deciduous forest to 10 m, over relatively shallow sediments, just behind the frontal dunes. For Capparis sepiaria (a thorny vine) on the relatively deeper sediments, it may be observed that at 4 a.m. the XPP of three individuals had a mean value of -18 ± 4 bars. Later in the day (1 p.m.) XPP drops to -39 bars, indicating that this species is photosynthetically active and drawing on substrate water supplies. After this time XPP increases (less negative) until, by 7 o'clock, equilibrium with the substrate is almost attained. For Capparis on the shallower sediments, it may be observed that this same trend is followed, only at consistently more negative XPP. The availability of substrate water in this latter situation then, is, as expected, relatively less favourable than in the deeper sediments. These same trends are observed with Celtis philippensis, a small evergreen tree.

* The range of XPP given here is derived statistically from the t-distribution. The values are, in fact, 95% Confidence Limits of the mean.
Figure 7: Measurements of xylem potential for two evergreen species, in two ecological situations at Point Stuart, October 10, 1983.
Plate 21: Semi-deciduous vine-forest on relatively deep shelly sediments; Point Stuart (Site 116). The photograph shows one of the sites chosen for study of XPP (see text).

Plate 22: Diffuse vine-thicket on granite rock outcrop, Goodparla (Site 129). Evergreen species were sampled here also for XPP. As might be expected the results indicated that water availability conditions in the late-dry season were xeric (i.e. very harsh). Many monsoon vine-forest species are tolerant of such conditions.
Of particular interest here however, is the magnitude of the predawn XPP. When it is considered that a well-watered garden soil has a pressure potential of around -2 bars, and that -15 bars is considered conventionally as the 'permanent wilting point', the values recorded here are exceedingly low (e.g. -47 ± 6 bars predawn for Celtis on the shallower sediments). Indeed, a third evergreen species sampled, Drypetes lasiogyna, started off before dawn at -62 ± 9 bars. Such values are more typical of arid zone plants. As well, when these same three species were sampled also on a granite outcrop at Goodparla, and on limestone karst near Katherine, the XPP responses were of similar magnitude. Quite clearly, these species are tolerant of seasonal drought. Furthermore, it follows that all the other species associated with them in these places are tolerant likewise. It is to be noted however, that most species growing under these conditions effectively avoid possible water stress through their deciduous habit.

In Figure 8, the pre-dawn XPP of a single species, Erythrophloeum chlorostachys (ironwood), occurring at two locations, is plotted at various intervals of the 1983 dry season. Figure 8(a) compares the XPP of ironwoods occurring in a deciduous vine thicket on top of a doleritic outcrop, with other individuals in the adjacent savanna. The rock outcrop concerned is near the abandoned Evelyn mine, north of Pine Creek. It may be observed that the XPP of individuals on the rock outcrop itself is consistently more negative than the XPP of individuals in the savanna. It follows therefore, that the vine thicket is occupying a situation relatively less favourable with respect to substrate water status than the areas immediately adjacent. The sharp improvement in water balance conditions evident in December is attributable to the onset of the wet season. The improvement evident in October however, is not easily explained.*

Figure 8(b) compares the predawn XPP of ironwoods occurring on three study plots at North Point, Kapalga. Plot B concerns the margin of a well-developed patch of semi-deciduous vine-forest adjacent the South Alligator River floodplain. Relative to plots C and D (in eucalypt forest at increasing distances from Plot B), the pre-dawn XPP of ironwood at Plot B indicates that this plot enjoys the most favourable substrate water status. Given that Plots C and D occur upslope, the occurrence of such relatively favourable conditions in Plot B is not surprising. However, when it is considered that vine-forest vegetation occurs at Evelyn where ironwoods in the same patch are registering pre-dawn XPP of -25 ± 1.5 bars, whereas at North Point the lowest value recorded is -13.5 ± 1 bar (Plot C), it presumably follows that substrate moisture status per se is not limiting the expansion of vine-forest at North Point.

A similar situation, but concerning an escarpment semi-deciduous vine-forest, is presented as Figure 9. This Figure compares the pre-dawn XPP of two species occurring inside a protected sandstone gorge at

*Ironwood is sometimes deciduous for very short periods in the late dry season (gurrung), quickly replacing old leaves. To support such growth one would assume that ironwoods would need to draw relatively heavily on substrate water supplies. Yet the pre-dawn XPP increases (i.e. is more positive) relative to earlier in the dry season. Detailed discussion of this phenomenon is, however, beyond the scope of this Report.
Figure 8: Pre-dawn measurements of xylem pressure potential for *Erythroploem chlorostachys* in two ecological situations.
Figure 9: Pre-dawn measurements of xylem pressure potential for two species on two study plots at Ngarradj Warde Djobkeng.
Ngarradj Warde Djokeng, with the same species on deep sands in nearby eucalypt forest. The course of predation XPP for each species in both these situations is very similar. As such, the restriction of vine-forest vegetation to the protected gorge must be attributable to some other factor.

11) Soil fertility

It is not my intention to discuss this at length since it is covered sufficiently elsewhere (Section 3.2, first Report). Suffice to say however, that, except in the case of organic rich soils such as occur with springs, and very localised occurrences of nutrient-rich parent materials (e.g. coastal chert, limestone), soils for the most part, acidic and very leached (see Aldrick 1976). Many vine-forest taxa therefore, do not exhibit any strict requirement for fertile soils. Rather, such fertility as does exist is mostly held in very shallow surface organic horizons (often < 5cm).

3.2.2 Resume

Given the wide range of substrates on which vine-forest vegetation occurs, and even more significantly, given that many species are tolerant of nutrient-poor and seasonally dry conditions, edaphic conditions per se are unlikely to exert any significant limiting influence on the distribution of vine-forests at the present time. An exception to this however, concerns vine-forests associated with rare perennially-wet habitats. In the general absence of such constraints it follows that fire, in combination with the competitive abilities of other floristic elements (e.g. eucalypts and grasses), is a determining factor of prime ecological significance.

3.3 Fire In Escarpment And Lowland Habitats

3.3.1 Escarpment vine-forests

Many exposed margins of escarpment vine-forests are being affected seriously by fire at the present time (see Table 2(a)). In many situations boundaries can be shown to be actively retreating. For example, burnt-out shells of vine-forest trees adjacent existing patches were observed in many, sometimes extensive, situations. In the course of this study only one instance was observed where the patch boundary could be shown, on structural grounds, to be expanding. This exception moreover, concerned but a portion of the boundary. The patch itself was as badly affected by fire as any seen (Site 162). Of the various habitat types of vine-forest, only those associated with topographically protected situations are incurring no significant impact.
As has been described elsewhere (Section 2.5, first Report), the fate of patch boundaries in most escarpment vine-forests is dependant on the adaptive traits of just one species, Allosyncarpia ternata. This evergreen tree is often the sole canopy species present and, as such, exerts a controlling influence on the subcanopy microclimate. It is tolerant of light fires given that it coppices readily; both as a tree or sapling. With increased fire severity however, saplings become susceptible given that regenerative tissues are held at, or just beneath, the soil surface. Mature trees also become susceptible in that they typically are piped by termites, and once fire enters through fire scars or other deformities are liable to smoulder for weeks or more. When individuals at the patch margin are killed by fire, the surrounding understorey and regeneration is exposed both to the full intensity of dry season conditions, as well as competition from invading grasses (e.g. the highly combustible spinifex grasses, Triodia and Plectrachne spp.), and other weedy types (e.g. Acacia spp., Triumfetta micrantha, Hibiscus spp., Cleome viscosa, and various legumes). If hot fires in the late dry season were to occur frequently, it is to be anticipated that exposed patch boundaries would recede rapidly.

A feature of these Allosyncarpia forests is the absence of any significant marginal vine-forest vegetation (ecotone) between the patch itself and the surrounding combustible vegetation (most commonly spinifex grasses). This is in marked contrast to seasonally lowland vine-forests where boundaries often comprise a profusion of shrubby vine-forest species which are tolerant even of frequent low intensity burning. In Allosyncarpia forests such an ecotone does not commonly occur. Tables 4(a) and (b) describe the occurrence of vine-forest seedlings and saplings along 8 transects which each run from under an Allosyncarpia forest canopy, across the margin, and into the surrounding vegetation. Table 4(a) describes the distribution of Allosyncarpia regeneration along these transects, and 4(b) the distribution of other vine-forest species. Each transect was sampled in the wet season at a time when the annual seed crops of Allosyncarpia and most other vine-forest species had germinated.

In Table 4(a) it may be observed that Allosyncarpia germinants are profuse under the closed canopy, much reduced in number at the margin, and are absent at distances greater than 2m from the parent canopy. Such a distribution is simply explained by the fact that the dry seeds of Allosyncarpia are relatively heavy and, as such, are dispersed only within the immediate vicinity of parent canopies. The distribution of Allosyncarpia seedlings/saplings, and the regeneration of other vine-forest species (Table 4(b)), observes the same pattern. Of note, however, is the occurrence of 2 Allosyncarpia saplings in the open (transect 2, Lightning Dreaming). These 2 individuals were clearly remnants of a former closed canopy given their occurrence beside a recently killed and fire-gutted large Allosyncarpia trunk.
TABLE 4
Potential recruitment of vine-forest species at the margins of four escarpment evergreen vine-forests dominated by Allosyncarpia ternata.

All data presented here collected in 1983/84 wet season. Data based on consecutive quadrats 1x2m² along transects at right angles to patch margins.

(a) Allosyncarpia ternata recruitment

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<td>Seedlings &lt;3cm DBH</td>
<td>No. of saplings</td>
</tr>
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</tr>
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<td>(iii) Oenpelli Rainforest</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>transect 1</td>
<td>53</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>transect 2</td>
<td>13</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>(iv) Djirrinbal Creek</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>transect 1</td>
<td>153</td>
<td>3</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>transect 2</td>
<td>78</td>
<td>2</td>
<td>10</td>
<td>0</td>
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</table>
### TABLE 4 (Continued)

(b) **Other vine-forest species recruitment**

<table>
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<th></th>
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<th>Edge of canopy</th>
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<tbody>
<tr>
<td></td>
<td>(0-5m)</td>
<td>(5-7m)</td>
<td>(7-50m)</td>
</tr>
<tr>
<td>No. of seedlings/saplings</td>
<td>No. of seedlings/saplings</td>
<td>No. of seedlings/saplings</td>
<td></td>
</tr>
<tr>
<td>No. of germinants &lt;3cm DBH</td>
<td>No. of germinants &lt;3cm DBH</td>
<td>No. of germinants &lt;3cm DBH</td>
<td></td>
</tr>
</tbody>
</table>

(i) **Mt. Howship**

<table>
<thead>
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<th>Transect</th>
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<th>Edge of canopy</th>
<th>In open</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transect 1</td>
<td>1 9 0 1 0 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transect 2</td>
<td>0 9 0 1 0 0</td>
<td></td>
<td></td>
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</tbody>
</table>

(ii) **Lightning Dreaming**

<table>
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<th>Transect</th>
<th>Under closed vine-forest canopy</th>
<th>Edge of canopy</th>
<th>In open</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transect 1</td>
<td>0 2 0 1 0 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transect 2</td>
<td>1 11 0 0 0 0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(iii) **Oenpelli Rainforest**

<table>
<thead>
<tr>
<th>Transect</th>
<th>Under closed vine-forest canopy</th>
<th>Edge of canopy</th>
<th>In open</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transect 1</td>
<td>0 2 0 1 0 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transect 2</td>
<td>4 14 1 4 0 0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(iv) **Djirrinbal Creek**

<table>
<thead>
<tr>
<th>Transect</th>
<th>Under closed vine-forest canopy</th>
<th>Edge of canopy</th>
<th>In open</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transect 1</td>
<td>4 6 1 0 0 0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transect 2</td>
<td>5 2 0 0 0 0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Given the low vagility of *Allosyncarpia* (i.e. its inability to disperse effectively much beyond the extent of the parent canopy), it may be appreciated that, in order for the patch margin to expand, seedlings at the margin have to be given the opportunity to reach sexual maturity, establish their own canopy, and the same process be repeated. When it is considered that sexual maturity is unlikely to be attained in less than 20 years*, it can be appreciated that expansion is a relatively slow process, requiring considerable periods of time in which hot fires do not occur.

At the present time however, hot fires lit in the late dry season are evidently occurring in the escarpment country at a high frequency (Day 1984; Helmut Schimmel pers. comm.). As is evident in the Landsat images of fire distribution mapped by Jon Day, such fires mostly originate in the south-east and arrive in Kakadu after having burnt-out considerable tracts of country on the way. This is corroborated by Helmut Schimmel, the lessee of Gimbat Station. Mr Schimmel recounts how, in the ten years or so he has held the Gimbat lease, *Callitris* populations on Gimbat have been decimated as a result of late dry season fires emanating from the direction of Katherine. While it is not known for how long this pattern of burning has existed, it is to be noted that such a burning pattern is unlikely to have operated under Aboriginal occupancy. Traditional informants (e.g. Nipper Kapirigi and George Mingam) recount that widespread burning in gurrung (the late dry season) was avoided, there being strict limitations put on the use of fire at this potentially hazardous time of year. Aboriginal burning practices will be considered in more detail, however, in Section 4.

While it is clear that the curtailment of such a burning pattern is dependant largely on the co-operation of people outside Kakadu, specifically to the south and south-east, it may be possible to restrict the impact of such fires as do occur by employing occasional aerial-ignition fuel-reduction burns in the early dry season. Although the development of an appropriate strategy is beyond the scope of the present Report, it is put as a suggestion that such burning could be most effectively deployed along the southern perimeter of the Park.

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*tthis is based on observations made from *Allosyncarpia* trees grown in suburban Darwin (Clyde Dunlop pers. comm.). Such observations furthermore, concern trees given every encouragement to grow. In natural situations, especially where water is seasonally scarce, the attainment of sexual maturity probably takes considerably longer.*
Plate 23: Looking onto the sharp and exposed boundary of a patch of *Allosyncarpia* forest. Note that the patch is surrounded by weedy species (e.g. *Acacia aulacocarpa*, *Grevillea pteridifolia*).

Plate 24: The same patch looking out. Note how the vine-forest understorey (comprising mainly *Allosyncarpia* coppice) stops abruptly at the edge of the canopy.
Plate 25: The retreating margins of an escarpment Allosyncarpia forest. The dead stems in the middle of the photo are mostly Callitris intratropica. Note how a large Allosyncarpia individual in the right foreground is isolated from the patch proper.

Plate 26: A closer view of a similar situation to that above. The main patch is in the background. Isolated individuals of Allosyncarpia are regenerating from coppice in the foreground.
Plate 27: Lightning-strike in dense Allosyncarpia forest. Such fires do not go far. The blurred vine in the bottom right of the picture is Muehlenbeckia rhyticarya, one of the few species in these forests which acts as a fire-weed.

Plate 28: Germinating seeds of Allosyncarpia ternata. Note the relatively large size. Given that the fruits are of a dry capsular type, they are not dispersed by birds. The inability of Allosyncarpia to disperse seeds more than 1-2m beyond the extent of the parent canopy has manifold ecological consequences (see text).
Plate 29: *Allosyncarpia* seedlings. Note the capacity for coppice in this species (i.e. 3 of the seedlings shown are clearly multi-stemmed). Such capacity enables *Allosyncarpia* seedlings to resprout after light fires. With hot fires however, this capacity is negated by the death of regenerative tissues held at, or just beneath the soil surface.

Plate 30: An *Allosyncarpia* sapling showing the largely lateral disposition of roots (thus easily damaged by buffalo compaction) and a former aerial shoot. In no regenerating individuals examined was there evidence of the production of rhizomes; i.e. *Allosyncarpia* does not reproduce vegetatively. As such it is totally dependant on the recruitment of canopy individuals from seed.
3.3.2 Lowland vine-forests

Most lowland vine-forest patches are being affected by fire similarly at the present time (Table 2(b)). As discussed in Section 2.4.2(ii) (this report) such impact is often promoted by the activities of feral animals.

In contrast to the typical escarpment vine-forest situation however, patch margins are often buffered to some extent by shrubby ecotones. The species which comprise these ecotones are characterised by a relative tolerance of even frequent light burns. In Table 5 is presented data concerning the occurrence of vine-forest seedlings/saplings along two narrow transects extending 70m from a patch margin into eucalypt forest savanna. It may be observed that considerable potential for recruitment of vine-forest species exists even 10-20m from the patch margin, with occasional individuals scattered as far as 50-70m. It may be anticipated furthermore, that, in the absence of disturbance, this boundary would be likely to develop rapidly. While this boundary (Site 3, Field Island; see Section 2.3.2(i)) is somewhat exceptional in the Kakadu region given that it is developing in the absence of feral animals or a recent history of frequent late dry season burning, it exemplifies the contrast which exists between escarpment and lowland seasonally dry vine-forest margins. The ecological significance of bird and wind dispersal agencies vis-a-vis dispersal by gravity (as in Allosyncarpia) is indicated also.

Despite this relative tolerance of fire exhibited by many species occupying the margins of lowland patches however, it is evident that patch margins have receded in the recent past (see Section 2.4.3, this Report). While this is attributable in part to feral animals, it is clear that relatively hot fires lit late in the dry season are responsible also (see also Day 1984, Hoare et al. 1980). Such observations reinforce the need to undertake early dry season fuel reduction burns so as to mitigate against impacts incurred by late dry season fires.
TABLE 5

Potential recruitment of vine-forest species in eucalypt woodland adjacent an incipient patch of semi-deciduous vine-forest, Field Island.

Data collected June and October 1983. Data based on alternate quadrats of 2x2m², along two transects at right angles to the patch margin.

<table>
<thead>
<tr>
<th>Species</th>
<th>0-10m²</th>
<th>10-20m²</th>
<th>50-70m²</th>
<th>Dispersal agent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ampellocissus acetosa</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>Bird</td>
</tr>
<tr>
<td>Breynia cernua</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>Bird</td>
</tr>
<tr>
<td>Bridelia tomentosa</td>
<td>12</td>
<td>0</td>
<td>2</td>
<td>Bird</td>
</tr>
<tr>
<td>Dioscorea bulbifera</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>Wind</td>
</tr>
<tr>
<td>D. transversa</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>Wind</td>
</tr>
<tr>
<td>Drypetes lasiogyna</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>Bird</td>
</tr>
<tr>
<td>Exocarpus latifolius</td>
<td>2</td>
<td>7</td>
<td>0</td>
<td>Bird</td>
</tr>
<tr>
<td>Glochidion macroporum</td>
<td>5</td>
<td>1</td>
<td>0</td>
<td>Bird</td>
</tr>
<tr>
<td>Micromelum minutum</td>
<td>3</td>
<td>13</td>
<td>0</td>
<td>Bird</td>
</tr>
<tr>
<td>Popowia australis</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>Bird</td>
</tr>
<tr>
<td>Pouteria sericea</td>
<td>6</td>
<td>11</td>
<td>0</td>
<td>Bird</td>
</tr>
<tr>
<td>Premna obtusifolia</td>
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<td>Bird</td>
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<td>Secamone elliptica</td>
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<td>Smilax australis</td>
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<td>1</td>
<td>0</td>
<td>Bird</td>
</tr>
<tr>
<td>Sterculia quadrifida</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>Bird</td>
</tr>
<tr>
<td>Trema aspera</td>
<td>15</td>
<td>2</td>
<td>2</td>
<td>Bird</td>
</tr>
</tbody>
</table>

1 Total area sampled = 24m²
2 Total area sampled = 16m²
3 Total area sampled = 80m²
Burning practices and the significance of vine forests in traditional Aboriginal economy

4.1 Burning practices in prehistorical perspective

Aspects of traditional Aboriginal burning practice in the Kakadu region have been discussed at length in Section 2.5 (first Report). For the purposes of the present Report however, some of that material is repeated here.

As is now well documented, continuous Aboriginal occupation of the region spans some 20,000 years at least (see Jones 1984 a, b; Kamminga and Allen 1973). For much of this period however, human population densities are likely to have been low; such occupation as occurring being, perhaps, sporadic and seasonal (Jones 1984 b). From about 2000 years B.P.* there are good indications to suggest that human populations began to increase dramatically; such increase being a response to the increased productivity of the region associated with the evolution of freshwater wetlands (Jones, ibid).

While burning of "country" is likely to have been undertaken throughout the period of Aboriginal occupancy, it is to be anticipated that the pattern and extent of burning is likely to have changed through time in response to changing ecological conditions. Thus, for example, the spatial pattern and extent of annual burning at the time of European contact, is unlikely to have been practised before the mid to late Holocene at most. It is only during this period that ecological resources similar to those occurring today have existed (see Jones 1984 b for development of this theme).

Furthermore, the evolution of extensive, freshwater wetland resources is likely to have involved significant changes to the seasonal movement and distribution of human populations in the landscape. The Badmaadi Clan serves as a good illustration for this. From their home base in Deaf Adder Gorge, Nipper Kapirigi relates how, at the end of the wet season (say banggerreng), his people would often move through the escarpment country, arriving in the Cannon Hill region commonly in the late dry season ("half gurrung"). From there, they, with many other peoples, would detamp to the South Alligator River floodplains for the late dry (gurrung), to avail themselves of abundant animal and plant resources, and water. With the arrival of the rains (gunumeleng) the clans would disperse to their wet season camps, the Badmaadi mob returning to the escarpment. Clearly, such patterns of seasonal movement and population distribution are unlikely to have occurred prior to the creation of the wetlands.

*before the present.
The point I simply wish to make from these examples is that patterns of human movement and distribution which existed at the time of European contact, pertain to only a relatively short period of Aboriginal occupancy. The spatial pattern and scale of traditional burning of country, has undoubtedly changed much through time.

4.2 Seasonality of burning

Through the course of a single year, traditional burning of country followed a relatively set pattern*. The essential elements of this are outlined in Figure 10 (see also Section 2.5, first Report). Commencing with the end of the wet season, at around Banggerreng, burning was undertaken in the vicinity of wet season camp-sites wherever grasses were sufficiently cured to carry a slow and cool fire. Such fires did not travel far. As people increasingly began to move around their country, "cleaning up" by burning was undertaken as a matter of course. By yekke, and through wurrgeng, burning could be undertaken in earnest given the cured state of most grasses. Fires were lit in the late morning (after the dew had evaporated) and would burn all day until nightfall. At night such fires would die out naturally as a consequence of the precipitating dew. By wurrgeng, areas burnt earlier in the season could often be burnt again - given the moisture still available in the ground to promote post-fire regeneration. The burning of floodplains occurred at this time. The ecological result of this early dry season 'pyromania' was that it created a mosaic of burnt and unburnt country (see Haynes, 1983).

Also at this time people in the escarpment would deploy fire to hunt kangaroos. Such fire drives were extremely well-planned affairs involving up to a dozen or so men. The basic procedure was to choose a small isolated hill (or hills), or patch of vine-forest ("anngarrey" in Mayial), and encircle it with a slow-burning fire. Kangaroos so entrapped would be forced to seek refuge from the flames on top of the central hill, or in the anngarrey. These could then be killed by hunters already stationed there. Such drives evidently were not undertaken by people who resided in some lowland areas (e.g. Bunidj country: pers. comm. Little Dolly and Bill Neidji).

In gurrung however, unrestricted burning ceased. A number of stated reasons were involved in this. Fires lit at such time have the potential to burn out vast tracts of country; such as happens in the present day (see Section 3.3.1, this Report). Given that dew is absent at this time of year, such fires are not extinguished at night - in fact they may be inflamed by the "salt water" wind, mapili. As such, gurrung fires may burn for a week or more, even trickling through fallen leaves on previously burnt patches. Not only may such a fire burn out your own camp (as well as near and distant neighbours) but, even more significantly, it destroys the food resources of important game species** (e.g. macropods) over a

* the following description is based on a number of oral sources, especially the knowledge of Nipper Kapirigi.

** also, by razing the ground-cover, yams and other vegetable foods are less easily obtained.
Figure 10: Seasonal calendar for Western Arnhem Land region in Mayiali/Kundjehmi and Gumwinngi languages showing main burning periods.

(Adapted from 'Seasonal calendar of Kakadu region'; Alderson, Gangali and Haynes, 1979).
vast area. The lighting of fires in gurrung, therefore, was undertaken with great circumspection. Fires could be lit however, where an area was topographically enclosed by rock and/or streams; i.e. where there was no possibility for fire escaping. Even here, however, an added problem concerns the ability of karrkayin, the chicken-hawk, to take up burning twigs and spread fire into other areas.

With the onset of the first rains in gumaeleng, such restrictions were lifted, and light burning was undertaken in much the same manner as occurred in yekke. Even in the wet season (gudjewk) burning was undertaken where possible; such burning being restricted to occasional dry periods. These fires never travelled far however.

Given that a highly seasonal climate has prevailed in this region throughout the period of Aboriginal occupancy (see Section 2.3, first Report), it may be anticipated that traditional burning practices have followed essentially the same seasonal pattern as that outlined here over a very long span of time. Such fire seasonality contrasts strongly, furthermore, with the seasonal pattern of fires under what may be termed the natural fire regime (see Section 2.5, first Report).

4.3 Aboriginal occupancy and vine-forests

While the effect(s) of Aboriginal burning on vine-forests over long spans of time is to some extent an academic question; an understanding of the factors which contribute to the present distribution of this vegetation is clearly useful. As such, throughout the two parts of this Report I have endeavoured to present a perspective in which the contribution of individual factors can be assessed in relation to the whole. These thoughts in mind, I conclude this discussion with an assessment of the status of Kakadu vine-forests through the period of Aboriginal occupancy. This is undertaken with reference to three periods of time: the recent, historical past; the Holocene; and beyond.

4.3.1 The recent past

Many vine-forest patches in the recent past have taken a battering. This applies especially to patches in topographically exposed situations. A primary contributory factor is the impact of feral animals, buffalo especially. These animals destroy the integrity of margin vegetation, disperse and promote the growth of weedy species (both natives and exotics) and, as a consequence of these activities, promote the impact of fire. Also, as indicated by the recent contraction of escarpment vine-forests where feral animal impact is non-existent, late dry season fires (i.e. in gurrung) are currently exerting a destructive influence on many patch boundaries.
4.3.2 The Holocene (i.e. the past 10,000 years)

(i) Lowland vine-forests

On the basis of the occurrence of lowland vine-forest on, or associated with Holocene landforms, it is likely that much of this vegetation is of relatively recent origin. For the most part such vegetation comprises taxa widespread in other coastal regions. Exceptions to this probably concern Ballyangardy spring, a small vine-thicket on a topographically-protected rock outcrop on Goodparla (Site 129), and at least some taxa at Nourlangie Camp (e.g. Callitris intratropica, Schizaea dichotoma). It is problematic whether the rising sea drowned possible riparian vine-forests associated with former river valleys.

There is no evidence to suggest that lowland vine-forests have been significantly more extensive within the Holocene than they are at present. Given the widespread occurrence of scrub fowl incubation mounds in these vine-forests, it may be assumed that broad-scale elimination of jungle habitats in the Holocene would leave some conspicuous evidence. There is no evidence for such broad-scale elimination. Rather, exposed mounds are known to occur only in a small number of localised situations - and at least some of these, it may be recalled, are a legacy of the historic past (see Section 2.4.3):

 Against this background it is improbable therefore, that Aboriginal burning has contributed significantly to the distribution of lowland vine-forest as witnessed today. Rather, it is evident that such vegetation has expanded in the Holocene. However, with a dramatic increase in human populations in the past 2,000 years or so, it is possible that such vegetation has come under increased burning pressure in localised situations. For example, when Little Dolly was asked whether people traditionally burnt angarrey at Bindji Bindji*, she responded: "of course; make'm open place, good place for camping".

(ii) Escarpment vine-forests

In contrast to lowland vine-forests, those in the escarpment comprise many species with widely disjunct population distributions (especially with other sandstone surfaces in the Top End, and northern Queensland). As well, the major canopy species in the majority of these forests, Alliosyncarpia ternata, has but a limited capacity to disperse (see Section 3.3.1). The patchy distribution of this vegetation is thus remnant of a former expanse.

* a favoured Bunitj clan camping area, both in the wet season and intermittently through the dry.
Given the evident tolerance of *Allosyncarpia* to harsh conditions (e.g. its occurrence on bare sandstone pavement at Gimbat, Site 133), it is probable that fire has been the major factor contributing to its relative demise. Its occurrence mainly in deeply dissected (i.e. topographically protected) terrain indicates this also.

The impact of Aboriginal burning on the greater expanse of this vegetation is not known. Certainly, in localised situations there is good, albeit indirect evidence to indicate that patch boundaries were at least maintained by Aboriginal fires (see Section 2.5, first Report). The use of isolated anngarrey in macropod fire drives is of relevance here also.

4.3.3 Beyond the Holocene

A first constraint is that the actual period of Aboriginal occupancy is unknown. For the demonstrated period of occupancy however (i.e. ca. 20,000 years), it is possible to make three general observations. The first is that the distribution of vine-forests associated with perennial spring habitats is unlikely to have been affected significantly by burning, Aboriginal or otherwise. Even in the relatively favourable climatic conditions of the present, potential habitats are rare. The patchy distribution of this vegetation is better attributed to the paucity of available habitat. Secondly, seasonally dry lowland vine-forests are unlikely to have been affected significantly either, given that the great majority of such vegetation did not exist. The coastline at the height of the last glacial period was some 300 km distant; the climate probably similar to that of Tennant Creek at the present day (e.g. Jones 1984 b, Schrire 1983: 7-8). And thirdly, seasonally dry forest in the escarpment would have been at its most vulnerable to fire given these postulated climatic conditions. The impact of fire at this time is not known.

Factors contributing to the fragmentation of vine-forests in the Top End at larger scales of time are discussed in Section 2 (first Report).

4.4 The significance of vine-forests in traditional Aboriginal economy

While it is evident from my interactions with local Aboriginal people that anngarrey constitute "special place", they existed also as an economic resource. In this latter context, anngarrey formed but one component of the greater landscape.

In Appendix 4 is presented a list comprising the Aboriginal names of plants and their uses. In Appendix 5, plants used traditionally in material culture are listed in their various categories of usage. Information concerning the distribution of food plants in 3 categories of habitat is summarised in Figure 11.

* this does not mean however, that anngarrey has its own djang (or "dreaming") - at least in Kakadu (N. Kapirigi pers. comm.). Certain anngarrey occur associated with places of djang however.
In part (a) of this Figure it may be observed that vine-forests provide an important source of fruits, especially around the time of the wet season (i.e. gudjewk/banggefreng and gunumeleng). None of these fruits however acted as a staple food, their being utilised more as "snacks" as described by Thomson (1949) for eastern Arnhem Land. Furthermore, only two plants in this fruit/seed category are known to have been utilised in sufficient quantity to be considered staples. Both these species, the grasses Oryza perennis and Panicum paludosum, occur in freshwater wetland habitats and were utilised in the late wet and early dry. The mature inflorescences were collected, dried in the sun, and then threshed to obtain the seeds. These were then ground in stone grinding hollows, and the resulting flour used to make dampers. Given the very sporadic occurrence of cycads in the Kakadu region, cycad "fruits" did not form an important part of late dry season (gurrung) diet as in eastern Arnhem Land (Thomson 1949).

In part (b) of this Figure it may be observed that vegetable foods constituted a significant part of people's diets through all seasons of the year. Yams were by far the most important vegetable foods. In the early part of the year (gudjewk through wurrgeng) the most important sources for yams were vine-forest habitats. Four principal species were utilised: Amorphophallus campanulatus, A. galbra, Dioscorea bulbifera, and D. transversa. From gurrung through gunumeleng vegetable gathering was focused mostly on remaining inundated areas of the floodplains. At this time rushes (Eleocharis spp.) and water lilies (Nelumbo nucifera, Nymphaea spp. and Nymphoides spp.) provided the main bulk of vegetable foods. The parts of these plants used as food, and methods of preparation, are outlined in Appendix 4. In passing it is observed that, as described by Thomson (1949) for eastern Arnhem Land, the occurrence of tarot (Colocasia esculenta) in the Kakadu region is both rare and highly localised. As such it is unlikely that tarot constituted a staple food in this region.

While this account is necessarily brief, it serves to illustrate that, despite the relative scarcity of such vegetation, vine-forests constituted a major seasonal source of plant foods for Aboriginal people. It is noted however that vine-forests did not constitute a major source of animal foods. Such few animal foods as were taken comprised possums, scrub fowl, and scrub fowl eggs in gunumeleng.

As for other aspects of material culture, vine-forests constituted major sources of hard and soft woods for the manufacture of implements and dug-out canoes, binding cord, and ceremonial paints (see Appendices 4 and 5).
Figure 11: Seasonal usage of food plants in three broad habitat types.
5.0 RECOMMENDATIONS

On the basis of preceding discussion it is concluded that vine-forests in the Kakadu region are being affected seriously by feral animals and late dry season fires at the present time. The only exceptions to this concern patches occupying topographically protected situations. The damage incurred by vine-forests clearly has accelerated within the time-span of Europeans' involvement in the region. Vine-forests continue to be affected despite the demonstrated general effectiveness of management prescriptions currently employed in Kakadu. To effectively conserve vulnerable vine-forest patches it is evident that further measures are required. To this end the following recommendations have been made in preceding discussion:

1. (pages 18-20)

The elimination of feral animals is a fundamental priority. Given that the current eradication programme is unlikely to curb destruction of many biogeographically outstanding and fragile patches (especially those associated with topographically exposed springs), consideration should be given to fencing biogeographically outstanding and threatened patches as a matter of urgency. To this end, two patches in particular have been designated as warranting immediate attention (Sites 169 and 185). As well as these, many others are in a very degraded and threatened state. Given the considerable costs involved in fencing isolated, individual situations, consideration should be given to fencing relatively large areas followed by desocking.

2. (page 20)

In order to identify biogeographically outstanding and threatened patches requiring management attention it is recommended that further ecological survey work be undertaken. In undertaking this, priority should be given to the investigation of topographically exposed spring habitats.

3. (pages 26-27)

While the impact of late dry season fires often is promoted by feral animal activities, fire is also exerting pressure on many exposed patch boundaries in the absence of such disturbance. It is suggested that consideration be given to undertaking early dry season burning along the southern perimeter of the Park to help protect escarpment vine-forests and other vegetation types from fires emanating from the south-east. Similar principles apply to the protection of lowland vine-forest patches. Fuel-reduction burning in gurrung is, of course, to be avoided.

4. (pages 19-20)

Three biogeographically outstanding patches are identified as requiring management attention on the basis of their sensitivity to either actual or potential visitor usage. Two of these patches are currently included in Kakadu; a small seepage forest near the Nourlangie Rock gallery (Site 9), and Radon Springs (Site 15). To protect the former situation with its associated specialised flora, it is recommended that it be fenced-
off with wooden railings. Consideration should be given to providing above-ground walkways in the Radon Springs forest, especially in sections where ground seepage occurs. Adequately protected moreover, this forest would provide an excellent interpretative destination.

As well as these situations, consideration should be given to assisting CSIRO protect major patches in the northern sector of Kapalga. Similarly, there is an urgent requirement for protection of biogeographically outstanding patches and regions on both Gimbat and Goodparla.

5. (page 17)

The planting of exotic species which are genetically related to native weedy types should be prevented.

Further to the above, two other recommendations are made here:

6. Given the evident detrimental significance of much disturbance, it is recommended that, wherever possible, tracks or roads which currently cut through patches be rerouted. A minimum distance of 50 m from patch margins is recommended.

7. As an aid to the rehabilitation of seriously-affected patches, consideration should be given to the planting of fast-growing endemic vine-forest species, especially those which throw dense shade. This would facilitate the early elimination of fire-promoting weeds. A useful species furthermore would be one with bird-attracting fruits. The choice of suitable species should be made to fit the particular conditions of each situation. As such, a list of potential species is not appropriate here. Professional advice in these matters is readily available locally (e.g. the Darwin Botanical Gardens, the N.T. Herbarium).
6.0 ADDITIONAL REFERENCES

The references listed here are only those not given in Part 1 of this Report.

DAY J.C., 1984

A report on the effects of fire in tall open forest and woodland with particular reference to fire management in Kakadu National Park in the Northern Territory. Unpub. Report to A.N.P.W.S.

JONES R., 1984(a)

JONES R., 1984(b)
Archaeological conclusions and recommendations for archaeological site management in Kakadu National Park. Prelim. draft of a chapter in the Final Report of the Kakadu Archaeological Consultancy.

THOMSON D.F., 1949
ACKNOWLEDGEMENTS

A great many people have contributed to the undertaking of this study, and to them all I extend my appreciation. I trust I will be forgiven if I single out, for special thanks, the inhabitants of East Alligator Ranger Station and the staff of the N.T. Herbarium. As well, I wish to acknowledge here the assistances provided me by Terry Baldwyn, Lindsay Barnett, Alex Carter, Géorgé Chaloupka, Sandra Cousins, Ken and Betty Couzens, Lyn Craven, Joy Djolom, Clyde and Adi Dunlop, Cliff Ellis, Stan Fisher, Malcolm Forbes, Judith Gallen, Danny Gillespie, Talking Billy Gunbunuka, Chris Haynes, Geoff Hope, Rhys Jones, Nipper Kapirigi, Hank Lewis, Dave Lindner, Diane Lucas, Greg and Jane Miles, George Mingam, Ian Morris, Rob Muller, Bill Neijji and his family, Des Pike, Sue Medway, Coleen Pyne, Mike Ridpath, Helmut and Joy Schimmel, Keith Taylor, Helen Thomson, Len Web, Glen Whishman, Penny Wilkins and Genesse Winch.

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Finally, the preparation of this Report could only have been made possible by the generous assistances of Val Lyon, Susan Clarke and Bob Dowhy.

To all these people, and many others not mentioned, thank-you.
APPENDIX 1:

SITE LOCATIONS FOR THE ECOLOGICAL SURVEY OF MONSOON VINE-FOREST VEGETATION IN KAKADU NATIONAL PARK
<table>
<thead>
<tr>
<th>SITE NO.</th>
<th>SITE NAME</th>
<th>GRID REFERENCE</th>
<th>LONG.</th>
<th>LAT.</th>
<th>LOCATIONAL NOTES</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Koongarra I</td>
<td>5472 682 793</td>
<td>132 52</td>
<td>12 51</td>
<td>1 km NW Koongarra Saddle.</td>
</tr>
<tr>
<td>2</td>
<td>Koongarra II</td>
<td>5472 682 787</td>
<td>132 52</td>
<td>12 51</td>
<td>0.5 km NW Koongarra Saddle.</td>
</tr>
<tr>
<td>3</td>
<td>Field Island</td>
<td>5472 679 592</td>
<td>132 55</td>
<td>12 07</td>
<td>Behind landing beach on SE.</td>
</tr>
<tr>
<td>4</td>
<td>Baralba Springs I</td>
<td>5472 705 810</td>
<td>132 52</td>
<td>12 50</td>
<td>Along creek in escarpment.</td>
</tr>
<tr>
<td>5</td>
<td>Baralba Springs II</td>
<td>5472 700 810</td>
<td>132 53</td>
<td>12 50</td>
<td>Along creek 1 km W of Site 5.</td>
</tr>
<tr>
<td>6</td>
<td>Anbangbang</td>
<td>5472 625 767</td>
<td>132 49</td>
<td>12 52</td>
<td>Around Anbangbang excavation.</td>
</tr>
<tr>
<td>7</td>
<td>Nourlangie Camp I</td>
<td>5472 450 884</td>
<td>132 49</td>
<td>12 52</td>
<td>Small spring 500 m from Site 7 (West).</td>
</tr>
<tr>
<td>8</td>
<td>Anbangbang Spring</td>
<td>5472 628 769</td>
<td>132 58</td>
<td>12 25</td>
<td>Floodplain forest.</td>
</tr>
<tr>
<td>9</td>
<td>Radon Gorge I</td>
<td>5472 723 892</td>
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<td>12 45</td>
<td>0.5 km NW Nourlangie Camp (CSIRO plots).</td>
</tr>
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<td>10</td>
<td>Radon Gorge II</td>
<td>5472 725 888</td>
<td>132 53</td>
<td>12 45</td>
<td>0.5 km S Nourlangie Camp.</td>
</tr>
<tr>
<td>11</td>
<td>Radon Gorge III</td>
<td>5472 728 891</td>
<td>132 53</td>
<td>12 45</td>
<td>Along creek in middle of gorge.</td>
</tr>
<tr>
<td>12</td>
<td>Radon Gorge IV</td>
<td>5472 729 890</td>
<td>132 53</td>
<td>12 45</td>
<td>Edge of Creek in middle of gorge.</td>
</tr>
<tr>
<td>13</td>
<td>Kumunkuw I</td>
<td>5472 336 813</td>
<td>132 52</td>
<td>12 49</td>
<td>Forest behind Kumunkuwi occupation site.</td>
</tr>
<tr>
<td>14</td>
<td>Kumunkuw II</td>
<td>5472 332 812</td>
<td>132 52</td>
<td>12 49</td>
<td>Site along flood plain edge 2 km N site 17.</td>
</tr>
<tr>
<td>15</td>
<td>Jim Jim I</td>
<td>5471 655 315</td>
<td>132 50</td>
<td>13 16</td>
<td>Along creek on N side of gorge.</td>
</tr>
<tr>
<td>16</td>
<td>Jim Jim II</td>
<td>5471 650 310</td>
<td>132 50</td>
<td>13 15</td>
<td>Along small creek on S side of gorge.</td>
</tr>
<tr>
<td>17</td>
<td>Goose Camp I</td>
<td>5472 380 904</td>
<td>132 35</td>
<td>12 44</td>
<td>Edge of floodplain.</td>
</tr>
<tr>
<td>18</td>
<td>Goose Camp II</td>
<td>5472 382 902</td>
<td>132 35</td>
<td>12 44</td>
<td>Edge of floodplain.</td>
</tr>
<tr>
<td>19</td>
<td>Deaf Adder I</td>
<td>5471 683 537</td>
<td>132 52</td>
<td>13 05</td>
<td>Creekline at S entrance to Deaf Adder.</td>
</tr>
<tr>
<td>20</td>
<td>Deaf Adder II</td>
<td>5471 683 533</td>
<td>132 52</td>
<td>13 05</td>
<td>0.5 km S of Site 24.</td>
</tr>
<tr>
<td>21</td>
<td>Deaf Adder III</td>
<td>5471 681 537</td>
<td>132 52</td>
<td>13 05</td>
<td>0.5 km W of Site 24.</td>
</tr>
<tr>
<td>22</td>
<td>Deaf Adder IV</td>
<td>5471 768 480</td>
<td>132 57</td>
<td>13 08</td>
<td>2 km SE of Djuwa waterhole.</td>
</tr>
<tr>
<td>23</td>
<td>Deaf Adder V</td>
<td>5471 795 473</td>
<td>132 58</td>
<td>13 08</td>
<td>4 km SE of Djuwa waterhole.</td>
</tr>
<tr>
<td>24</td>
<td>Deaf Adder VI</td>
<td>5471 810 555</td>
<td>132 59</td>
<td>13 04</td>
<td>Creek line flowing from Ywingiyi.</td>
</tr>
<tr>
<td>25</td>
<td>Deaf Adder VII</td>
<td>5471 810 560</td>
<td>132 59</td>
<td>13 04</td>
<td>Entrance to Ywingiyi.</td>
</tr>
<tr>
<td>26</td>
<td>Deaf Adder VIII</td>
<td>5471 750 497</td>
<td>132 56</td>
<td>13 06</td>
<td>Along Djuwa.</td>
</tr>
<tr>
<td>27</td>
<td>Deaf Adder IX</td>
<td>5471 763 495</td>
<td>132 56</td>
<td>13 06</td>
<td>0.5 km SW from Djuwa campsite.</td>
</tr>
<tr>
<td>28</td>
<td>Deaf Adder X</td>
<td>5471 690 557</td>
<td>132 52</td>
<td>13 04</td>
<td>Along Deaf Adder Creek at entrance to gorge.</td>
</tr>
<tr>
<td>29</td>
<td>Deaf Adder XI</td>
<td>5471 690 498</td>
<td>132 54</td>
<td>13 07</td>
<td>1 km SW of Nauwalabila.</td>
</tr>
<tr>
<td>30</td>
<td>Deaf Adder XII</td>
<td>5471 672 498</td>
<td>132 54</td>
<td>13 07</td>
<td>0.5 km N of site 34.</td>
</tr>
<tr>
<td>31</td>
<td>Deaf Adder XIII</td>
<td>5471 731 495</td>
<td>132 56</td>
<td>13 07</td>
<td>Spring 0.5 km SW of Nauwalabila.</td>
</tr>
<tr>
<td>32</td>
<td>Deaf Adder XIV</td>
<td>5471 768 495</td>
<td>132 56</td>
<td>13 07</td>
<td>1 km SW of Djuwa camp.</td>
</tr>
<tr>
<td>33</td>
<td>Little Nourlangie Rock</td>
<td>5472 600 775</td>
<td>132 47</td>
<td>12 51</td>
<td>North Western edge.</td>
</tr>
<tr>
<td>34</td>
<td>Cooinda</td>
<td>5472 326 736</td>
<td>132 32</td>
<td>12 53</td>
<td>1.5 km N Cooinda airstrip.</td>
</tr>
<tr>
<td>35</td>
<td>Baralba Springs III</td>
<td>5472 690 808</td>
<td>132 53</td>
<td>12 50</td>
<td>Out on sand sheet along creek.</td>
</tr>
<tr>
<td>36</td>
<td>Baralba Springs IV</td>
<td>5472 696 807</td>
<td>132 53</td>
<td>12 50</td>
<td>Escarpment surrounding creek.</td>
</tr>
<tr>
<td>37</td>
<td>The Flats</td>
<td>5472 290 863</td>
<td>132 30</td>
<td>12 47</td>
<td>Laterite promontory 8 km due N Leichhardt bill.</td>
</tr>
<tr>
<td>SITE NO.</td>
<td>SITE NAME</td>
<td>MAP NO.</td>
<td>X</td>
<td>Y</td>
<td>LONG.</td>
</tr>
<tr>
<td>---------</td>
<td>-------------------------</td>
<td>---------</td>
<td>------</td>
<td>------</td>
<td>-------</td>
</tr>
<tr>
<td>43</td>
<td>Flats Island</td>
<td>5472</td>
<td>32</td>
<td>860</td>
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</tr>
<tr>
<td>44</td>
<td>Malangganbalk I</td>
<td>5472</td>
<td>312</td>
<td>912</td>
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</tr>
<tr>
<td>45</td>
<td>Malangganbalk II</td>
<td>5472</td>
<td>258</td>
<td>912</td>
<td>132 31'</td>
</tr>
<tr>
<td>46</td>
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<td>5472</td>
<td>310</td>
<td>918</td>
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<tr>
<td>47</td>
<td>Couramoul I</td>
<td>5472</td>
<td>322</td>
<td>970</td>
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</tr>
<tr>
<td>48</td>
<td>Couramoul II</td>
<td>5472</td>
<td>329</td>
<td>969</td>
<td>132 32'</td>
</tr>
<tr>
<td>49</td>
<td>South Alligator Inn I</td>
<td>5372</td>
<td>268</td>
<td>977</td>
<td>132 29'</td>
</tr>
<tr>
<td>50</td>
<td>South Alligator Inn II</td>
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<td>263</td>
<td>980</td>
<td>132 29'</td>
</tr>
<tr>
<td>51</td>
<td>Ybooyok I</td>
<td>5472</td>
<td>737</td>
<td>817</td>
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<tr>
<td>52</td>
<td>Ybooyok II</td>
<td>5472</td>
<td>738</td>
<td>814</td>
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<tr>
<td>53</td>
<td>Ybooyok III</td>
<td>5472</td>
<td>768</td>
<td>838</td>
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</tr>
<tr>
<td>54</td>
<td>Ybooyok IV</td>
<td>5472</td>
<td>762</td>
<td>841</td>
<td>132 56'</td>
</tr>
<tr>
<td>55</td>
<td>Ybooyok V</td>
<td>5472</td>
<td>715</td>
<td>792</td>
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</tr>
<tr>
<td>56</td>
<td>Ngarradj I</td>
<td>5473</td>
<td>739</td>
<td>204</td>
<td>132 55'</td>
</tr>
<tr>
<td>57</td>
<td>Barramundie Creek I</td>
<td>5371</td>
<td>215</td>
<td>246</td>
<td>132 26'</td>
</tr>
<tr>
<td>58</td>
<td>Barramundie Creek II</td>
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<td>221</td>
<td>250</td>
<td>132 26'</td>
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<tr>
<td>59</td>
<td>Barramundie Creek III</td>
<td>5371</td>
<td>222</td>
<td>248</td>
<td>132 26'</td>
</tr>
<tr>
<td>60</td>
<td>Barramundie Creek IV</td>
<td>5371</td>
<td>216</td>
<td>247</td>
<td>132 26'</td>
</tr>
<tr>
<td>61</td>
<td>Evelyn</td>
<td>5370</td>
<td>882</td>
<td>892</td>
<td>132 07'</td>
</tr>
<tr>
<td>62</td>
<td>Koolpin Gorge I</td>
<td>5471</td>
<td>398</td>
<td>070</td>
<td>132 35'</td>
</tr>
<tr>
<td>63</td>
<td>Koolpin Gorge II</td>
<td>5471</td>
<td>375</td>
<td>062</td>
<td>132 35'</td>
</tr>
<tr>
<td>64</td>
<td>Moline Rockhole I</td>
<td>5370</td>
<td>030</td>
<td>980</td>
<td>132 15'</td>
</tr>
<tr>
<td>65</td>
<td>Moline Rockhole II</td>
<td>5370</td>
<td>025</td>
<td>975</td>
<td>132 15'</td>
</tr>
<tr>
<td>66</td>
<td>Koolpin Gorge III</td>
<td>5471</td>
<td>376</td>
<td>061</td>
<td>132 35'</td>
</tr>
<tr>
<td>67</td>
<td>Billy Spring</td>
<td>5370</td>
<td>040</td>
<td>016</td>
<td>132 16'</td>
</tr>
<tr>
<td>68</td>
<td>Goodparla Jumpup</td>
<td>5371</td>
<td>025</td>
<td>073</td>
<td>132 15'</td>
</tr>
<tr>
<td>69</td>
<td>Cannon Hill</td>
<td>5473</td>
<td>786</td>
<td>324</td>
<td>132 97'</td>
</tr>
<tr>
<td>70</td>
<td>Yarrawalaya</td>
<td>5473</td>
<td>760</td>
<td>388</td>
<td>132 58'</td>
</tr>
<tr>
<td>71</td>
<td>E.A. Ranger Station</td>
<td>5473</td>
<td>775</td>
<td>245</td>
<td>132 57'</td>
</tr>
<tr>
<td>72</td>
<td>Oenpelli Rainforest</td>
<td>5473</td>
<td>860</td>
<td>298</td>
<td>133 02'</td>
</tr>
<tr>
<td>73</td>
<td>Munmarlary I</td>
<td>5473</td>
<td>365</td>
<td>423</td>
<td>132 14'</td>
</tr>
<tr>
<td>74</td>
<td>Munmarlary II</td>
<td>5473</td>
<td>373</td>
<td>530</td>
<td>132 35'</td>
</tr>
<tr>
<td>75</td>
<td>Munmarlary III</td>
<td>5473</td>
<td>380</td>
<td>519</td>
<td>132 35'</td>
</tr>
<tr>
<td>76</td>
<td>East Alligator River I</td>
<td>5473</td>
<td>797</td>
<td>225</td>
<td>132 58'</td>
</tr>
<tr>
<td>77</td>
<td>East Alligator River II</td>
<td>5473</td>
<td>795</td>
<td>233</td>
<td>132 58'</td>
</tr>
<tr>
<td>78</td>
<td>Ngarradj I</td>
<td>5473</td>
<td>739</td>
<td>203</td>
<td>132 55'</td>
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<tr>
<td>79</td>
<td>Ngarradj II</td>
<td>5473</td>
<td>742</td>
<td>202</td>
<td>132 55'</td>
</tr>
<tr>
<td>80</td>
<td>Ja Ja I</td>
<td>5472</td>
<td>724</td>
<td>154</td>
<td>132 54'</td>
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<tr>
<td>81</td>
<td>Ja Ja II</td>
<td>5472</td>
<td>719</td>
<td>155</td>
<td>132 54'</td>
</tr>
<tr>
<td>82</td>
<td>Yawakaka I</td>
<td>5573</td>
<td>865</td>
<td>278</td>
<td>133 02'</td>
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<tr>
<td>83</td>
<td>Yawakaka II</td>
<td>5573</td>
<td>860</td>
<td>274</td>
<td>133 02'</td>
</tr>
<tr>
<td>84</td>
<td>Yawakaka III</td>
<td>5573</td>
<td>872</td>
<td>294</td>
<td>133 02'</td>
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<tr>
<td>SITE NO.</td>
<td>SITE NAME</td>
<td>MAP NO.</td>
<td>GRID REFERENCE</td>
<td>LONG.</td>
<td>LAT.</td>
</tr>
<tr>
<td>---------</td>
<td>-------------------------------</td>
<td>---------</td>
<td>----------------</td>
<td>--------</td>
<td>-------</td>
</tr>
<tr>
<td>99</td>
<td>Twin Falls I</td>
<td>5471</td>
<td>594</td>
<td>132 47'13 19'</td>
<td>Forest to the left of falls on ledge.</td>
</tr>
<tr>
<td>100</td>
<td>Twin Falls II</td>
<td>5471</td>
<td>600</td>
<td>132 47'13 20'</td>
<td>Creekside in escarpment.</td>
</tr>
<tr>
<td>101</td>
<td>Bindjil Bindjil I</td>
<td>5473</td>
<td>680</td>
<td>132 52'13 17'</td>
<td>Edge of floodplain margin.</td>
</tr>
<tr>
<td>104</td>
<td>Evelyn Creek</td>
<td>5370</td>
<td>889</td>
<td>132 07'13 41'</td>
<td>Edge of floodplain margin.</td>
</tr>
<tr>
<td>105</td>
<td>Kapalga billabong</td>
<td>5372</td>
<td>207</td>
<td>132 26'12 36'</td>
<td>East of Kapalga billabong.</td>
</tr>
<tr>
<td>106</td>
<td>North Point, Kapalga</td>
<td>5373</td>
<td>120</td>
<td>132 22'12 22'</td>
<td>Floodplain margin.</td>
</tr>
<tr>
<td>116</td>
<td>Point Stuart</td>
<td>5273</td>
<td>150</td>
<td>132 54'12 13'</td>
<td>Coastal cheniers.</td>
</tr>
<tr>
<td>128</td>
<td>Pandanus Spring</td>
<td>5370</td>
<td>028</td>
<td>132 32'12 20'</td>
<td>Spring.</td>
</tr>
<tr>
<td>129</td>
<td>Goodparla Hill</td>
<td>5371</td>
<td>055</td>
<td>132 16'13 26'</td>
<td>Small hill 1 km NW of Goodparla turnoff.</td>
</tr>
<tr>
<td>130</td>
<td>Gibbat I</td>
<td>5470</td>
<td>526</td>
<td>807 43'13 38'</td>
<td>Spring in sandplain.</td>
</tr>
<tr>
<td>131</td>
<td>Gibbat II</td>
<td>5470</td>
<td>445</td>
<td>807 43'13 38'</td>
<td>Edge of creek.</td>
</tr>
<tr>
<td>132</td>
<td>Gibbat III</td>
<td>5470</td>
<td>445</td>
<td>803 43'13 38'</td>
<td>0.5 km S of Site 131.</td>
</tr>
<tr>
<td>133</td>
<td>Gibbat IV</td>
<td>5470</td>
<td>460</td>
<td>770 46'13 39'</td>
<td>Patch of forest on side of highway (North).</td>
</tr>
<tr>
<td>134</td>
<td>Gibbat V</td>
<td>5470</td>
<td>393</td>
<td>951 35'13 36'</td>
<td>'Island' surrounded by Magela floodplain.</td>
</tr>
<tr>
<td>135</td>
<td>Gibbat VI</td>
<td>5470</td>
<td>327</td>
<td>132 32'13 32'</td>
<td>'Island' at edge of floodplain.</td>
</tr>
<tr>
<td>160</td>
<td>West Alligator Spring</td>
<td>5372</td>
<td>983</td>
<td>132 13'12 37'</td>
<td>Edge of river.</td>
</tr>
<tr>
<td>161</td>
<td>Munmarkary Fence</td>
<td>5472</td>
<td>405</td>
<td>132 37'12 37'</td>
<td>Spring at edge of floodplain.</td>
</tr>
<tr>
<td>162</td>
<td>Djirrirbal I</td>
<td>5473</td>
<td>766</td>
<td>190 57'12 29'</td>
<td>1 km N of Three Pools (Djirrirbal).</td>
</tr>
<tr>
<td>163</td>
<td>Djirrirbal II</td>
<td>5473</td>
<td>750</td>
<td>132 56'12 30'</td>
<td>Along Djirrirbal creek.</td>
</tr>
<tr>
<td>164</td>
<td>Djirrirbal III</td>
<td>5473</td>
<td>761</td>
<td>175 57'12 30'</td>
<td>Edge of escarpment top country.</td>
</tr>
<tr>
<td>165</td>
<td>Hypit's Hill (Djalmarr)</td>
<td>5473</td>
<td>655</td>
<td>340 51'12 21'</td>
<td>'Island' at edge of floodplain.</td>
</tr>
<tr>
<td>166</td>
<td>Cannon Hill Floodplain Island</td>
<td>5473</td>
<td>775</td>
<td>132 67'12 22'</td>
<td>'Island' at edge of floodplain.</td>
</tr>
<tr>
<td>167</td>
<td>Hawk Dreaming</td>
<td>5473</td>
<td>752</td>
<td>313 56'12 23'</td>
<td>Edge of Hawk Dreaming escarpment.</td>
</tr>
<tr>
<td>168</td>
<td>Munmarkary Abatt.</td>
<td>5473</td>
<td>281</td>
<td>132 30'12 28'</td>
<td>Around billabong edge.</td>
</tr>
<tr>
<td>169</td>
<td>Ballyangardy Spring</td>
<td>5473</td>
<td>372</td>
<td>132 35'12 15'</td>
<td>0.4 km NE of Ballyangardy Spring.</td>
</tr>
<tr>
<td>170</td>
<td>Bindjil Bindjil II</td>
<td>5473</td>
<td>670</td>
<td>955 55'12 18'</td>
<td>Edge of floodplain margin.</td>
</tr>
<tr>
<td>173</td>
<td>Mayitdjiura</td>
<td>5473</td>
<td>728</td>
<td>128 55'12 27'</td>
<td>Crevices in small sandstone outlier.</td>
</tr>
<tr>
<td>174</td>
<td>Djurlayn</td>
<td>5472</td>
<td>772</td>
<td>105 57'12 34'</td>
<td>5 km SE Hades crossing of Winwuyurr.</td>
</tr>
<tr>
<td>175</td>
<td>Ibangu</td>
<td>5472</td>
<td>735</td>
<td>123 55'12 32'</td>
<td>1.5 km NE Hades crossing of Winwuyurr.</td>
</tr>
<tr>
<td>176</td>
<td>Mt. Howship I</td>
<td>5572</td>
<td>010</td>
<td>133 10'12 35'</td>
<td>Facing escarpment in amphitheatre.</td>
</tr>
<tr>
<td>177</td>
<td>Mt. Howship II</td>
<td>5572</td>
<td>010</td>
<td>133 10'12 35'</td>
<td>Spring in rock face.</td>
</tr>
<tr>
<td>178</td>
<td>Mt. Howship III</td>
<td>5572</td>
<td>000</td>
<td>133 10'12 35'</td>
<td>Spring/creek.</td>
</tr>
<tr>
<td>179</td>
<td>Mt. Howship IV</td>
<td>5572</td>
<td>999</td>
<td>133 10'12 34'</td>
<td>Escarpment gorge.</td>
</tr>
<tr>
<td>180</td>
<td>Lightning Dreaming I</td>
<td>5572</td>
<td>845</td>
<td>133 01'12 55'</td>
<td>Escarpment face.</td>
</tr>
<tr>
<td>181</td>
<td>Lightning Dreaming II</td>
<td>5572</td>
<td>851</td>
<td>133 01'12 55'</td>
<td>Creek/spring.</td>
</tr>
<tr>
<td>182</td>
<td>The Gorge I</td>
<td>5471</td>
<td>685</td>
<td>132 52'13 19'</td>
<td>South side of gorge in escarpment.</td>
</tr>
<tr>
<td>183</td>
<td>The Gorge II</td>
<td>5471</td>
<td>685</td>
<td>132 52'13 19'</td>
<td>Centre of gorge.</td>
</tr>
<tr>
<td>184</td>
<td>The Gorge III</td>
<td>5471</td>
<td>701</td>
<td>132 52'13 19'</td>
<td>Isolated spring forest in steep terrain.</td>
</tr>
<tr>
<td>185</td>
<td>The Gorge IV</td>
<td>5471</td>
<td>707</td>
<td>132 52'13 20'</td>
<td>Isolated spring forest, sandplain.</td>
</tr>
<tr>
<td>186</td>
<td>The Gorge V</td>
<td>5471</td>
<td>711</td>
<td>132 53'13 20'</td>
<td>Isolated spring forest, sandplain.</td>
</tr>
<tr>
<td>187</td>
<td>Magela Falls I</td>
<td>5572</td>
<td>914</td>
<td>133 05'12 46'</td>
<td>Protected south running gorge.</td>
</tr>
<tr>
<td>188</td>
<td>Magela Falls II</td>
<td>5572</td>
<td>915</td>
<td>133 05'12 46'</td>
<td>Along Magela creek.</td>
</tr>
<tr>
<td>189</td>
<td>Magela Falls III</td>
<td>5572</td>
<td>933</td>
<td>133 06'12 46'</td>
<td>Steep escarpment face.</td>
</tr>
</tbody>
</table>
APPENDIX 2:
HIGH PLANT SPECIES OCCURRING AT SURVEY SITES IN THE KAKADU REGION

This list is presented in alphabetical order of Linnaean generic names. Where specific nomenclature is unknown a specimen collection number is given. All specimens are lodged in the N.T. Herbarium, Conservation Commission of the Northern Territory.

The occurrence of species are given for all sites surveyed, not just the 127 occurring in the vicinity of Kakadu. Numbers in brackets following the site number provide an indication of the abundance of taxa at sampling sites. The abundance scale used here is as follows:

1. 1 mature individual present
2. 2-6 individuals present
3. 7-20 individuals present
4. 21-50 individuals present
5. >50 individuals present

Where maturity is assumed when the characteristic adult growth form of the particular species is realised.

A small number of vine-forest taxa not encountered in this survey are included also. These taxa have been recorded in other regional studies by Webb and Tracey (1979) and by Lyn Craven as part of the Kakadu Fauna Survey. Where included in this list such records are given by:

Webb & Tracey = (W & T # [site no.])
Craven = (RB # [site no.])

After the abbreviated Family name (e.g. Malv. = Malvaceae; Myrt. = Myrtaceae), the growth form of the taxa is denoted by a letter where:

T = tall tree (>8m)
H = herb
v = vine

ge = geophyte
gr = graminoid (e.g. sedge or grass)
e = epiphyte/epiphytic parasite
f = fern
x = exotic species
p = palm

Taxa more typically associated with vegetation types other than vine forest are indicated by an asterisk (*).
Abras precatorius Fab. v

Abutilon indicum Malv. s
61(4), 107(5), 110(2), 116(5), 120(5), 136(5)

Abelmoschus moschatus Malv. *h
150(5)

Acacia alleniana Mimos. *s
132(3), 164(3), 183(3), 188(5)

A. aulacocarpa T.t

A. auriculiformis T.t

A. consperse *s
1(5), 38(3), 194(2)

A. difficilis *s

A. dimidiata *s
45(5), 58(3), 59(2), 132(3)

A. diasticha *t
136(2)

A. holosericea *s

A. humifusa *s/c
1(5), 2(3), 7(3), 9(1), 14(2), 16(9), 38(4), 41(3), 66(4), 100(3)

A. latifolia *s
31(3), 58(4), 59(3)
A. mimula *t*s
  3(2), 132(3)
A. montfordiae *s
  97(2)
A. pellita *s
  112(5)
A. plectocarpa *t*, *s
  27(3), 163(5), 164(5)
A. producta *s
  21(4), 58(5), 59(3), 132(4), 164(3)
A. rothii *s
  21(5)
A. sublanata *s
  21(5), 27(2), 35(3), 180(4)
A. torulosa *t*, *s
  29(5), 33(3), 66(5); 56(5), 163(5), 183(3), 38(5)
A. umbellata *s
  66(5)
Acanthus ilicifolius Acanthaceae *m
  192(2)
Achyranthes aspera *s* Amaranth h
Acmena hemilampra Myrt. T
  141(5), 142(5), 140(4)
Acrostichum aureum Pterid f
  124(4), 127(2), 143(5)
Actephyla sp. Euphorb. *t*
  (W & T #5)
Adansonia gregorii Bombac T
  111(2)
Adenia heterophylla Passiflor. *v*
  69(3), 70(5), 72(5), 78(5), 84(2), 82(5), 83(4), 85(4), 87(3), 90(4),
  92(4), 93(2), 94(3), 95(3), 97(3), 100(3), 101(4), 106(5), 108(3),
  110(4), 111(4), 113(5), 116(4), 120(3), 123(4), 129(3), 134(2), 139(4),
  191(4)
Adenanthera pavonina Mimos. *t*
  85(2), 115(2), 116(5), 152(2)
Adiantum philippense Adiant. *f*
  24(4), 60(5), 61(4), 96(2), 107(3), 150(5), 165(5), 179(5), 182(5), 188(5),
  189(5)
Aglaia elaeagnoida Mel. T, *t*
  78(5), 79(4), 81(5), 82(5), 85(5), 137(4), 145(5)
Aglaia sapindina T
  142(4), 143(3), 146(5), 147(4)
Aglaia sp. Mel. *t*
  (W & T #5)

Albizia lebbek Mimos. t 28(4), 87(1), 137(3)


Alphitonia sp. t 143(3), 148(2)


A. ophiolyoides T 109(4), 111(3)


A. galbra ge, h

Ampelocissus acetosa Vit. ge,v

Ampelocissus sp. (small-leaved) *ge,v
168(5)

Ampelocissus sp. (granite) *ge,v
61(3), 149(3), 150(5), 151(5)

Amyema vib...leflorum Loranth. e,p.
3(2), 22(2), 42(3), 45(3), 73(2), 94(2)

Aneilema siliculosum Commelin. h

Annona reticulata Annon
61(5), 98(2), 104(2)

Antiar~s toxicaria Mor. T (RB #1)
78(5), 79(3), 81(2), 82(5), 86(5), 87(4), 120(5), 143(2)

Antidesma ghaesembilla Euphorb. s

A. parvifolium s

Aristolochia sp. (CRD 6392) Aristoloch. v
152(5), 155(5), 157(5), 158(5)

Arthrochilus irritabilis Orchid. h

Artocarpus glaucus Mor. t,T

Asparagus racemosus Liliac. v

Atalaya variifolia Sapind. *t
56(2), 91(1), 102(3), 167(2), 175(2)

Atalaya salicifolia v
2(3), 178(2)

Atylosia cinerea Fab. s
27(5), 28(4), 36(3), 59(5), 133(3), 159(5)
Bacemia intratropica Myrt. *t, s
164(2)

Bambusa arnheimica Poac. gr
127(5), 135(5)

Banksia dentata Prot. *t
33(2), 58(3), 64(3), 65(2), 128(3), 131(3), 141(2), 148(3)

Barringtonia acutangula Barrington. *t
193(5)

Berrya cordifolia Til. *t
78(9), 79(3), 82(5), 83(3)

Bidens bipinnata Aster. *h
170(5)

Blainvillea dubia Aster. *h
39(5), 113(5), 119(4)

Blechnum indicum Blechn. f.
145(5), 148(5), 150(5)

Blechnum orientale Blechn. f
19(4), 20(3), 24(5), 36(5), 52(4), 53(3), 55(5), 60(4), 64(3), 67(5),
185(5), 186(1), 187(4), 189(5)

Blepharocarya depaupe.rata Blepharocary. *t
7(3), 9(1), 14(2), 16(3), 20(1), 21(2), 35(2), 38(3), 57(2), 69(1),
72(2), 95(1), 97(3), 112(2), 164(2), 167(3), 173(4), 180(5), 182(3)

Boerhavia diffusa Nyctagin. *ge,v

Bombax ceiba Bombac. T
10(5), 11(4), 17(5), 18(3), 22(2), 23(4), 42(2), 43(4), 44(4), 45(2),
47(1), 50(4), 70(4), 78(4), 79(4), 81(2), 82(5), 83(3), 84(3), 86(3),
87(3), 88(2), 91(1), 101(3), 102(2), 106(4), 111(2), 116(5), 120(3),
123(4), 137(4), 143(2), 144(5), 145(4), 152(4), 153(4), 154(4), 155(5),
156(4), 158(3), 165(5), 167(4), 170(1), 190(3), 191(2), 192(3), 193(3)

Boronia grandisepala Rutac. *s
26(4), 180(5)

B. lanceolata *s
94(2), 95(2), 97(3), 162(5), 163(5), 164(4), 171(3), 194(4)

Brachychiton diversifolius Stercul. *T,t
3(3), 73(1), 74(2), 91(3), 104(3), 135(2), 144(2), 151(2), 153(3),
167(2), 190(2)

B. paradoxus *t,s
7(3), 12(4), 18(4), 27(2), 41(2), 42(2), 59(3), 66(5), 70(2), 91(1),
100(3), 103(3), 107(2), 136(2), 145(5), 149(2), 151(5), 159(3), 164(2),
168(3), 172(3), 174(3), 176(3)
Breynia cernua Euphorb. t,s
53(3), 57(2), 65(3), 66(5), 68(4), 70(5), 73(3), 75(3), 76(3), 78(4),
192(3), 193(4)
B. rhynchocarpa t,s
16(5), 26(3), 33(2), 35(3), 56(3), 57(3), 59(2), 62(2), 63(2), 66(3),
69(2), 71(2), 72(3), 73(2), 90(3), 94(2), 95(1), 98(3), 100(3), 132(3),
134(2), 162(3), 163(5), 164(2), 167(4), 168(1), 171(1), 176(4), 182(5),
184(2)
Bridelia tomentosa Euphorb. s
70(5), 72(4), 75(1), 76(3), 78(5), 81(3), 82(5), 83(2), 86(5), 88(4),
91(1), 92(1), 93(4), 97(2), 98(4), 100(5), 101(3), 102(5), 103(5),
104(4), 105(4), 106(4), 107(5), 108(5), 110(2), 111(3), 113(5),
116(5), 120(5), 123(3), 125(4), 134(2), 138(4), 139(4), 144(5),
145(5), 149(2), 150(4), 151(5), 152(5), 157(5); 158(5), 159(5),
170(3), 172(5), 174(2), 175(2), 176(5), 179(5), 180(5), 182(5),
189(5), 190(5), 191(3), 194(3)
Brucea javanica Simaroub. s
90(2), 91(1), 155(5), 167(5), 174(4), 176(5), 179(5)
Buchanania arborescens Anacard. T
26(1), 30(3), 31(3), 32(2), 34(2), 35(2), 37(2), 40(2), 52(2), 62(3),
63(4), 70(4), 72(5), 77(2), 85(4), 87(3), 94(2), 95(2), 96(4), 97(1),
98(3), 101(4), 102(4), 104(2), 114(4), 115(3), 117(4), 118(2), 119(2),
121(2), 122(5), 134(2), 135(3), 137(4), 138(4), 143(4), 144(5),
146(5), 152(4), 154(4), 155(4), 156(4), 163(5), 170(2), 179(5),
B. obovata *t
7(4), 9(2), 12(3), 17(2), 18(3), 20(1), 21(3), 22(2), 26(2), 27(2),
33(2), 35(2), 38(2), 41(3), 42(3), 45(5), 57(2), 59(4), 66(5), 70(2),
73(1), 61(2), 93(2), 103(2), 104(2), 107(2), 108(2), 125(4), 132(2),
136(3), 138(2), 149(1), 151(5), 158(2), 159(3), 160(2), 162(3),
163(5), 170(2), 184(1), 194(1)
Bulbostylis barbata Cyper. *gr
61(5), 91(5), 151(5)
Bursaria spinosa var. incaha Pittospor. t,s
132(3), 133(3)
Burtonia subulata Fabac. *s
58(3), 66(5), 132(3), 162(3)
Caesalpinia bonduc Caesalpin. s/c
70(1), 82(3), 86(5), 116(5), 120(4), 123(3), 144(5), 192(1)
Callicarpa candicans Verben. s
101(2), 103(4), 107(4), 108(4), 133(3), 151(4), 152(5), 155(5)
Callitris intratropica Cupress. T
Calliphylum sif Clus. T
C. soulattri T
Calopogonium mucunoides Fab. V.X.
114(5), 172(5)
Calytrix extipulata Myrt. s
7(3), 12(3), 54(3), 69(3), 91(4), 132(3), 151(4)
C. megaphylla s
59(3)
Canarium australianum Burser. T
Canavalia sp. (BD475) (aff. papuana) Fabac.v
Cansjera leptostachya Opil. v
86(5), 109(5), 110(5), 116(5), 120(5), 144(5)

Canthium sp. aff. lucidum Rub. t.s
29(3), 31(3), 33(4), 62(3), 63(2), 65(2), 102(3), 114(5), 120(5),
121(4), 122(5), 135(4), 142(3), 156(5), 188(5)

Canthium sp. 920 sfrm
7(2), 14(5), 16(4), 19(3), 26(2), 28(2), 30(2), 32(2), 38(2),
71(2), 72(5), 77(5), 80(2), 82(5), 83(3), 84(3), 85(3), 90(3),
92(2), 93(3), 94(2), 96(2), 97(2), 100(3), 112(4), 117(4),
139(3), 144(5), 155(4), 162(3), 163(5), 167(3), 171(2), 173(1),
176(5), 179(4), 180(5), 182(5), 189(5), 190(4)

Capparis jacobsii Cap r±d.
21(2), 100(4), 133(2), 180(3), 182(5)

C. sepiaria s
3(5), 8(3), 10(5), 17(5), 18(3), 22(3), 24(3), 42(3),
70(3), 76(4), 78(5), 79(2), 81(2), 82(5), 83(5), 86(5), 87(3),
127(5), 129(4), 137(4), 139(4), 144(5), 153(5), 155(5), 157(4),
193(5)

C. sp. aff. sepiaria (small leaved) v
107(4), 108(3), 136(5)

C. umbonata *s,t
21(3), 26(2), 28(3), 41(2), 57(1), 184(1)

Capsicum sp. Solan. s,x
126(1)

Carissia lanceolata Apocyn. *s
31(2)

Carallia brachiata Rhizophor. T.t.
33(4), 34(4), 35(2), 36(2), 40(3), 44(2), 46(2), 52(2), 53(2),
55(2), 58(2), 60(3), 62(3), 63(3), 65(5), 67(2), 68(3), 72(5),
73(5), 75(3), 77(3), 87(3), 88(5), 89(4), 93(1), 96(1), 98(2),
99(2), 100(2), 101(4), 102(3), 105(2), 106(2), 112(4), 114(5),
126(4), 131(4), 134(4), 135(3), 137(2), 138(4), 141(4), 142(5),
143(4), 146(4), 147(4), 148(4), 150(5), 152(3), 153(4), 154(4),
156(4), 158(3), 160(4), 161(3), 162(2), 163(5), 166(2), 167(4),
184(3), 188(5), 189(5), 194(2)

Cardiospermum halicacabum Sapind. h
10(5), 193(5)

Carpentaria austinata Areccac. P
35(1), 40(3), 46(1), 57(1), 58(3), 60(5), 63(3), 67(4), 73(5),
72(5), 77(5), 80(1), 85(3), 87(2), 88(5), 89(4), 96(5), 97(3),
99(4), 101(2), 102(4), 105(1), 106(2), 112(2), 114(5), 115(2),
117(2), 119(5), 121(5), 122(5), 124(5), 126(5), 131(2), 142(3),
143(2), 146(3), 148(4), 150(4), 152(5), 153(3), 154(5), 155(5),
Cassia fistula Caesalpin. T,X
11(2), 126(1)
C. leptocladia s
26(2)
C. obtusifolia x,s
126(3), 192(5), 193(5)
C. occidentalis x,s
170(5), 172(5), 192(5)
C. timorensis s
107(3), 108(3)
Cassytha filiformis Laur. v
120(5), 132(2), 139(4), 164(5), 179(5)
Cayratia aeris Vitae. v
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Claoxylon tenerifolium Euphorb. t

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*C. floribundum as listed here may comprise other taxa as well (e.g.
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Gymnanthera nitida Asclepiad. v

Gyrocarpus americanus Hernand. T,t

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H. tillicaeus  t
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I. velutina v
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*I. pentamera t
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I. tomentosa (syn. Pavetta brownii) t
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* Note that various Rubiaceae (e.g. Ixora, Pavetta, Tarenna) require taxonomic revision. See also Pavetta.
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J. simplicifolium v

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Leptocarpus spatheus Restion. *gr
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57(2), 58(3), 132(3), 140(5)

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Lindernia ensifolia Lindernia. f

L. ensifolia ssp. agatii f
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Lomandra spp. (741, 742) Xanthorrh. gr


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Lysiphylgium *cunninghamii* Caesalpin. T 136(3).

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Malaxis acuminata Orchid. ge, h
  122(5), 143(2)
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  190(2)
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Mangifera Anacard. x, T
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Marsdenia velutina Asclepiad. v
Marsdenia sp. (J 1540) v
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Marsdenia sp. 940 v.
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182(2)

Asclepiadaceae sp. 898

?Dichapetalaceae sp. 1164 s/c
176(3), 180(4), 187(5), 189(5)

Rubiaceae sp. 718 (CRD 6707)
3(4), 116(5), 120(5), 123(5), 144(5), 190(4), 191(5)

Rubiaceae sp. 818
128(2)

?Euphorbiaceae sp. (GW 1807) t
191(5)

Malvaceae sp. (CD 6395) t
155(4)

Tiliaceae sp. 820 s.
136(5)

Rubiaceae sp. (W924) t
143(4)

Cucurbitaceae sp. (CD6394) v
152(3)
APPENDIX 3

OCCURRENCES OF RARE VINE-FOREST TAXA IN THE KAKADU REGION

This Appendix is presented in two parts. In part (a) the occurrences of rare taxa are listed by sampling site. The locations of these sites have been given previously in Figure 6. In part (b), an alphabetic listing of rare taxa is given, as well as brief notes regarding their wider distributions.

As used here, 'rare' denotes taxa which are very restricted in their distributions, at least within the N.T.; i.e., only populations which are known to occur at one to a small number of localities are included. Not included are taxa such as Antiaris toxicaria, Macaranga spp., Mimusops elengi, and Marsdenia velutina, which, whilst rare to uncommon in the Kakadu region, are widespread in other parts of the N.T., especially coastal regions. As well, a number of apparently rare taxa collected by Webb and Tracey (1979) are not included. There is some indication that, for a number of taxa at least, the nomenclature employed by these workers differs from that employed by the N.T. Herbarium. Until this is examined more thoroughly the omission of these taxa here is warranted.

(a) Occurrences of Rare Taxa

<table>
<thead>
<tr>
<th>Site No.</th>
<th>Rare Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Suregada glomerulata</td>
</tr>
<tr>
<td>2.</td>
<td>Suregada glomerulata, Tragia novae-hollandiae</td>
</tr>
<tr>
<td>3.</td>
<td>Rubiaceae sp.</td>
</tr>
<tr>
<td>9.</td>
<td>Taenites blechnoides</td>
</tr>
<tr>
<td>14.</td>
<td>Suregada glomerulata</td>
</tr>
<tr>
<td>15.</td>
<td>Psilotum nudum, Schizaea digitata</td>
</tr>
<tr>
<td>16.</td>
<td>Suregada glomerulata</td>
</tr>
<tr>
<td>19.</td>
<td>Tournstroemia cherryi</td>
</tr>
<tr>
<td>38.</td>
<td>Tiliacora australis</td>
</tr>
<tr>
<td>51.</td>
<td>Tiliacora australis, Tragia novae-hollandiae</td>
</tr>
<tr>
<td>54.</td>
<td>Suregada glomerulata</td>
</tr>
<tr>
<td>60.</td>
<td>Schizaea digitata, Taenites blechnoides</td>
</tr>
<tr>
<td>68.</td>
<td>Sterculia sp. 756</td>
</tr>
<tr>
<td>72.</td>
<td>Morinda jasminoides, Taenites blechnoides</td>
</tr>
<tr>
<td>75.</td>
<td>Hydrastele wendlandiana</td>
</tr>
<tr>
<td>96.</td>
<td>Taenites blechnoides</td>
</tr>
<tr>
<td>99.</td>
<td>Histiopteris sp. 703, Taenites blechnoides</td>
</tr>
<tr>
<td>104.</td>
<td>Planchonella sp. 771</td>
</tr>
<tr>
<td>116.</td>
<td>Rubiaceae sp.</td>
</tr>
<tr>
<td>128.</td>
<td>Rubiaceae sp.</td>
</tr>
<tr>
<td>129.</td>
<td>Embilia sp. 816</td>
</tr>
<tr>
<td>130.</td>
<td>Cyclosorus interruptus, Sterculia sp. 756</td>
</tr>
<tr>
<td>131.</td>
<td>Pterideum esculentum, Sterculia sp. 756</td>
</tr>
<tr>
<td>Site No.</td>
<td>Rare Taxa (Continued)</td>
</tr>
<tr>
<td>---------</td>
<td>-----------------------</td>
</tr>
<tr>
<td>132</td>
<td>Bursaria spinosa, Rubiaceae sp.</td>
</tr>
<tr>
<td>133</td>
<td>Bursaria spinosa</td>
</tr>
<tr>
<td>169</td>
<td>Embilia sp.816, Hydriastele wendlandiana, Morinda sp.930</td>
</tr>
<tr>
<td>176</td>
<td>Remusatia vivipara, Tragia Tragia novae-hollandiae, Trichosanthes sp. (D6266)</td>
</tr>
<tr>
<td>177</td>
<td>Nephrolepis obliterata, Remusatia vivipara, Taenites blechnoides, Tournstroemia cherryl</td>
</tr>
<tr>
<td>178</td>
<td>Atalaya sp., Nephrolepis obliterata, Tournstroemia cherryl, Tragia novae-hollandiae</td>
</tr>
<tr>
<td>179</td>
<td>Cayratia sp. (D6649), Croton sp. (D6650), Doryopteris concolor, Marsdenia sp. (J1540), Nephrolepis obliterata, Remusatia vivipara, Trichosanthes sp. (D6266)</td>
</tr>
<tr>
<td>180</td>
<td>Croton sp. (D6650), Suregada glomerulata, Typhonium sp. (J1380), Annonaceae sp.</td>
</tr>
<tr>
<td>182</td>
<td>Croton sp. (W1330), Ophioglossum intermedia, Psychotria sp. Tiliacora australis</td>
</tr>
<tr>
<td>183</td>
<td>Psychotria sp. (DJ 1331), Psilotum nudum, Schizaea digitata, Tiliacora australis, Tournstroemia cherryl</td>
</tr>
<tr>
<td>184</td>
<td>Tournstroemia cherryl</td>
</tr>
<tr>
<td>185</td>
<td>Dendrobium lobbii, Hydriastele wendlandiana; Ophioglossum intermedia</td>
</tr>
<tr>
<td>187</td>
<td>Polysciad australianum, Schizaea digitata, Selenodesmium obscurum, Suregada glomerulata, Taenites blechnoides, Annonaceae sp.</td>
</tr>
<tr>
<td>189</td>
<td>Suregada glomerulata, Tragia novae-hollandiae, Annonaceae sp.</td>
</tr>
</tbody>
</table>

(b) Alphabetical Listing of Rare Taxa — * denotes threatened status

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Sites</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atalaya sp.</td>
<td>178</td>
<td>possibly Atalaya salicifolia.</td>
</tr>
<tr>
<td>Bursaria spinosa</td>
<td>132, 133</td>
<td>evidently rare in Top End.</td>
</tr>
<tr>
<td>Cayratia sp. (D6649)</td>
<td>179</td>
<td>possibly Cayratia sp. (WT=60): collections being examined by D.L. Jones.</td>
</tr>
<tr>
<td>Cheilanthes spp.</td>
<td>various</td>
<td>collections require examination.</td>
</tr>
<tr>
<td>Clerodendrum spp.</td>
<td>various</td>
<td>evidently rare.</td>
</tr>
<tr>
<td>Croton sp. (D6650)</td>
<td>179, 180</td>
<td>evidently rare.</td>
</tr>
<tr>
<td>Croton sp. (W1330)</td>
<td>182</td>
<td>rare in Kakadu and possibly Top End as well.</td>
</tr>
<tr>
<td>*Cyclosorus interruptus</td>
<td>130</td>
<td>only known occurrence in N.T.</td>
</tr>
<tr>
<td>*Dendrobium lobbii</td>
<td>185</td>
<td>only known occurrence in N.T.</td>
</tr>
<tr>
<td>Doryopteris concolor</td>
<td>179</td>
<td>‘odd’ distribution in Kakadu, (2.3.2.iii), widespread in Darwin region.</td>
</tr>
<tr>
<td>Embilia sp.816</td>
<td>129, 169</td>
<td>only known occurrence in Top End.</td>
</tr>
<tr>
<td>Histiopteris* sp. 703</td>
<td>99</td>
<td>‘odd’ distribution in Kakadu, widespread in coastal regions.</td>
</tr>
<tr>
<td>*Hydriastele wendlandiana</td>
<td>75, 169, 185</td>
<td></td>
</tr>
<tr>
<td>Taxa</td>
<td>Sites</td>
<td>Notes</td>
</tr>
<tr>
<td>-----------------------------</td>
<td>-------------------</td>
<td>----------------------------------------------------------------------</td>
</tr>
<tr>
<td>Lygodium spp.</td>
<td>various</td>
<td>collections being examined by D.L. Jones.</td>
</tr>
<tr>
<td>---</td>
<td></td>
<td>evidently rare.</td>
</tr>
<tr>
<td>Marsdenia sp. (J1540)</td>
<td>179</td>
<td>rare in Kakadu and possibly Top End as well.</td>
</tr>
<tr>
<td>Morinda jasminoides</td>
<td>72</td>
<td>rare in Top End at least.</td>
</tr>
<tr>
<td>Morinda sp. 930</td>
<td>169</td>
<td>rare in Top End, sandstone regions.</td>
</tr>
<tr>
<td>Nephrolepis obliterata</td>
<td>177, 178, 179</td>
<td>rare in Top End.</td>
</tr>
<tr>
<td>*Ophioglossum intermedia</td>
<td>182, 185</td>
<td>collections require examination.</td>
</tr>
<tr>
<td>Phyllanthus spp.</td>
<td>various</td>
<td>rare in Top End.</td>
</tr>
<tr>
<td>Planchonella sp. 771</td>
<td>104</td>
<td>one known occurrence in Kakadu region, otherwise known from Melville Island in the Top End.</td>
</tr>
<tr>
<td>Polyscias australianum</td>
<td>187</td>
<td>rare in Top End.</td>
</tr>
<tr>
<td>Psilotum nudum</td>
<td>15, 183</td>
<td>possibly Psychotria loniceroides, and then known otherwise only from Webb and Tracey Site 15, in the N.T.</td>
</tr>
<tr>
<td>Psychotria sp. (DJ1331)</td>
<td>182, 183</td>
<td>rare in Top End.</td>
</tr>
<tr>
<td>Pteridium esculentum</td>
<td>131</td>
<td>rare in Kakadu, but otherwise in North Queensland and widespread elsewhere.</td>
</tr>
<tr>
<td>Remusatia vivipara</td>
<td>176, 177, 179</td>
<td>collections require examination.</td>
</tr>
<tr>
<td>Scleria spp.</td>
<td>various</td>
<td>one known occurrence in Kakadu region, otherwise known from Melville Island in the Top End.</td>
</tr>
<tr>
<td>Selenodesmium obscurum</td>
<td>187</td>
<td>rare in Top End.</td>
</tr>
<tr>
<td>Schizaea digitata</td>
<td>15, 60, 183</td>
<td>restricted to Kakadu region in the Top End.</td>
</tr>
<tr>
<td>Sterculia sp. 756</td>
<td>15, 68, 130, 131</td>
<td>restricted to Kakadu region in the N.T.</td>
</tr>
<tr>
<td>Suregadà glomerulata</td>
<td>1, 2, 14, 16, 56, 180, 187, 188, 189</td>
<td>restricted to Kakadu region in the N.T., otherwise North Queensland, New Guinea.</td>
</tr>
<tr>
<td>Taenites blechnoides</td>
<td>9, 60, 72, 96, 99, 177, 187</td>
<td>restricted to Kakadu region in N.T., possibly also in Nth Qld.</td>
</tr>
<tr>
<td>Tiliacora australis</td>
<td>38, 51, 182</td>
<td>status unknown, requires examination.</td>
</tr>
<tr>
<td>Ternstroemia cherryi</td>
<td>19, 177, 178</td>
<td>status of specimens indeterminate</td>
</tr>
<tr>
<td>Tragia novae-hollandiae</td>
<td>2, 51, 178, 178, 178, 184</td>
<td>status of specimens indeterminate</td>
</tr>
<tr>
<td>Typhonium sp. (J1380)</td>
<td>180</td>
<td>Family Rubiaceae requires revision.</td>
</tr>
<tr>
<td>Genus indeterminate</td>
<td></td>
<td>restricted to Kakadu region in N.T., otherwise status unknown.</td>
</tr>
<tr>
<td>Rubiaceae spp.</td>
<td>3, 116, 128, 132</td>
<td>restricted to one occurrence in N.T., otherwise status unknown.</td>
</tr>
<tr>
<td>? Annonaceae sp.</td>
<td>180, 187, 189</td>
<td></td>
</tr>
<tr>
<td>?</td>
<td>176</td>
<td></td>
</tr>
</tbody>
</table>
APPENDIX 4:
ABORIGINAL PLANT NAMES AND USES IN KAKADU NATIONAL PARK:
LISTINGS IN MAYIALI/KUNDJEYIMI AND GUNWINNGU LANGUAGES.

This list of Aboriginal plant names and uses is based on information provided by Nipper Kapirigi and George Mingam (MAYIALI), and Talking Billy Gunbunukâ and Joy Djolom (GUNWINNGU). The list does not provide a complete listing of the plants and their uses known to these people. It does represent, however, a substantial body of information recorded over one and a half years wherever opportunities to spend time with these people presented themselves. I thank each of them for the many enjoyable days we passed together and for their patience.

Plants are listed alphabetically according to their Linnaean name. The Linnaean names employed are those currently in use by the Northern Territory Herbarium (Conservation Commission of the Northern Territory). Where it has not been possible to ascribe a specific name, the generic name is given followed by a collection number (e.g. Typhonium sp. 1170). Collection numbers refer to specimens lodged by myself in the N.T. Herbarium. Where the generic name has not been determined (e.g. sterile grass specimens) these are listed at the end as with other Linnaean plant determinations given in this Report. The generous assistance of Mr Clyde Dunlop of the N.T. Herbarium is gratefully acknowledged.

Aboriginal Names:

Names of plants in Mayiali language are underlined (e.g. Andjeerrweerr), whereas names in Gunwinggi are not (e.g. Manganbirr). Where the Mayiali and Gunwinggi names are the same, the name is preceded by an * (e.g. *kindjilkindjil). It is to be noted however, that since most Gunwinggi names have as their prefix, 'man-', whereas most Mayiali names commence with 'an-', names which are essentially the same, differing only in the prefix, are given as *(m)an (e.g. *(m)andjarran). In summary then:

- andjeerrweerr - Mayiali name only.
- manganbirr - Gunwinngu name only.
- *kindjilkindjil - Common to both languages.
- *(m)andjarran - Common to both languages.

In contrast to the Linnaean classification system which is genetically based, the traditional Aboriginal classification of plant taxa may be described as being essentially a functional system. Thus, in the Aboriginal system names are given to any plants which are conspicuous, useful, or significant in some way. Plants which do not fulfill such criteria are described collectively, and individually, as *gundalk; that is, they are given no name of their own. Such plants include the great majority of herbaceous types (e.g. most grasses, sedges, annual herbs, small shrubs). Only a relatively few trees have no name, and this is probably best summed up in the remark, "must have a name somewhere".
Skin Names:

In most cases, skin names (i.e. whether a plant belongs either to Yirritja or Duwa moieties) of individual Aboriginal taxa have not been given. Where these have been given (e.g. Livistona humilis = mangulurut (D); Livistona inermis = mandjandad (Y)), this is because in recording ethnobotanical information such skin names were emphasised. For most plants, the affiliation of a plant taxon with one or the other moiety is not consciously remembered. Apart from the situation where plants are ascribed skin names on the basis of connections with creation stories, ceremonies and so on, there are, however, general rules which may be applied to determine whether a plant taxon belongs to one moiety or the other. These are presented diagramatically below. It is to be emphasised however that, as this is a relative system which requires a broad knowledge of plant morphologies, usages, habitats and the like (as well as a firm grounding in Aboriginal mythology), it is not possible (usually) to say that plants with long leaves are Yirritja, and those with short leaves are Duwa. Rather, where there are two taxa with recognised similar properties (e.g. two morphologically similar species), the taxon with the longer leaf may be identified as Yirritja, and the taxon with the smaller leaf, Duwa.

Spelling of Aboriginal Names:

The conventions followed in the spelling of Aboriginal names are as follows:

<table>
<thead>
<tr>
<th>Consonants</th>
<th>Pronunciation</th>
</tr>
</thead>
<tbody>
<tr>
<td>b</td>
<td>as in bed</td>
</tr>
<tr>
<td>d</td>
<td>as in dead</td>
</tr>
<tr>
<td>rd</td>
<td>as in hard</td>
</tr>
<tr>
<td>dj</td>
<td>as in dune</td>
</tr>
<tr>
<td>tj</td>
<td>as in tune</td>
</tr>
<tr>
<td>k or g</td>
<td>as in coal or goal</td>
</tr>
<tr>
<td>h</td>
<td>as in bu'er (cockney pronunciation of butter)</td>
</tr>
<tr>
<td>m</td>
<td>as in mouse</td>
</tr>
<tr>
<td>rm</td>
<td>as in farm</td>
</tr>
<tr>
<td>n</td>
<td>as in noose</td>
</tr>
<tr>
<td>nn</td>
<td>as in barn</td>
</tr>
<tr>
<td>ny</td>
<td>as in onion</td>
</tr>
<tr>
<td>ng</td>
<td>as in sing</td>
</tr>
<tr>
<td>nk</td>
<td>as in fink</td>
</tr>
<tr>
<td>l</td>
<td>as in colour</td>
</tr>
<tr>
<td>rl</td>
<td>as in earl</td>
</tr>
<tr>
<td>rr</td>
<td>as in trilled scottish words</td>
</tr>
<tr>
<td>r</td>
<td>as in rice</td>
</tr>
<tr>
<td>w</td>
<td>as in water</td>
</tr>
<tr>
<td>y</td>
<td>as in yellow</td>
</tr>
</tbody>
</table>
Vowels

a       as in hut
i       as in pit
e       as in merry
o       as in hot
u       as in put
aa      as in task
ay      as in buy
ee      as in their
oo      as in poor
ey      as in bait
oy      as in boy

Seasonality:

In describing the seasonality of plant usage, reference has been made to the Aboriginal seasonal calendar (which is the same for Mayiali and Gunwinngu), as opposed to the European monthly calendar. A Mayiali/Gunwinngu Seasonal calendar has been presented previously as Fig. 10. The main elements of this calendar are as follows:

- **gudjewg** (monsoon season) January through March approx.
- **banggerreng** (the knock 'em down storm time) April approx.
- **yegge** May into June approx.
- **wurrgeng** (cold weather season) June into August approx.
- **gurrung** (hot sand time) August into October approx.
- **gunumeleng** (first storm time) October through December approx.

Growth Forms:

After the Linnaean name, subscript letters have been used to denote the growth forms of plants as follows:

- (a) aquatic
- (e) epiphyte or epiphytic parasite (e.g. mistletoes)
- (f) fern
- (g) graminoid (grass, sedge)
- (h) herb
- (p) palm
- (q) shrub
- (t) tree
- (v) vine

Taxa commonly occurring in vine-forests are denoted by IDTH, and Mangroves by (m).
<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Botanical Name</th>
<th>Meanings</th>
<th>Uses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abrus precatorius</td>
<td>(v) <em>kindjilkwindjil</em></td>
<td>seeds used for ornamentation, bracelets etc. Apparently poisonous.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia auriculiformis</td>
<td>(t) manyarrngark (large tree) (s) burdadaburdada (small tree)</td>
<td>seeds used as fishpoison. Seeds are crushed, wrapped in grass, and the water of small billabongs beaten vigorously. Stunned fish float to the surface.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia aulacocarpa</td>
<td>(t,s) (i) (ii) (i) in escarpment country manganbirr, andjeerrweerr (ii) in lowlands yeringendjen, kaa(l)mang</td>
<td>flowering cue for banggerring season.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia conserverse</td>
<td>(t) angambalbal</td>
<td>strong wood for use as woomeras, yamsticks, spear shafts.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia difficilis</td>
<td>(s) <em>(m)andj</em></td>
<td>fibrous bark strips used for the extraction of honey. Also used to make a string for binding (e.g. wrapping up Cycas dampers). Flowering cue for banggerring.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia dimidiata</td>
<td>(s) manburrel, anbarrada</td>
<td>foliage used as a fish poison in gurrung. As with other foliage fish poisons, a large bunch of leaves is tied up with string and small water-holes are beaten vigorously. The fish are stunned and float to the surface.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia gonocarpa</td>
<td>(s) andjendjen</td>
<td>foliage used as a culinary herb in the cooking of meats, especially kangaroos. Leaves are placed in the stomach cavity.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia holosericea</td>
<td>(s) mandulk, anlaabey</td>
<td>young straight stems used as shovel-nose and stone-spear shafts.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
2.

*Acacia humifusa* (s) *anmayitbaalen*  
(see *Acacia* sp. 1086)

*Acacia latescens*  
(s) *burdarburdar, anbilabila*

*Acacia latifolia*  
(s) *anbuluk, ankomkok*

*Acacia mimula*  
(t,s) *(m)* *andjarran*

this species has ‘big story’. The wood is also used for digging sticks.

*Acacia oncinocarpa*  
(s) *ankanbirr*

*Acacia platycarpa*  
(s) *anbarrkela*

*Acacia plectocarpa*  
(s) *anmulurdum*

*Acacia producta*  
(s) *manyqilminal, anyol*

*Acacia sublanata*  
(s) *anminam*

*Acacia torulosa*  
(t,s) *anbaandjen*

*Acacia umbellata*  
(s) *anlarrbe*

*Acacia sp. 1011*  
(s) *andjandjan*

*Acacia sp. 1086*  
(s) *anmayitbalem*  
*(see *Acacia humifusa)* Another species not collected which is apparently morphologically similar to *anmayitbalem*, but with thorns, is called *worukmud.*

*Acanthus ilicifolius*  
(m) *angellekberrk*

*Adenia heterophylla*  
(v) *?anbure, ?kumfluk*

no good for anything

(ii) *?manambopo*

fruit tucker in gunumeleng, gudjewk
#Aidia cochinchinensis  \( (t) \)  *djidu \( (d) \)
red-brown fruit tucker in gudjewk. See Celtis philippensis for Yirritja counterpart.

#Allosyncarpia ternata  \( (t) \)  *(m)anbinik
A 'special' tree providing shade in the escarpment, as well as an important source of honey.

Alloteropsis semialata  \( (g) \)  *(m)anyokkolomud
'sugarbag' grass, green stems chewed like sugarcane.

#Alphitonia excelsa  \( (t,s) \)  *(m)anbaarrkela
leaves used to wrap up meats for roasting. Fruits as pigeon tucker, flowers as possum, emu tucker.

#Alstonia actinophylla  \( (t) \)  *(m)andjendjok
white latex used as ceremonial paint. Large stems hollowed out for canoes.

#Alyxia ruscifolia  \( (s) \)  manminim, anmerriyi

#Amorphophallus campanulatus \( (h) \)  *kaarmayin, andikandu
\( (= A. variabilis) \)
An important yam species. The large 'mother' yam is called kaarmayin. The young ones, which are eaten preferentially, are called moorlkalk. The yams are roasted all night before being eaten. Gudjewk through banggerreng.

#Amorphophallus galbra  \( (h) \)  mandjingmi, amunyurri
Also an important yam which is prepared in the same manner as that above. The red fruits are eaten in gudjewk.

#Ampellocissus atetosa  \( (v) \)  mandjalgey, manwaak, anwaak
yam gudjewk time. fruit tucker (grape) also available gudjewk. Leaves can be used in place of paperbark (Melaleuca spp.) to wrap up meat for cooking in earth ovens.
Ampellocissus sp. aff acetosa (fine leaves) (v) madjaabey, an(k)unyek
uses as above. At least one other Ampellocissus occurs in the region, and this too is used similarly.

Amyema bifurcatum (e) mandayigandey, andjirran, andjinirran
Leaves are pounded, steeped or boiled in water and the white exudate used for washing sores. See also Decais-nina spp.

Aneilema siliculosum (h) mankowang, arbirrigowang
Yam tucker which can be eaten raw, gudjewk.

Antidesma ghaesembilla (s,t) (m)andjurukomalba
black ('currant') fruit available at banggerreng. If fruits are boiled or soaked in water, they provide a purple dye for basket making.

Antidesma parviflora (s) manyuku, andjerrukomalba
as above

Aponogeton elongatus (a) *(m)ankodbang
Yam tucker which can be eaten raw, gudjewk, banggerreng.

Aristida browniana (g) *(m)anbullambullam
inflorescences are dangerous to chew as can stick in throat.

Asparagus racemosus (v) geen, andolkbang, durrukkunyidmi
roots are pounded, steeped or boiled in water, and the exudate applied to sores. No. 1 medicine.

Atalaya variifolia (t) (i)(ii)
escarpment country anbirrimbirrim lowlands ankambalaari

Atylosia (= Cajanus) acutifolia (s) *mowwurrmbul, mowrumbul
leaves used for fish poison.
Atylosia (=Cajanus) cinerea (s) bildjekminyoh
Leaves used for fish-poison. (see Acacia dimidiata)

Austrodolichos errabundus (v) *(m)ankoorlapbang
Yam, banggerreng time.

Avicennia marina (m) mandoorrk, andjunggurruk
Hard wood, good for burning.

Baeckea intratropica (s) anyurroh

*Bambusa arthemia (g) *(m)ankoley
Young stems used for spear shafts, especially shovel nose and stone spears.

Banksia dentata (t) *goybuk
Young inflorescences are used to carry fire as they will smoulder all day. When inflorescences are more developed they are cleaned back to expose the 'velvet', and these are used as nostril ornaments.

*Barringtonia acutangula (t) *(m)ankangki
Itchy tree. The name derives from caterpillars which can cause severe irritation.

*Blepharocarya depaullata (t) anbidjanga, manbindey.

*Bombax ceiba (t) *gorroh, *gohdoh, *korroh
Stems hollowed out for making canoes.

Boronia lanceolata (s) anmiri

Boronia sp. 1120 (s) *(m)anbidwen

Bossiaea bosioides (s) anbirrim

Bothriochloa bladhii (g) baandulbaandul

Brachychiton diversifolius (t) manbadbad, ankojko(h)
Bark is stripped from young/small plants and rolled to make string for basket manufacture.
Brachychiton paradoxum (t) manmaarnayin, andjeermayin, andjaarmayin
Bark strips from young individuals used to make string for baskets. Young stems also used as a firestick. Fruit tucker, "bush peanut" (called anbadbad), available yekke.

Breynia rhynchocarpa (s) annowoorknowoork
Black fruit tucker, banggerreng.

Bridelia tomentosa (s) *(m)anwworknowoork
Black fruit tucker, banggerreng.

Buchanania arborescens (t) *(m)anbiggurrid
Black fruit tucker, gunumeleng.

Buchanania obovata (t) *(m)andwimi, *(m)andudjmi
Green fruit tucker, gunumeleng.

Callitris intratropica (t) *(m)anlarr
Hard wood used for making hooked spears, woomeras, corroboree sticks.

Callitris arborescens (t, s) *(m)anbandarr
No. 2 wood for hooked spears and corroboree sticks.

Callitris brachychaeta (s) andjimbak
No. 2 wood for hooked spears and corroboree sticks.

Calycopeplus casuarinoides (s) anbiddegdeng

Calytrix achaeta (t, s) andjimbak
Good fire wood, 'kerosene' wood, for starting fires when wet.

Calytrix arborescens (t, s) *(m)anbandarr

Calytrix brachychaeta (s) andjimbak

2 No. 2 refers to anything that is second-rate.
No. 1 is good stuff

1 Callitris (cypress pine) is not strictly a vine-forest species, but commonly grows in association with vine-forest in Kakadu.
Calytrix decussata  
(s) anyilwin

Calytrix exstipulata  
(s) anbandarr, manbirrbirr

No. 2 wood for hooked spears and corroboree sticks.

#Canarium australianum  
(t) mandey, andidi

Soft wood for making dug-out canoes.

#Canthium lucidum  
(t) anmomdwak, manmarrembollem

Red fruit tucker, gunumeleng.

#Canthium sp. 920  
(s,t) andulkmin


Capparis umbonata  
(t) bukbuk, Kayiwom

Good 'guava' tucker, gudjewg. Green and soft when ripe.

#Capparis sepiaria  
(v) ngil, kin

Thorny vine.

#Carallia brachiata  
(t) *(m)anwidu

Small red fruit tucker, gunumeleng.

Cardiospermum halicacabum  
(h) anyilwin

If leaves are touched, one has to wash one's hands. Leaves are evidently toxic.

#Carpentaria umbonata  
(t,p) yirrigiyirrigi, ankanbayin

The pith of the meristem is eaten raw or lightly cooked. This 'cabbage' is considered a delicacy. The basal sheaths of the fronds are used as water carriers and temporary storage containers.

Cartonema sp. 992  
(h) yarrambaam(Y)

Perennial geophytic herb with multiple tubers. Only the young tubers are used as yams, banggerreng-wurrgeng. The tubers have to be peeled and cooked at least 2 times before eating. Little bit cheeky. Found only in sandy country.

1 'cheeky' refers to anything bitter or of nuisance value (e.g. thorny vines, spiky grasses).
Cartonema sp. 1070

(h) *(m)anmortidjak, ankanbelu (D)

Tubers eaten in gudjawg. Needs to be peeled and cooked only once. Found in rocky ridges and in the escarpment. Good kangaroo tucker.

Carissa lanceolata
(s) ?andalkbayin

Cassia lateriflora
(s) manbunbarr, ankurrkkurrkmoor

Leaves used as culinary herb in the cooking of kangaroo. Leaves placed in stomach cavity.

Cassia leptoclada
(s) *mowwurrumbul(k)

Leaves used as fish poison see Acacia dimidiata). Also when cooked in water may be used for treatment of sores.

Cassia venusta
(s) ankomkorrk

Possible fish poison.

#Cassytha filiformis
(v) *(m)anburrunburrun

No. 2 tucker fruit, yekke. Emu tucker.

#Cathormion umbellatum
(t) *ganadjulin

Shade tree on edge of floodplain.

#Cayratia maritima
(v) *(m)ankodbey, ankodbi (D)

Black grape tucker, gudjawg. Tuberous roots peeled and roasted, gudjawg.

#Cayratia trifolia
(v) *(m)ankodbey, ankodbi (Y)

As above

#Celtis philippensis
(t) djidu (Y), andjarrdaakin

See Aidia cochinchinensis for Duwa counterpart: Fruits ripen gudjawg, gunumeleng, but are not eaten.

#Cheilanthes spp.
(f) mankobin, mankoorbin, anwoytwoy

#Choriceras tricorne
(s) ?

Good wood for woomera handle.
Chrysopogon fallax  (g) mayikolobarr
Roots good tucker for agile wallabies in gurrung.

Chrysopogon latifolius  (g) mandalbang, bundarr
Leaf blades with sharp cutting edges.

#Cissus adnata  (v) ankorrwan
black (grape) tucker, banggerreng.

#Cissus sp. aff. adnata  (v) anmalkgrruwa
Black (grape) tucker, banggerreng.
Root stock eaten by rock wallabies.

Cleome viscosa  (s) anyururr, ankamulkamul

#Clerodendrum floribundum  (s,t) *(m)anmoorlorrk, *(m)anmolorrk
No. 1 firestick. Hollow young stems used as smoking pipes.

#Clerodendrum sp. 978.  (s) ankoorrkoorr
Bark of young stems used for making string. Firestick.

Cochlospermum fraseri  (t) *(m)andjed (D)
Young stems used as No.2 firestick.

Cochlospermum gillivraei  (t) anbiyarrang (Y)
Cochlospermum gregorii  (t) anbiyarrang (Y)
Swollen roots of young trees cooked like yams, wurrgeng. Tastes like cassava.
Important escarpment country tucker.

Coelorrhachis rotthoellioides  (g) *(m)ankanbalde

#Coelospermum reticulatum  (s) mandjundum, andjurrunder
Fruit tucker banggerreng. Roots provide yellow dyes for basket, etc. Roots are dug up, peeled to expose yellow sap, and, then steeped in water to develop the dye colour.

Comesperma aphyllum  (s) ankulurrkmoor
Culinary herb for cooking of kangaroos at any season except gurrung, when it is too dry.
Commelina ensifolia  (h) anbidkalkbed (D)
Yam tucker, banggerreng

Corchorus psidioides  (s) manbodjub, anwalngwalng

Corynotheca lateriflora (h) *(m)anbunbarr
Culinary herb used in the cooking of meats (emu, macropods, goanna).

Crinum asiaticum  (h) djiladdjilad, ankilkil
Bulbous yams too cheeky to eat.

Crotalaria crassipes  (s) anlerrelerre
Foliage used as fish poison.
(see Acacia dimidiator).

Crotalaria linifolia  (s) anbidjibidji

Croton arnhemicus  (t) kundaaminaabek, anlangaakmarrey
Firestick.

#Croton byrnesii  (t) anmayitgulba, andjuin
Light wood good for woomera.

#Cryptocarya cunninghamii  (t) yirrikol, anbindungjarra
Pigeon tucker (fruits).

#Cryptocarya triplinervis  (t) anloorlorr, ankorrnan
As above.

#Cupaniopsis anacardioides  (t) anndjarrwoor

Cucurbitaceae sp. 960 (possibly Cucumis melo)  (v) mandoldol
bush 'watermelon', gudjewg.

#Curcuma australasica  (h) gulumuduk, anbindjarra
Cheeky 'onion'. No good tucker.

Cycas armstrongii  (s) mandingu, ankoorkboh
Not common in region, but a food staple of much significance elsewhere. "Fruits" are placed in water to rot for "about a month Ready for use when starting to ferment. Drain. Knead into a damper loaf. Wrap in paperbark bound with string (especially from Acacia difficilis). Roast in coals or antbed oven.
Cymbopogon procerus

Leaves used for making a lemon scented 'tea'. Given to children to quieten them.

Cynanchum pedunculatum

Good yam tucker, yekke, sometimes gudjewg. 'Fruits' can also be eaten. cooked or raw.

#Cyperus diffusus, C. javanicus

Leaf blades of these species and other large-fronded Cyperus are used for the making of baskets.

Cyperus sp. 1000

Ripened seeds (in banggerreng) are rubbed into head hair and then follows the fun of getting them out. The name doort also refers to the head louse.

Cyperus sp. 1132

Root bulb provides a red dye, for basket making. If pandanus or Cyperus leaves are left to steep for 2-3 days then dye colour turns black. As well, if this species is burnt (in wurrgeng) along with the floodplain habitat generally, the dye colour is automatically black.

Decaisnina brittenii

Strong medicine for sores. Leaves are steeped in water and boiled.

Decaisnina signata

As above.

#Dendrobium dicuphum

Pseudo-bulbs are smashed to extract green exudate for use as a ceremonial paint.

#Denhamia obscura

Yellow underbark used as a fish poison. Bark strips are tied up with grass and used similarly as for a foliage fish poison (see Acacia dimidiata).
**#Dioscorea bulbifera** (v) *mangindjek, ankindjek*

Water yam. A most important yam which becomes available in banggerreng, and may be utilised through to gunumeleng. Even though aerial shoots die back in the dry season, the yams may be located by tracing along the vines from conspicuous seed capsules. This yam needs to be leached before cooking. It is sliced up thinly and placed in water overnight before roasting.

**#Dioscorea transversa** (v) *gorrbada, gayiwol*

Long yam. Another important yam which is available year round. Does not require leaching, but may be eaten after simple roasting. The 'mother' yam is called *mandiley* and when it is dug up, some of the side branches ('young yams') may be left behind, ensuring the perpetuation of the resource.

**#Diopyros ferrea var. ferrea** (t) *murrunkun*

Good yellow fruit tucker, gunumeleng.

**#Distichostemon hispidulum** (s) *anloorrloorr*

Foliage and fruits used as fish poison. (see Acacia dimidiata).

**Dolichandrone filiformis** (t) *mayindengabek, andergaabek*

Hardwood for digging sticks, axe handles and woomeras.

**#Drynaria quercifolia** (e,f) *mankobin, djilladdjillad*

Rhizomes can be roasted and eaten anytime. Apparently not a major food.

**#Drypetes lasiogyna** (t) *?guluwuk*

Wood makes for good woomeras, axe handles.

**#Dysoxylum oppositifolium** (t) *ularr*

Strong wood for fighting stick.
Elaeocarpus arnhemicus (t) andjeerdwe
Pigon tucker, gunumeleng.

Eleocharis sp. aff. brassii (a) ankulyayitj
Edible corms available from late wurrung through to gunumeleng. Good tucker for magpie geese and humans. Eaten raw or roasted (water chestnut).

Eleocharis sp. aff. dulcis (a) mankuladj, ankulyayitj
As above.

Eleocharis sp. M33. (a) bunda, manbinmuk
Corms only as goose tucker, gurrung.

Eleocharis sp. M6 (a) mandjirrikaala, anwayinwayin
Little corms available in banggerreng. Roasted.

Eriachne obtusa (g) ankarrndalk

Eriachne triiseta (g) *(m)anbullumbullum

Eriosema chinense (s) mankurri, anbulpi
Roots roasted, banggerreng.

Ervatamia orientalis (s) mandoorr, andoorrbakbak
Red fruit, gudjewg.

Erythrina vespertilio (t) *marraka, karran
Good wood for woomeras.

Erythrophloeum chlorostachys (t) *(m)andubang
Extremely hard dense wood which is good for posts, burning, and the spear shafts of hook and fighting spears. A gum extracted from the roots called gaarbi-kalweyid is used as an adhesive for binding spear points on to spears etc. The gum is warmed over a fire until pliable and soft, applied until set, and then fined with a sharp instrument. Mandubang also features in mythology.
Eucalyptus alba
Eucalyptus alba var. australasica
Eucalyptus bleeseri
Eucalyptus clavigera
Eucalyptus confertiflora
Eucalyptus dichromophloia
Eucalyptus ferruginea
Eucalyptus herbertiana
Eucalyptus jensenii
Eucalyptus kombolgiensis
Eucalyptus latifolia
Eucalyptus miniata
Eucalyptus papuana
Eucalyptus patellaris

(t) mankombolo(k)

(t) manbenben

(t) mankalarr, andjuid

Small hollow stems (eaten by termites). Used for making didjeridoos.

(t) mankombolo(k)

Good cooking wood, burns slowly.

*birrkul

(t) mandjadbag
When flaky barked = angoori.
When white barked = annaabarrek.

Good trees for sugarbag.

(t) andjoney

Eucalyptus herbertiana

(t) *(m)anbunheay

Small hollow stems used for making didjeridoos. Good sugarbag trees.

(t) andjibin, anbaaderre

Eucalyptus jensenii

(t) manyarryan

Eucalyptus latifolia

(t). *(m)andooroork

Eucalyptus miniata

(t) *(m)andjalen (long barked)
*(m)anarakmi (short barked)

Long fibrous bark strips good for lighting fires. The bark of *(m)anarakmi however is not as useful. The onset of flowering taken as a sign for the start of wurrgeng, and as well, that the dry time is properly arrived. The seeds may be eaten raw.

*(m)anbenben

Eucalyptus papuana

(t) *(m)anbenben

Eucalyptus patellaris

(t) andjalwuk

Good dense wood for cooking fires.
Eucalyptus phoenicea (t) anmadba
Eucalyptus polycarpa (t) manbuney, bunoy
   Flowering cue for the start of yekke.
Eucalyptus porrecta (t) bayiru, anngal
Eucalyptus ptychocarpa (t) mankaorlanglang, anngal
Eucalyptus setosa (t) mandangdlang,
   Hollow stems used for making didjeridoos.
Eucalyptus tectifica (t) mayinyowgoth
Eucalyptus tetrodonta (t) manborrogoo, manbologoor, anrevel
   Stringy bark used for multiple purposes:
   for stringybark houses in the wetseason,
   bark canoes (bilem) and didjeridoos.
   The end of flowering is a cue for the arrival of gurrung.
#Exocarpus latifolius (t,s) *(m)andumu(k)
   The wood is burnt as a mosquito repellent. Strong wood for yamsticks etc.
#Ficus benjamina (t) ankarakin
   Fruits eaten by birds only.
#Ficus leucotricha (t) mandarreybulgey, anbaanek
   Small edible tucker available year-round.
#Ficus opposita (t) *larr, mambula
   Black fig tucker available year-round.
   Leaves used as sandpaper to smooth wooden implements. Small stems used as fire sticks.
#Ficus platypoda (t) mandarreybulgey, anundjelk
   Small edible fig tucker available year-round.
**Ficus racemosa**
(t) *manmanaawan*
large yellow figs, good tucker year-round.

**Ficus scobina**
(t) *larr, anbambula*
Good sweet black tucker available year-round. Leaves used as sandpaper for wooden implements.

**Ficus virens**
(t) *(m)anboornde*
Good shady tree on edges of floodplains, near patches of jungle *(m)anggarrey* especially. The bark and the fire aerial roots used to fashion string for the making of fishnets.

**Flacourtia territorialis**
(s) *gunkulurr, gundun*
Black fruit tucker, gudjewg.

**Flagellaria indica**
(v) (i) *arrawuka, midjaakol*
(in closed forest) used for making armbands, for wrists on forearms.

(ii) *anrong* (in jungle springs only)
When vine is flexible (i.e. midjaakol, arrawuka) it is used as a very strong binding rope (e.g. in the making of bark canoes - see Eucalyptus tetrodonta) When vine is rigid (i.e. anrong) it is fashioned into sharp pointed for sticks for testing honey hives. Anrong is often found in the same habitats as Allosyncarpia ternata *(m)anbînik*, an important "sugarbag" tree.

**Ganophyllum falcatum**
(t) *kuluwuk*
Large stems used to make dug-out canoes.

**Gardenia fucata**
(t) *(m)andjunggurk*
Culinary herb for cooking kangaroos.

**Gardenia megasperma**
(t) *(m)anbarbirr - escarpment country, andjarrbiwarra - lowlands

**Gardenia sp. 815**
(t) *manbarbirr, andjarrbiwarra*
#Glochidion xerocarpum (s) andjibil, anwaak
#Glycosmis pentaphylla (s) kyrumbu
Comphrena sp. (h) ankalakirrud
Goodenia cirriferata (h) manbulbul, 'ankamulkamul

Fish may be cooked on leaves of this plant.

Gossypium hirsutum (s) gaarbadja

Introduced cotton bush.

Grevillea decurrens (s,t) (i) *(m)anbadbad - escarpment, country
(ii) andjangeerreerr - lowlands
Seeds extracted from pods and eaten raw.

Grevillea dryandri (s) *anjamgoh
Grevillea goodii (v) *anjamgoh
Grevillea heliosperma (s,t) *(m)anbadbad - escarpment
andjangeerreerr - lowlands
Seeds extracted from pods and eaten raw.

Grevillea mimosoides (t) ammandoerbid
Grevillea pteridifolia (t) manbanggoh, andjandjek, andayidjek
Grevillea pteridifolia (s) anbirrim

#Grewia multiflora (s) *(m)alabandja

Good fire-stick. Bark is stripped and rolled to make string.

#Grewia retusifolia (s) mandjodmong, andjodmoh

Red-brown sweet fruit tucker, banggerreng. New leaves in gunumeleng, gurrung used to make a 'tea'. Médicinal?
Grewia xanthopetala  (s) *(m)alabandja.

As for Grewia multiflora.

Gronophyllum ramsayi  (t,s) marrun, marruin

Growth apex cut out and eaten as 'cabbage'. Water container made from basal sheaths of old frond. Leaves of young plants may be eaten raw.

Gymnanthera nitida  (v) andildil

White latex used for ceremonial purposes.

Gymnema sp. 1018  (s) *(m)anbun

Haemodorum brevicaule  (t) waardagid, anmangilaapoh

Young stems used for shafts of fish spears.

Haemodorum corymbosum  (g) wirdlwirdil, balbolbin

Roots used as a red dye for making of baskets etc. Roots pounded and then steeped in water to develop colour. Strings and prepared fronds for basket making are then added.

Haemodorum sp. 1126  (g) *wirndilk

Uses as above.

Hakea arborescens  (t) ankaladjeerdid

Hard wood for spears, digging sticks, corroboree sticks, axe handles.

Helicia australasica  (t) ?anbiggurrid

Black fruit tucker, gudjewg.

Helicteres sp. 903,922  (s) mandjodmong, alabandja

Seeds edible in yekke. Bark is stripped and rolled to make string.
Helicteres sp. 1106
Heliotropium indicum
Heteropogon contortus
Heteropogon triticeus
Hibbertia oblongata
Hibbertia species
Hibbertia sp. D120
Hibiscus arnhemensis
Hibiscus byrnesii
Hibiscus leptocladus
Hibiscus merawkensis
Hibiscus simensis
Hibiscus tiliaceus

(s) anmayimilinggoh
(h) andjilawat
(g) Bangdulbaandul
(g) mayiaardja

Sugar cane grass, stalks chewed in gunumeleng.

Hibbertia oblongata
(s) *(m)anyilingbilk, *(m)anyirringbilk

Nearly all species of Hibbertia are recognised as good fire sticks.

Hibbertia species
1008, 1033, 1056, 1061
(s) As above

Hibbertia sp. D120
(s) ankulabum

Carrot-like yam which is peeled before eating raw or cooked, banggerreng through gunumeleng.

Hibiscus arnhemensis
(s) *(m)annyaal(k)nyal

Little bit fire stick.

Hibiscus byrnesii
(s) *(m)annyaal(k)nyal

As above.

Hibiscus leptocladus
(s) *(m)annyaal(k)nyal

As above.

Hibiscus merawkensis
(s)ฤดูกาลดิจุ้นเจนเจน, ้ออกเป็นกิ้งก่าม่วงลับพรหม

"emu’s foot": refers to the leaf shape.

Hibiscus simensis
(s) *(m)annyaal(k)nyal

Little bit fire stick.

Hibiscus tiliaceus
(t) *alabandja

An important wood for the making of spear shafts. These may be straightened over fire. The bark may be used for making string. Young stems are a favoured fire-stick.
Hibiscus sp. 918  
(s) barrkar  
Fire-stick and straight stems used for fighting spear shafts.

#Horsfieldia australiana  
(t) ammayitkulba  
Fruit kernels eaten raw, gudjewg.

#Hoya australis  
(v) andildil  
Milky latex used as a ceremonial paint.

#Hypoestes floribunda  
(s) andulkban  

Hypoxis marginata  
(g) maadudjak  
Yam tucker ready banggerreng. Roasted.

Hypoxis sp. 953  
(g) djarrbal, anburra  
Long yam tucker ready banggerreng. Roasted.

#Hyptis sauveolens  
(h) *widni  
No. 2 fire-stick.

#Ichnocarpus frutescens  
(v) andildil  
Milky latex used as a ceremonial paint.

Imperata cylindrica  
(g) *(m)angarnbaldje, angaardid  
The perennating underground organs are very sharp and will 'killem foot' if trodden on.

Indigofera saxicola  
(s) *(m)ankandqork  
When these plants are burnt they leave behind very sharp stubs which will 'killem foot' if trodden on.

#Ipomoea abrupta  
(v) *(m)anburrey  
Long yam tucker available end of gudjewg through to gurrung.

Ipomoea diversifolia  
(v) *gaarrbilk  
'long potato' yam. Anytime. Roasted.
Ipomoea gracilis  (v) *gaarrbilk' (D)
Yam tucker, banggerreng. Roasted.

Ipomoea sp. 1175  (v) *gaarrbilk (Y)
Differs from the above species through possession of narrower leaf blades. No tucker.

Ipomoea graminea  (v) mankongkong, anwoorpmi

Ixora tomentosa  (t) did, anbalowaark
Black fruit tucker, gunumeleng. 'moon tree'.

Jacksonia dilatata  (s) manbirrimanyak
ankunyun (escarpment), ankundilm (lowlands).

Jacksonia vernicbsa  (s) manwulnikoork, ankunbilarri

Jacquemontia browniana  (s) anmurrungi

Jasminum simplicifolium  (v) manleklek

Jasminum sp. 1107  (s) anmayinbiimayin

Lekea rubra  (s) *(m)anwaak
Black fruit tucker, gudjew.

Leptocarpus spatheus  (g) anyayityayi,
*(m)angallerek (Y) - lowlands.
(D) - escarpment
Hollow-stemmed, segmented graminoid which is broken into small parts and made into bracelets.

Lindsaea ensifolia  (f) mankoorbin

Litsea glutinosa  (t) *wurr
Wood used for making woomeras.
Livistona benthami
(t,p) *barbinbarbin

Livistona humilis
(t,p) (d) mankulturut

marrabi (large),
kulurut (small),

Apices cut out and eaten raw or roasted (cabbage).

'Cabbage' also provides a pink dye if soaked in water. If left this colour will eventually turn black.

The stem is cut off at the base and the pith extracted. This is pounded and then steeped in water to make a beverage.

Livistona inermis
(t,p) (Y) mandjandad djangelerr

Cabbage eaten as above. 'Tea' made similarly.

Lophopetalum arnhemica
(t) *(m)anwolbon

Light wood used for making woomeras.

Lophostemon grandiflorus
(t) mandad, anngbutdj

Good tree for sugarbag.

Lophostemon lactifluus
(t) *(m)anwurrben

Lumnitzera racemosa
(m) gundaabarr

Ludwigia octovalvis
(h) dabayiyin

#Luffa cylindrica
(v) mandofild, andowk

Yams too cheeky; pig tucker.

#Lygodium flexuosum
(f,v) *annyilm

Macarthuria apetala
(s) ankurkurrkmoor

Culinary herb for cooking of goanna, kangaroo.
Mackinlaya macrosciada (s) *(m)anbonking
Malaisia scandens (v) milil
Long strands of this vine are used for making fishing nets.
Malachra fasciata (s) *(m)anyalknyal (D), anumwen (Y)
Maranthes corymbosa (t) maagulurr, maagurrul, ammoorkkulurr
Large stems hollowed out for canoes.
Maytenus ferdinandi (t) mankaawarrk, anbinmoh
Kerosene wood when green or dry, for starting fires when wet.
Melaleuca argentea (t) maardel, ankoorgoh
As with other paperbark types of Melaleuca, the bark is used for a variety of uses: as bedding; for wrapping up meats and fish in cooking; for wrapping up dampers made from Cycas in cooking; in shelters; for paperbark watercraft; for use as temporary water containers; in food storage, fire tinder; and for wrapping up human corpses for burial.
Melaleuca cajuputi (t) manmu(l)mu, maarmoormoor.
Uses as above.
Melaleuca dealbata (t) manbarra
Very strong wood which never rots.
Since the paperbark is tightly bound to the tree it is not used for many of the uses described as for M. argentea.
Melaleuca leucadendron
(t) sp. 966 *m(andal)
sp. 963 manbulbul - very thick paperbark.
sp. 963 barridbarr, angot, angwot - very tall.

M. leucadendron paperbark is used for the full range of uses as described for M. argentea. The leaves are also used to flavour roasting meat, and the wood is also used for making wooden rafts. The thick-barked form (manbulbul) is especially prized for making shelters.

Melaleuca magnifica
(s) anambopo

Melaleuca nervosa
(t) *(m)ankulkul

Used similarly as for M. dealbata

Melaleuca punicea
(s) *(m)anbandarr

Very strong wood used for making spear tips and digging sticks etc.

Melaleuca symphyocarpa
(t,s) manlombeng, anboorndum

Very strong wood used for making fighting spears. The leaves may be boiled or soaked to make a 'tea' for cough medicine.

Melaleuca viridiflora
(t) *(m)anbididubu
*kaadakka - when in flower, early gudjewg

Uses as for M. argentea but bark often compact and as such is not widely used.

Melaleuca sp. 1036
(t) mandjim, andjil

Uses as for M. argentea in building of shelters especially.

Melastoma malabathricum
(s) anberramberram

Melochia corchorifolia
(s) *mayitdenge

Bark is stripped and rolled to make string for use in small fishing nets.

Melochia sp. 1130
(s) ankumbe
Micaira spp. (spiky types) (g) anyokkorrol (D) e.g. sp. 1068

Micaira spp. (soft types) (g) anyokkorrol (Y) e.g. sp. 1097

Resurrection grasses. Spiky types dry out and can be very painful to walk on.

Microstemma tuberosum (h) *badju

Bush potato available gunumeleng, gudjewg. Eaten raw or cooked.

#Morinda citrifolia(t,s) manngukmayin, manbowelarrk, anbalawok

The bark of the roots is boiled and used as a yellow dye in making baskets etc. Fruit tucker, banggerreng.

Mukia sp. 1044 (v) mandowk, anyunggerreng

Yams too cheeky to eat.

Murdannia gigantea (h) *(m)ankowang

Yam tucker, banggerreng, yekke. Eaten raw or roasted lightly.

Murdannia graminea (h) *(m)anbidkalkbed

Yam tucker, banggerreng. Eaten raw or roasted lightly.

Murdannia sp. 950 (h) mankowang

Yam tucker, banggerreng. Eaten raw or roasted lightly.

Murdannia sp. 1104 (h) mankowang, anbirrigowang

Yam tucker, banggerreng. Eaten raw or roasted lightly.

#Myristica insipida (t) ammayitkulba

Good hard wood for woomeras, digging sticks, axe handles.

#Nauclea orientalis (t) *(m)ammarreywahwah

Edible but bitter fruit tucker, gunumeleng.
Nelumbo nucifera
(a) *wurrunining
An important floodplain plant food at gurrung. The seeds (anmin) are available at this time, as are the fleshy roots or rhizomes, (anmeer) which are dug up and roasted.

*Nervilia holochila

Nymphaea gigantea
(a) *(m)andem
Another important floodplain 'yam' tucker available from gurrung. At this time the edible portion is enclosed in a hard shell, which is cracked open. The edible 'flesh' is then boiled. The whole corm is called mimdubey, the 'mother yam'. In gunumeleng more corms are formed. After the first rains the shoots are also eaten, as are the flower stems *(m)anbadmoh and seeds (garnwerrra, angan, annayin) in gudjewg.

Nymphaea gigantea
var. violacea
(a) *barrddjunga
Similar to above but the corms are eaten raw. Available from gurrung through gudjewg.

Nymphoides hydrocharoides
(a) manmarreybulmarreybul
Nymphoides indica
(a) manmarreybulmarreybul
Nymphoides sp. 994
(a) manmarreybulmarreybul, marreybul (Y)
white flowers.
Nymphoides sp.
(a) mandem, yalgey (D)
yellow flowers. Corms eaten raw or roasted, gurrung.
Nymphoides sp. 1110
(a) andemdoorrken, andoorrken
Olax pendula
(t) wurrumbu
Small red fruit tucker, gunumeleng.
Opilia armentacea (v) manleklek, ?anbin

Creamy fruit tucker, gunumeleng. Fruit peeled and leached, and applied to sore eyes and other inflammations.

Oryza perennis (g) manrol

A floodplain rice which is available gudjewg, banggerreng. Flower stalks are collected, dried in the sun, and shaken to collect the seeds. The seeds are ground up in grinding hollows etc., and used to make a damper.

Osbeckia australiana (s) mandjarrandjarran, yarrangkan

Developing fruit eaten, gurrung. Tastes like 'black jam'.

Owenia vernicosa (t) manbalarr, anbanadja

Inner red bark used as a fish poison.

Pachynema complanatum (s) manbalk, anbidjibidji

Pachynema sp. 1058 (s) djangkooroor

No. 2 fire stick.

Pandanus aquaticus (t,s) *(m)andjimdjm

Kernel inedible.

Pandanus basedowii (t,s) manmurringnyam, anporrgey

Kernel extracted and roasted before being eaten.

Pandanus spiralis (t) manbelk, anyakngarra

Kernel extracted from drupes and roasted. Leaf blades stripped of their outer layers, dried, dyed, and used in manufacture of baskets, mats, dillybags, etc. A beverage can be prepared from the smashed fruits.

Panicum paludosum (g) manrol

A floodplain 'rice' which flowers and seeds in gudjewg, banggerreng. Preparation as for Oryza.

Parinari nonda (t,s) manngukbut, anbilimanyak

Parsonsia velutina (v) anwoytwoy, dijyelkun
Paßiflora foetida  
Edible fruits available throughout the year.

Patersonia macrantha  
Flowers are emu tucker.

Persoonia falcata  
Favoured fruit in gudjewg, gunumeleng.

Petalostigma pubescens  
Good fire wood. Fruits are possum and emu tucker.

Petalostigma quadrilobulare  
Emu tucker.

Phragmites karka  
Shafts used for fish spears.

Phyllanthus ciccoides  
Leaves used as fish poison. (see Acacia dimidiata).

Pimelea punicea  
Kangaroo tucker.

Pimelea sp. 1063  
(see Acacia dimidiata).

Pityrodia jamesii  
Kangaroo tucker.

Pityrodia sp. 1051  
Light wood good for woomera and shafts of hook spears. The fruits are possum tucker.

Pityrodia sp. 916  
Light wood good for woomera and shafts of hook spears. The fruits are possum tucker.

Planchonella arnhemicus  
Light wood good for woomera and shafts of hook spears. The fruits are possum tucker.
Planchonella pohlmanniana (t) djjmed, andjimmit
Fruit tucker, yekke.

Planchonia careya (t) *(m)ankol - large tree
'Mango' fruit available gunumeleng.
(s) djjulba - shrub
String made from bark strips by rolling.

Platyzoma microphyllum (f) andjifat (y)
Plectrachne pungens (g) *(m)anbarrowwalk
Spiky leaf blades are very sharp and unpleasant to walk through.

#Polyalthia holtzeana (t) *yirrbin
Good wood for woomera.

#Polyalthia nitidissima (t) *yirrbin
Good wood for woomera.

Polycarpæa sp. 1111 (h) djeedjewu
Black wallaroo tucker.

Polygonum attenuatum (a) arldan
Hollow stems used as pipes for smoking tobacco.

#Popowie australis (t) *yirrbin
Good wood for woomera

#Pouteria sericea (t) *(m)andangnud
'Black plum' fruit tucker, gunumeleng, gudjewu.

#Premna acuminata (s,t) gundjaakol, andjaakol
No. 1 fire stick.
Pterocaulon sphacelatum (h) baki
Leaves are dried in the sun and smoked as substitute for tobacco.

Ptilotus sp. 107f (h) anbanogin

#Rauwenhoffia leichhardtii (s,v) *(m)anbadbirri
'White banana'. A sweet and favoured fruit, gudjewg.

#Rhodamnia cinerea (t) andjarrwootr
Good purple tucker, gudjewg.

Scaevola angulata (s) andulkwoytwoy

Schoenus sp. 1095 (g) andalkboorla

#Scleria spp. 949, 1100 (g) mayiyikmud, warekmud, wayiyikmud
Sedge with sharp leaf blades. The names warekmud etc. may be applied to any sharp cutting sedge and grass types.

#Securinega melanthesoides (s) mankalelle, andel
White fruit tucker, gunumeleng.

Solanum cannabina (s) manbunda, meleerrweb
Good light fuel for starting fires.

Setaria apiculata (g) gunbedmud djarran, bakadji gunbedmud
Flowerhead resembling tail of white tailed possum.

#Smilax australis (v) *(m)amorrong
Spiny vine.

Solanum asymmetriphyllum (s) anbambulbambul
Fruit eaten by rock kangaroos.

Solanum clarkiae *(s) *(m)andjabuljagbul, *(m)andjaveldjavel
Fruit is kangaroo tucker only.

Solanum echinatum *(s) *(m)andjabuljagbul, *(m)andjaveldjavel
Fruit is kangaroo tucker only.
Sonneratia caseolaris
Sorghum intrans
Sorghum plumosum
Spermacoce exserta
Spermacoce spp. 951, 952, 1081
Sporobolus virginicus
Stemodia caerulea
Stenocarpus cunninghamii
Stephania japonica
Sterculia quadrifida
Striga curviflora
Strychnos lucida
Syzygium armstrongii

(m) *ngulurr
(g) *manbedje (Y) atal
(g) *naadjarr (D)
(h) *bambulbambul

mankodmonmon, mankaladjirrak

Emu tucker.

(g) *maawaagil

(s) *anlowak

Medicine for rock kangaroos. These animals rub themselves with these plants to get rid of lice and, as well, as a cure for sores.

(t) *anmayinkohdjej

Good wood for woomeras, digging sticks etc.

(v) *anburrey

?Good yam, gunumeleng

(t) *mankarrayikmayin-large individual
angogoh-small individual

No. 1 'bush peanut' fruit, eaten raw. Available gunumeleng. Bark of small individuals makes good string.

(h) *baka, *baki

Bush tobacco. Leaves dried in the sun and smoked as a replacement for Nicotiana tobacco.

(t) *mankudu, ankoordu

Leafy branches, often used in conjunction with other fish poisons, used to stun fish in small water holes. Fruits are bird and possum tucker only.

(t) *mankarradjirr, *mankarradjil

Edible, (but not favoured), 'white apple' tucker, gunumeleng - gudjew.
Syzygium eucalyptoides ssp. bleeseri(t)  
mandjalbidoh, andjobirroh
'White apple' tucker, gunumeleng.

Syzygium eucalyptoides ssp. eucalyptoides(t)  
*(m)anbongbong
'White apple' tucker, gunumeleng - gujewg.

'Syzygium forte (t) *(m)anboyerre
'White apple' tucker, gujewg.

'Syzygium minutuliflora (t) ?
'Small white apple' tucker, gunumeleng.

'Syzygium operculata (t) ?
'Red apple' tucker, gunumeleng.

'Syzygium suborbiculare (t) mandjaardu, ankerribuwi
No. 1 'red apple' tucker, gunumeleng.

'Tacca leontopetaloides (h) moornayin, annunyurri
Fruits eaten banggerreng. The yams are not eaten by themselves, but may be cut up and leached along with (m)angindjek (Dioscorea bulbifera) before being eaten.

Templetonia hookeri  
*(m)ankaanharri, goopa
Wood used for making 'hose' of womberras.

Tephrosia conspicua (s) *mowwurrumbul(k)
No. 1 fish poison, foliage. (see Acacia dimidiata),

'Tephropsia flamma' (g) *bulndubuldu, amirri
Fish poison, foliage.

Tephrosia phaeosperma (s) *mowwurrumbul(k)
Fish poison, foliage.
Tephrosia spp. 1042, 1043, 1062
(s) *mowwurrumbul(k)
Fish poison, foliage.
(see Acacia dimidiata).

Tephrosia sp. 1053
(s) ankanbilarri
Fish poison, foliage.

Tephrosia sp. 990
(s) animmimigan

Tephrosia sp. 1069
(s) *(m)aninam
Leaves are good medicine for black wallaroo. These kangaroos rub themselves with these plants to remove lice and cure sores.

#Terminalia carpentariae
(t) mammoorban, anmarrbila
No. fruit tucker, eaten raw, from wuirrgeng through to gunumeleng. A red gum, exudate (angurrk) of this tree may be eaten raw or lightly cooked.

Terminalia ferdinandiana
(t) *(m)amnolak
No. 1 'billy goat plum', eaten raw, gunumeleng.

Terminalia grandiflora
(t) *(m)anbaardenre
Nuts are split open to reveal a kernel inside which is considered very good tucker. Available budjuwng, gunumeleng. Strong wood good for womeras etc.

Terminalia pterocarya

#Terminalia sericocarpa
(t) *maarkulurr
Sweet purple 'plum', gunumeleng. Favoured food of Torres Strait pigeons.

Terminalia volucris
(t) *(m)ankunbulk

#Timonius timon
(t) ankudwud
Firewood.
#Tinospora smilacina
(v) gulaggulag, anbalbail, andjilikum

#Trema aspera
(s) *(m)annwoorknowoork
Small black fruits sometimes eaten, gunumeleng.

Trichosanthes cucumerina
(v) manworrmanyak angurrungkirring
Fruits too cheeky.

Tricostularia undulata
(g) anaardenge
Roots may be eaten after roasting.
Yam tucker available anytime.

Triglochin procerum
(a) *(m)anbulet.
Good yam tucker, roasted, yekeke wurrungeng.

Triodia/Plectrachne spp.
These grasses provide the main ground cover in many escarpment/sandstone habitats. Many taxa are spiky or have sharp-edged leaf blades. The latter can cause severe skin irritation. Given the discomfort or impedance to walking they provide, and the very high combustibility of these grasses in general, it is not surprising that such ground cover was/is 'cleaned up' by burning as a matter of course. It is to be noted that the Linnaean taxonomy is uncertain for the following taxa listed under Triodia given that they were collected mostly in a sterile state, as well as being relatively difficult to identify.

Triodia microstachya
(g) *(m)angarrandalk
'Kerosene grass', a highly combustible fuel for starting camp fires.

Triodia plectracooides
(g) *(m)andjakmlnial
A spinifex grass with a resinous leaf which is both a good mosquito repellent when added to a camp fire, and a good medicine for bruises or internal pains. For application of the medicine, the grass may be heated in sand and applied to sore areas. As well, it can be boiled/steeped in water and the beverage applied to the hurting area, or drunk as a cough medicine. Good rock kangaroo tucker.
Triodia spp.  ankaarney (D) which are small and spiky  ankaarney (Y) which are long and spiky

Triodia sp. M27  (g) gundeerde

Triodia/ Plectrachne spp.

Tylophora sp. aff. crebriflora

Tylophora sp. 1116  (v) *ngarlbn, andildil

Typhonium alismifolium  Milky latex used for ceremonial purposes. The ripe fruit pods may be eaten raw or cooked, gudjewg.

Typhonium angustilobum  (v) *andjilat

Typhonium sp. 1170  Ripe fruit pods may be eaten raw or cooked, gudjewg:

Unona wardiana (=Uvaria goeziana)  madjalkbat, andjaanek

Unona wardiana  Tuber 'little bit cheeky', Yams have to be sliced up and roasted ('Softened'). Yekke, wurrgeng.

Vernonia cinerea  (h) *gubulurr

Verticordia cunninghamii  Yam, uses as above, yekke, wurrgeng.

Vigna lanceolata  (h) manamburpinya, mitdjenge

Vigna vexillata  Good yam tucker. As above.

Uraria lago podioides  (s,v) *Mankarrbad

Uraria lagopodioides  Black 'grape' tucker, banggerreng.

Vernonia cinerea  *(m)angandowwalk

Vigna lanceolata  (v) anyarrkeyyarrnkey, ankalarrandjek

Vigna vexillata  (s,t) anbirrbirr

Vigna vexillata  (v) ankoornak

Yam available all year. Has to be roasted, and even then is a bit chewy.

(g) badjubarr, drur (D)

Yam available all year. Does not need to be cooked. Flowers are emu tucker.
Vigna vexillata var. angustifolia

(V) badjubarr, drur (Y)
Uses as above. A finer leafed type than that above.

Vitex acuminata

(T) *(m)anbalindja
'Kerosene wood', good for starting fires in the wet season. Fruit tucker in gupumeleng, gudjewg. Nipper says that the fruit is eaten in his country, whereas Talking Billy says it is not in his.

Vitex glabrata

(T) *(m)ankundal(k)
Black plum tucker, gudjewg.

Whiteochloa capillipes

(G) anbullumbullum

Wrightia pubescens

(T) *(m)anben (D)
Wood good for woomera.

Wrightia saligna

(T) *(m)anben (Y)
Uses as above.

Xanthostemon eucalyptoides

(T) anngalimalk, mankindjilkindjil

Xanthostemon paradoxus

(T) *(m)anbulu

Xanthostemon psidioides

(T) anwanbu
Very strong wood used for making yam sticks, fighting spears.

Xanthostemon umbrosus

(T) anbilapbilap

Indeterminate taxa

Poaceae sp.

(G) djarradjaja (Y), marradup (D)
A grass which flowers in banggerreng.
APPENDIX 5

Plants Used Traditionally As Foods And In Material Culture
In The Kakadu Region

The data provided here are derived from Appendix 4. The food plants
are listed in generic alphabetical order, and information is provided as to
their occurrences in 5 broad habitat types, the seasonality of usage, and
their relative importance. These characteristics may be deciphered with
reference to the following keys:

Habitats

(1) lowland vine-forests
(2) escarpment vine-forests
(3) floodplains
(4) escarpment open forests, woodlands etc.
(5) lowland open forests and woodlands

Seasonality of Use

(1) gudjewk - banggerreng
(2) yekke - wurrgeng
(3) gurrung
(4) gunumeleng

Importance

(**) staple
(*) favoured food
( ) eaten occasionally

In the remainder of the Appendix species used in other aspects of material
culture are listed by usage. Not included in this Appendix are lists of
species whose flowering, fruiting, leaf fall etc. are used as seasonal
cues; which provide good fuel for burning (especially in wet weather); or
which are involved in mythological stories or ‘business’. Furthermore, it
is noted that many woody species other than those listed here can be used
for wooden implements (digging sticks, spears, woomeras etc.); only those
specifically mentioned in these contexts have been listed.
### A. Foods

#### (1) Fruit/Seeds

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<td>Ervatamia orientalis</td>
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(2) Vegetable Foods (yams, "cabbage", etc.)

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(3) Culinary herbs

Acacia gonocarpa, Cassia lateriflora, Comesperma aphyllum, Corynotheca lateriflora, Gardenia fucata, Macarthuria apetala, Melaleuca leucadendron.

(4) "Teas" and "Sugar-canedes"

Alloteropsis semialata, Cymbopogon procerus, Grewia retusifolia, Heteropogon triticus, Livistona humilis, Livistona inermis, Melaleuca symphyocarpa, Pandanus spiralis, Triodia plectrachnoides.

\( \text{\textdagger} \) none of these taxa are vine-forest species.
B. Fish poisons

Acacia auriculiformis, A. dimidiata, Atylosia crassipes, Denhamia obscura, Distichostemon hispidula, Owenia vernicosa, Pimelea sp. 1063, Strychnos lucida, Tephrosia conspicua, T. flammea, T. phaeosperma, Tephrosia spp. 1042, 1043, 1053, 1062.

C. Medicines and "Tobaccos"

(1) Medicines for human use
Amyema bifurcatum, Asparagus racemosus, Cyperus sp. 1000, Decaisnina spp., Crewia retusifolia, Melaleuca symphyocarpa, Opilia armentacea, Pityrodia sp. 916, Triodia plectranoides, and various fish poisons as above.

(2) Medicines used by rock kangaroos
Pityrodia sp. 916, Stemodia caerulea, Tephrosia sp. 1069.

(3) "Tobacco"
Pterocaulen sphecalatum, Striga curviflora.

D. Mosquito Repellants

Exocarpus latifolius, Triodia plectranoides.

E. Materials

(1) Wooden implements (spear shafts, digging sticks, etc.)

(2) Piped stems for didjeridooos
Eucalyptus blesseri, E. herbertiana, E. setosa, E. tetrodonta, Terminalia pterocarya.

(3) "Sandpaper"
Ficus opposita, F. scobina.

* also root gum used as an adhesive.
E. Materials (Continued)

(4) Firesticks
Brachychiton paradoxum, Clerodendrum spp., Cochlospermum fraseri, Croton arnheimicus, Ficus opposita, Grewia spp., Hibbertia spp., Hyptis suaveolens, Fachynema sp. 1058, Premna acuminata.
(Banksia dentata cones used to carry fire when travelling.)

(5) Pipes
Clerodendrum spp., Polygonum attenuatum.

(6) Canoes (dug-outs, rafts, paperbark types).
Alstonia actinophylla, Bombax ceiba, Canarium australianum, Eucalyptus tetrodonta, Carophyllum falcatum, Maranthes corymbosa, Melaleuca spp.

(7) House-sheeting
Eucalyptus tetrodonta, Melaleuca spp. (paperbark types, especially M. leucadendron, M. sp. 1036).

(8) "String" and "cord"
Acacia difficilis, Brachychiton spp., Clerodendrum spp., Picud virens, Flagellaria indica, Grewia spp., Helicteres sp. 903, Hibiscus tiliaceus, Malaisia scandens, Phyllanthus ciccoides, Plachonia careya, Sterculia quadrifida.

(9) Leaf blades used in manufacture of baskets etc.
Cyperus spp. (wide-bladed types), Pandanus spiralis, Triodia spp. (wide-bladed types), and various of the species whose bark is used to make string as above.

(10) Dyes
Antidesma ghaesembilla, Coelospermum reticulatum, Cyperus sp. 1132, Haemodorum spp., Livistona humilis, L. inermis, Morinda citrifolia.

(11) Cooking etc.
A. difficilis, Alphitonia excelsa, Ampellocissus spp., Carpentaria acuminata, Goodenia cIRRifera, Cronophyllum ramsayi, Melaleuca spp. (paperbarks).

(12) Ornamentation
Abrus precatorius, Banksia dentata, Leptocarpus spp.

(13) Ceremonial uses (paints etc.)
Alstonia actinophylla, Dendrobium dicuphum, Ervatamia orientale, Gymnanthera nitida, Hoya australis, Ichnocarpus frutescens, Melaleuca spp. (paperbark used for wrapping the dead), Tylophora spp.
THE STATUS OF MONSOON VINE-FOREST IN THE WESTERN ARNHEM LAND REGION, NORTHERN AUSTRALIA. I. DISTRIBUTION AND DISPERsal

Jeremy Russell-Smith
Unpublished manuscript, March 1986
Abstract:

The disjunct distribution of monsoon vine-forest across northern Australia has been considered to represent the fragmentation of a former, expansive vegetation; such fragmentation being a consequence of Late Cainozoic climatic deterioration and/or more recent human burning impact. Alternatively, this disjunction is considered to express also elements of colonization. This is the first paper of a two-part study which explores the status of monsoon vine-forest in western Arnhem Land. On the basis of studies concerning, (1) the distribution of defined monsoon vine-forest Community Types in that region, (2) the dispersal capacities of component species, and (3) the biogeographical affinities of the flora, it is shown that, (4) the great majority of species are highly vagile and (5) a significant proportion of monsoon vine-forest vegetation is of Recent origin, whereas, (6) a few ecologically significant species exhibit very restricted dispersal capacities; (7) whose disjunct distributions may thus be attributed to fragmentation. In discussion, the means by which species disperse is explored, and implications for patch dynamics are considered. In the final section, following a review of the known vegetation and climatic history of the region, the status of monsoon vine-forest in western Arnhem Land is assessed. Such assessment reveals that developing Late Cainozoic aridity, by itself, is insufficient explanation for the extant distribution of seasonal Community Types.
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1.0 INTRODUCTION

The extant distribution of Australian rainforest is characterised both by its patchiness, as well as by often marked disjunctions in the occurrences of individual taxa or assemblages (Webb & Tracey 1981a,b). Both these features are prominent in the scattered distribution of monsoon vine-forest (MVF) vegetation occurring across monsoonal northern Australia, from the Kimberleys in the west to northern Queensland in the east (Kikkawa et al. 1981). Patches are not scattered continuously throughout this region, but are concentrated, for example, in certain coastal areas (e.g. Keenally & Beard 1984; Lavarack & Goodwin 1984; Russell-Smith & Dunlop 1984). There is nevertheless a general gradient of declining species numbers from Cape York through to the Kimberleys. These patterns notwithstanding, a number of studies have commented on the relative floristic continuity of the north Australian MVF flora (Byrnes et al. 1977; Kikkawa et al. 1981; Specht 1958; Specht et al. 1977; Webb et al. 1984).

The term "monsoon forest", as defined originally by Schimper (1903:260), is a climatic formation which is "more or less leafless during the dry season, especially towards its termination, is tropophilous in character, usually less lofty than the rain forest, rich in woody lianes, rich in herbaceous, but poor in woody epiphytes". In the structural classification of Australian rainforests (Webb 1968, 1978; Webb & Tracey 1981a,b), the term "monsoon forest" is applied to all rainforest vegetation types occurring in tropical monsoonal regions, independent of leaf fall phenomena. Under this definition therefore, monsoon forest encompasses a range of canopy foliage conditions, from evergreeness through to seasonal deciduousness. In contrast to this Australian usage, the term "monsoon forest" is used in the Indo-Malesian region to denote a range of woody dominated vegetation, including those dominated by Eucalyptus, occurring under a markedly seasonal rainfall (i.e. monsoonal) regime (e.g. van Steenis 1957; Walter 1971; Whitmore 1984a,b). In order to
avoid confusion, therefore, the term "monsoon vine-forest" is used here to distinguish monsoonal rainforest vegetation types from other north Australian forest and woodland vegetations dominated principally by Eucalyptus and Melaleuca.
A variety of hypotheses have been advanced to account for this distribution pattern. Specht (1958: 422) considers the scattered patches of MVF occurring across northern Australia as being "relics of a previously widespread, relatively continuous flora", the larger part of which has been decimated through "climatic sifting of species" as a consequence of periodic Pleistocene aridity (Ibid: 439-40). In a subsequent study, Specht et al. (1977:36) propose that the establishment of a seasonal rainfall regime in the Quaternary, through its effect on seasonal soil moisture availability, may be attributed the primary factor responsible for the fragmentation of north Australian rainforest vegetation. The determinism of climate is evident also in a palaeoclimatic modelling study of the north Australian - New Guinea region for the period 20 000 years BP to the present, by Nix and Kalma (1972). These authors suggest that major shifts in the distribution of vegetation structural types have occurred throughout this period in response to changing water balance conditions. Following elimination of rainforest from all but locally favourable sites in northeastern Australia at the height of the last Glacial period (ca. 20 000 - 14 000 BP), they suggest that flooding of the broad northern continental shelf associated with rising sea-level, would have given rise to water balance conditions favourable for at least localised expansion of closed canopy forests across northern Australia. With a slight decline in the sea-surface temperature of the shallow north Australian epicontinental sea following the breaching of Torres Strait ca. 8 000 BP (Chappell 1976), Nix and Kalma suggest that rainfall may have declined by as much as one third to its present level, with the result that only scattered and depauperate rainforests would have survived across north Australia.

Stocker and Mott (1981:435-37) likewise subscribe to the relic hypothesis, but attribute the fragmentation of MVF vegetation to Aboriginal burning practices. Gillison (1983:184-85) considers that the retreat of MVF to their present "fire-shadow refugia" is the result of fluctuating climatic cycles during the Quaternary, in combination with Aboriginal burning.
This view gains support from the palynological studies of Kershaw (eg. 1976, 1978, 1981, 1985; Kershaw et al. 1984; Singh et al. 1981), who interprets the late Pleistocene vegetation history of the Atherton Tablelands in humid northeastern Queensland as reflecting the dominant control of climatic change, with Aboriginal burning as a major contributing factor after 38 000 BP. This latter hypothesis is questioned, however, by Horton (1982) and Clarke (1983).

Taking an essentially holocenotic view (see Sarmiento & Monasterio 1975:230), Kikkawa et al. (1981:48), and Russell-Smith & Dunlop (1984) suggest that as well as fire and deteriorating water balance conditions, the interaction of a variety of factors and processes have been contributive. These authors suggest also that disjunctions in the distribution of MVF vegetation express processes of colonisation as well as fragmentation. The widespread occurrence of MVF on Holocene sedimentary facies such as coastal dunes and riverine floodplains, and on Late Pleistocene basalt lava flows (Kahn & Lawrie 1984), may be cited as evidence for the former. Similarly, Gillison (1984) suggests that the littoral affinities of many inland vine-thickets may represent past colonisation associated with marine incursion(s). Beard (1976) also has attributed the occurrence of MVF vegetation in the Kimberleys to colonisation de novo following the last post-glacial rise in sea-level, with its attendant climatic amelioration: a position he has abandoned recently however, in favour of fragmentation attributable to Aboriginal burning (Beard et al. 1984; Clayton-Greene & Beard 1985).

It is clear from this discussion that a variety of hypotheses are entertained concerning the derivation of these extant patterns. However, the paucity of relevant palaeorecords for the region precludes any realistic assessment of competing viewpoints. Such evidence as is available is considered in later discussion.

The purpose of this contribution is to relate the findings of
a combined study of biogeographical and ecological relationships of MVF vegetation, and aspects of traditional Aboriginal land management practice, in the western Arnhem Land region of the Northern Territory. It is considered here that the results of these investigations can contribute usefully to academic debate concerning north Australian vegetation history, as well as having relevance to contemporary land management practice.

1.1 The Study

The results of this study are presented in two papers. This first paper explores biogeographical relationships of the regional MVF vegetation and flora: the spatial distributions of defined floristic and habitat types are described; aspects of population structure are outlined; and the significance of dispersal in the development of these patterns is assessed. In discussion, evidence concerning the regional extent of diverse MVF vegetation types through time is assessed.

The second paper explores the significance of fire (Russell-Smith 1986a).

This work was undertaken as part of two consultancies for the Kakadu National Park, in the western Arnhem Land region of the Northern Territory. The first of these was part of a multidisciplinary investigation of human prehistory and associated palaeoenvironments. The second concerned an investigation of the biogeographical and ecological status of regional MVF ecosystems, and the significance of such habitats in traditional Aboriginal economy. Various aspects of these studies have been reported elsewhere (Jones 1985; Russell-Smith 1984, 1985; Russell-Smith & Dunlop 1984).
2.0 REGIONAL ENVIRONMENT

2.1 Regional definition

As used here, western Arnhem Land describes a coastal to subcoastal region of the northern "Top End" of the Northern Territory confined generally between Latitudes 12°-14°S and Longitudes 132°-133°E. Within this region, the study is focused particularly on that area encompassing Stages I and II of Kakadu National Park, and Goodparla and Gimbat pastoral leases in the south (Fig.1). These pastoral leases are proposed for future inclusion in Kakadu. The eastern boundary is the Arnhem Land Aboriginal Reserve.

2.2 Climate

Climatic features of the region are described by McAlpine (1969, 1976). The climate is dominated by the regular annual alternation of an almost rainless dry season from May to September, and a rainy season from November to March. This pattern reflects complementary seasonal latitudinal shifts of the intertropical convergence zone (ITCZ), and the northern and southern hemisphere subtropical anticyclones. Most rainfall is associated with the location of the ITCZ over northern Australia during the summer months, its imminent arrival heralded by rain-bearing winds of the north-westerly monsoon in November. Also at this time, cyclones provide an additional, albeit erratic source of precipitation. With the retreat of the ITCZ to the northern hemisphere, the southeasterlies generated at the northern margin of the southern hemisphere anticyclone resume dominance, bringing with them relatively dry air after their passage over continental eastern Australia.

Only one meteorological station in the region, Oenpelli, provides a relatively long record of rainfall and temperature observations. A second station, El Sherana, provides a shorter
Fig. 1: Location of study area and distribution of MVF sampling sites (•). Where a number of sampling sites occur in close proximity, only one site is indicated.
Table 1: Rainfall, temperature and evaporation data for regional and selected Northern Territory recording stations.
Numbers in parentheses following station name refer to max. no. records available.

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Fig. 2: Median annual rainfall (mm) distribution in the northern sector of the Northern Territory (Source: Commonwealth of Australia 1977).
record of rainfall observations only, for the southern part of the region. These data are presented in Table 1, along with observations made at Darwin, Katherine and Tennant Creek. These latter records are included to indicate both the regional extent of the summer rainfall phenomenon, as well as the marked attenuation in annual rainfall away from coastal regions (Fig. 2).

For the western Arnhem Land region, mean annual rainfall is approximately 1400 mm in both the Oenpelli and El Sherana records, but is evidently highly variable from year to year (Table 1). Of these mean totals, 91.5% and 89.5% occur in the five months between November-March, for Oenpelli and El Sherana, respectively. Temperatures are high year-round, the mean approaching 28°C (McAlpine 1976). Frosts are unknown. As would be expected under such a climatic regime, evaporation is excessive.

2.3 Landforms, Geology, Soils

Information concerning these aspects is taken largely from various contributions in Story et al. (1969, 1976), supplemented by a number of other sources. For accounts of the geological and geomorphological history of the region, the reader is referred to Galloway (1976), Hays (1967), Williams (1969a,b), and Veevers (1984). Three broad landform types, each characterised by different geological and pedological features, may be differentiated thus:

(i) Arnhem Land plateau. This is the dominant landform type of the eastern margin of the study region. The plateau rises precipitously from the adjacent lowlands in the north-east (Fig. 3), but relief in the south-east is more subdued. Generally the plateau rim is 200-300 m a.s.l., attaining a maximum elevation of 508 m at Mt. Gilruth. The plateau is composed mainly of Middle Proterozoic quartzose sandstone with minor inclusions of interbedded volcanics (Galloway 1976). The terrain is rugged and deeply dissected, especially near the plateau rim and along major watercourses. Soils are mostly absent, or at best skeletal. Away
Fig. 3: Sharp differentiation between the Arnhem Land plateau and adjacent lowland Koolpinyah Surface (see text) (Photo: Diane Lucas).
from sites of active erosion sand plains are commonly interspersed among low rocky ridges. Such sandy mantles are nowhere very deep however, seldom being more than 150cm thick (Aldrick 1976a).

(ii) Koolpinyah Surface. Stretching westwards from the Arnhem Land escarpment towards Darwin is a gently undulating lowland plain termed the Koolpinyah Surface. This surface extends from Lower Proterozoic remnant hills in the south of the region, to the north where it is overlain by Quaternary riverine and coastal sediments (see below). This surface rarely exceeds 30m in depth and is composed of clay, silt, sand and gravel sediments derived originally as erosion products of scarp retreat and pediplanation (Williams 1969a,b). These sediments have in turn been further eroded, resorted, deeply weathered and laterised. Where remnant Lower Proterozoic strike ridges or granitic and doleritic outcroppings protrude this surface, soils are skeletal on slopes greater than 5% (Hooper 1969, Aldrick 1976a). As with the soils of the Arnhem Land plateau, those of the Koolpinyah surface exhibit very low concentrations of mineral nutrients (Aldrick 1976b).

(iii) Coastal and Subcoastal Lowland Plains. Such plains occur in low-lying areas, at elevations just above/below present sea-level, associated with the lower reaches of all major river systems in the region (Fig. 1). The plains are geologically young, comprising mostly clay sediments deposited in association with the last post-glacial rise in sea-level (e.g. Hope et al. 1985; Woodroffe et al. 1985a,b). In sections of these plains no longer under tidal influences, extensive areas of freshwater wetlands are developed. The great majority of these latter ecosystems have developed only within the last few thousand years (Ibid.). In these situations soils comprise organic, black cracking clays of variable depth (generally less than 1.5-1.0m) which overlie grey to bluish-grey estuarine clays. While totally inundated during the wet season, surface water is available only in the deepest depressions and billabongs in the late dry season.
2.4 Vegetation

The vegetation of the region is described in a number of studies. General accounts are given by Burgman & Thompson (1982), Christian & Stewart (1953), Story (1969, 1973, 1976), and Taylor & Dunlop (1984). Descriptions of specific vegetation components include studies of floodplain vegetation (Williams 1979), mangroves (Hegerl et al. 1979) and MVF vegetation (Russell-Smith 1984; Webb & Tracey 1979). The outline presented here does not include description of MVF vegetation since this is covered elsewhere in this paper. However, figures given in Story et al. (1969, 1976) indicate that of a total area of 28000 km² surveyed in their regional study, MVF was estimated to cover 520 km² (i.e. ca. 2.2%).

Unless otherwise stated, nomenclature follows Chippendale (1971). Authorities of all MVF species mentioned in the text are given in Appendix 1. Where given, an asterisk following a species name indicates an obligately or facultatively deciduous species. Vegetation structural typology follows Story (1969, 1973, 1976).

(i) Vegetation of the Arnhem Land Plateau. The greater part of the plateau is either bare or covered by a scanty, but diverse shrubland vegetation dominated principally by low leguminous (e.g. Acacia, Atylosia, Tephrosia) and myrtaceous (e.g. Calytrix, Melaleuca, Verticordia) shrubs over sedges and spinifex (i.e. Plectranche, Triodia) and resurrection (Micraira) grasses. In situations of local soil accumulation, or on talus, small trees generally less than 10m occur also and a woodland type of vegetation is expressed (Fig. 4). This woodland is dominated characteristically by eucalypts (e.g. E. bleeseri, E. dichromophloia*, E. herbertiana, E. kambolgiensis, E. miniata, E. phoenicea and E. tetrodonta), with lesser components of various other taxa (e.g. Callitris intratropica, Gardenia spp., Terminalia spp., Cochlospermum spp.*, Livistona inermis, Owenia vernicosa and Erythrophloeum chlorostachys). On deeper sandy soils, open forest communities
Fig. 4: Vegetation of the Arnhem Land plateau. Note the expression of a woodland type vegetation on shallow sands in the foreground, and the absence of significant vegetation cover on broken sandstone in the background.

Fig. 5: Tall open-forest dominated by Eucalyptus miniata and E. tetradonta on a deep red earth (sandy loam).
dominated largely by *Eucalyptus miniata* and *E. tetrodonta*, with occasional clumps of *Callitris*, occur over sparsely grassed groundcover (e.g. *Plectrachne* spp., *Eriachne* spp.).

(ii) **Vegetation of the Koolpinyah Surface.** The very great proportion of this vegetation is of an open forest or woodland type dominated by *Eucalyptus* spp. On deeper, well-drained soils, open forest is dominated by various admixtures of *E. miniata* and *E. tetrodonta* (Fig. 5), with lesser components of *Erythrophloeum chlorostachys*, *Terminalia ferdinandiana*, *Xanthostemon paradoxus*, *Buchanania obovata*, *Gardenia megasperma*, *Grevillea* spp., *Planchonia careya*, *Livistona humilis* and various *Acacia* spp. The ground cover tends to be dominated by annual grasses (e.g. *Sorghum* spp., *Thaumastochloa major*, *Schizachrium* spp., *Setaria* spp., *Ectrosia* spp. and *Eriachne ciliata*) with lesser contributions of perennials (e.g. *Allocloropsis semialata*, *chrysopogon* spp., *Heteropogon triticeus*, *Cochlocha* *rothoellioides*, *Eriachne triseta* and *Themeda* spp.). Where soils are shallower, as on rocky hills or semi-exposed concretionary laterites, open forest typically gives way to woodland communities dominated by broad-leaved bloodwoods (*E. foelschoeana*, *E. latifolia*) or other eucalypts (e.g. *E. alba*, *E. clavigera*, *E. confertiflora*, *E. dichromophloia*, *E. ferruginea*, *E. grandifolia*, *E. miniata*, *E. patellaris*, *E. phoenicea*, *E. teetifera*, *E. terminalis*, and *E. tetrodonta*) (Fig. 6). Other woody components include the taxa outlined above plus *Brachychiton* spp.*, *Cochlospermum fraseri*, *Hakea arborescens*, *Persoonia falcata*, *Petalostigma* spp., and *Stenocarpus cunninghamii*. In contrast to open forest communities however, sedges (e.g. *Pimbristylis* spp.) and perennial grasses are more abundant. In situations where seasonal waterlogging occurs, as in fine-textured soils associated with drainage depressions, *Eucalyptus* is replaced by *Melaleuca* (e.g. *M. nervosa*, *M. viridiflora*).
Fig. 6: Eucalypt-dominated woodland savanna over tall, cured grasses (Sorghum intrans). Note the gravelly, shallow soil in the foreground exposed by an early dry season back-burn.

Fig. 7: Freshwater wetland communities interspersed with tall open-forest patches of Melaleuca spp. on the subcoastal riverine plains (Photo: Allan Fox).
Open forest communities occur also as narrow riparian strips along the upper reaches of major watercourses and their tributaries. While these communities tend to be dominated by paperbarks (Lophostemon lactifluus, Melaleuca argentea, M. leucadendron) a variety of other species are characteristic also (e.g. Eucalyptus alba, E. papuana, E. ptychocarpa, Syzygium armstrongii, and Xanthostemon eucalyptoides). The great majority of streams are seasonal, however.

(iii) Vegetation associated with coastal and subcoastal plains. All these communities are inundated to some greater or lesser extent during the wet season (Fig. 7) and as such occur on substrates which typically are alternately waterlogged and desiccated for varying periods each year. Occupying areas which are inundated for only short periods are a variety of upland fringing communities which range in structure from open forest to woodland types. These comprise arborescent taxa such as Acacia auriculiformis, Eucalyptus alba, E. clavigera, E. papuana, E. polycarpa, Lophostemon lactifluus, Melaleuca nervosa, M. viridiflora, Pandanus spiralis, and Planchnoria careya. At the edges of the plains, and frequently in depressions of the floodplains as well, open forests of tall paperbarks (Melaleuca cajuputi, M. leucadendron) commonly overtop a lower stratum of Barringtonia acutangula, the so-called freshwater-mangrove. The vegetation of the open plains themselves ranges between herbaceous swamp types occupying the deepest depressions, to annual sedgelands and saline grasslands occupying relatively elevated situations and tidally inundated areas, respectively. As such, the vegetation of the plains in any one locality commonly forms a mosaic reflecting interactions between often subtle changes in surface relief, the duration of dry season surface water availability, and saline influences. The activities of the introduced water buffalo (Bubalis bubalis) are also of significance to floodplain vegetation pattern at the present day, given their demonstrated impact on landform processes (e.g. Letts et al. 1979). Mangrove communities line most tidal channels, but are best expressed in the lower, coastal
réaches of major rivers and their tributaries.

2.5 Fire

While aspects of traditional Aboriginal burning practice and the role of fire on MVF boundaries are considered elsewhere (Russell-Smith 1986a), it is pertinent to note here that, at the present time, fires lit either accidentally or for management purposes burn over considerable tracts of country each year. In a study of burning patterns in Stage I of Kakadu National Park using Landsat imagery, Day (1985) found that for the four years studied (i.e. 1972, 1980-82) the area burnt each year was 59%, 41%, 38% and 66% of the total area, respectively. When seasonality of fires was considered in relation to three land units corresponding to the landform types described in this paper, the results summarised in Table 2 were obtained. Of special significance in these results is the relatively high contribution of late dry season fires. This follows the work of Hoare et al. (1980) and Braithwaite & Estbergs (1985), which suggests that the current pattern of late dry season, and thus relatively high intensity fires, if sustained, may lead to structural degradation of open forest and woodland communities. The potential for regular burning, moreover, is high. The relatively long growing period available to shallow rooted herbaceous species, estimated by McAlpine (1969) and Mott et al. (1985) to be of the order of 20 weeks annually, followed by a long rainless period, gives rise to the production of a predominantly grassy fuel load which can sustain annual burning (Walker 1981). Crown fires are virtually unknown (Stocker & Mott 1981).

2.6 Environmental determinants of regional vegetation pattern: a summary

Mean annual rainfall for the region is apparently in the vicinity of 1400mm. The two records available however, probably mask considerable regional variation, especially a possible gradient in declining rainfall away from the coast (Fig. 2). The
Table 2: Areas burnt in Stage 1 of Kakadu National Park for the years 1972, 1980-1982 (km²). Early fires refer to those occurring prior to 1st August in any one year. Late fires refer to those occurring from August onwards. All data from Day (1985).

<table>
<thead>
<tr>
<th>Year</th>
<th>(i) Arnhem Land Plateau (2024 km²)</th>
<th>(ii) Koolpinyah Surface (2830 km²)</th>
<th>(iii) Coastal/Subcoastal Plains (830 km²)</th>
<th>Total Area (5684 km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1972</td>
<td>1034 (51%)</td>
<td>1920 (68%)</td>
<td>400 (48%)</td>
<td>3354 (59%)</td>
</tr>
<tr>
<td>1980 Early</td>
<td>19 (1%)</td>
<td>527 (18%)</td>
<td>116 (14%)</td>
<td>662 (11%)</td>
</tr>
<tr>
<td>Late</td>
<td>144 (7%)</td>
<td>1352 (48%)</td>
<td>202 (24%)</td>
<td>1698 (30%)</td>
</tr>
<tr>
<td></td>
<td>163 (8%)</td>
<td>1879 (66%)</td>
<td>318 (38%)</td>
<td>2360 (41%)</td>
</tr>
<tr>
<td>1981 Early</td>
<td>3 (0.1%)</td>
<td>424 (15%)</td>
<td>165 (20%)</td>
<td>592 (11%)</td>
</tr>
<tr>
<td>Late</td>
<td>444 (22%)</td>
<td>945 (33%)</td>
<td>156 (19%)</td>
<td>1545 (27%)</td>
</tr>
<tr>
<td></td>
<td>447 (22%)</td>
<td>1369 (48%)</td>
<td>321 (39%)</td>
<td>2137 (38%)</td>
</tr>
<tr>
<td>1982 Early</td>
<td>353 (17%)</td>
<td>1106 (39%)</td>
<td>193 (23%)</td>
<td>1652 (29%)</td>
</tr>
<tr>
<td>Late</td>
<td>1033 (51%)</td>
<td>900 (32%)</td>
<td>190 (23%)</td>
<td>2123 (37%)</td>
</tr>
<tr>
<td></td>
<td>1386 (68%)</td>
<td>2006 (71%)</td>
<td>383 (46%)</td>
<td>3775 (66%)</td>
</tr>
</tbody>
</table>
dominant feature of the climatic regime relevant to plant growth, however, is marked rainfall seasonality. Such seasonality is expressed differentially in the regional vegetation through the modifying influence of substrate water balance characteristics, especially those which affect drainage and moisture storage capacity. For the greater part of the region therefore, the occurrence of skeletal, shallow soils supports at best a woodland vegetation. Where deeper and not obstructed by lateritic hard-pans, open forest is developed. Where alternately waterlogged and desiccated, Melaleuca forests and woodlands give way to sedgelands. Except for the organic soils developed under floodplain conditions, dryland soils, where present, are infertile, being derived from oligotrophic parent materials (e.g. sandstone) or highly weathered and leached sediments (e.g. Koolpinyah surface). And finally, the collective interaction of these various conditions contribute, in the present day, to produce a vegetation highly conducive to frequent burning.
3.0 METHODS

The study has three components: an ecological survey of MVF vegetation; a study of dispersal capacities in selected habitats; and an analysis of the biogeographical relationships of the MVF flora. Methods used in undertaking these separate components are set out below.

3.1 Ecological Survey

3.1.1 Data Collection.

In order to provide an ecological framework for the study as a whole, a survey of MVF vegetation was undertaken over three field-work periods between 1981-84. The guiding principle of this survey was to sample as many MVF patches in as many ecological situations and different areas as constraints of time and accessibility would permit. While maps and aerial photographs were consulted in site selection as a matter of course, practical considerations concerning accessibility were largely determinant. To gain access to certain outstanding patches in otherwise intractable terrain, use was made of a helicopter.

Sampling was undertaken without resort to defined plots of fixed dimension. Rather, the whole patch was sampled as a single entity. However, where a patch might comprise more than one ecologically distinguishable facet (eg. in escarpment gorges where MVF vegetation associated with watercourses is often floristically and structurally distinct from that occurring away from the stream), these were sampled separately. Similarly, care was taken to distinguish between edge communities (ecotones) and internal patch vegetation.

While the sampling programme concentrated on the western Arnhem Land region and its near vicinity (127 sites), a further 76 sites were sampled in the north-west of the Northern Territory to place western Arnhem Land MVF vegetation in a broader regional
context. Of these latter sites, however, 9 were incompletely sampled and have been omitted from analysis. Thus a total of 194 sites are considered here. The distribution of sampling sites is given in Fig. 1.

Sampling of individual sites was conducted with reference to a standard proforma comprising essentially two parts. In the first part, environmental characteristics of each site were recorded. Such characteristics included the physiographic setting, geology, soils, evidence of fires, and the impact of feral animals. In the second part, characteristics of the vegetation were recorded. Such characteristics included structural parameters, physiography, a complete species list, the size of the patch, and the area actually sampled. Population sizes of individual species were estimated using a 5-point Abundance Scale, where: 1 = 1 sexually mature individual present; 2 = 2-6 individuals; 3 = 7-20 individuals; 4 = 21-50 individuals; and 5 = > 50 mature individuals present. Sexual maturity was assumed where individuals had attained the characteristic mature growth form of the species concerned. This scale was developed during field trials of the proforma when it became evident that individual population sizes in many patches are small.

With experience, sampling of a patch 1-2ha extent could be undertaken in a few hours. For larger patches, or small patches with highly diverse species assemblages, at least a day might be required and even then only a representative section might be sampled effectively. While sampling of sites was undertaken, whereever practicable, both in wet and dry seasons, the majority of sites were sampled only once. Since many MVF taxa (i.e. annual herbs, herbaceous geophytes, geophytic vines) are conspicuous only in the wet season however, it follows that, where given in following analysis, species numbers occurring at any one site are to be taken as a minimum number. For the same reason, discussion of population sizes is restricted mostly to perennially identifiable woody taxa.
All specimens collected were identified either at the Northern Territory Herbarium, Darwin, or at the Australian National Herbarium, Canberra. A complete listing of the data collected in this survey is given in Russell-Smith 1986(b).

3.1.2 Data analysis.

Over 500 taxa were recorded through the course of this survey. Of these, 388 are considered typical MVF constituents on the basis of their capacity to regenerate successfully in more-or-less closed canopy vine-forest situations, or in gaps (Russell-Smith & Dunlop 1984). A number of native and exotic weedy taxa which are typical of disturbed situations have been included also (see Appendix 1).

Using only perennally identifiable taxa occurring at at least 5 sites, a data matrix of 235 taxa X 194 sites was subjected to numerical analysis to reveal floristic patterns in the data set. Since the purpose of this analysis was to explore floristic patterning per se, presence-absence data were used. Classification was undertaken using the Jaccard measure, followed by polythetic agglomerative fusion using the unweighted Group Average (UPGMA) sorting strategy (Sokal & Mitchener 1958) to produce a dendrogram. This analysis was conducted using computational facilities available in the Numerical Taxonomic Package (NTP) (Belbin et al. 1984).

The choice of fusion strategy was made easily given that UPGMA is both mathematically simple and, as well, being a space-conserving strategy, is not given to distortional effects such as occur with certain other strategies (Abel & Williams 1985; Belbin 1982; Reddy 1983). The essential feature of UPGMA is that fusion of an entity (site) with a cluster (previously grouped sites), or one cluster with another, occurs at the similarity level equal to the average similarity of an entity/entities in one group to each entity in the other. A worked example is provided in Legendre & Legendre (1983:231).
The selection of association measure is not so obvious. Discounting those association measures suitable for presence-absence data which take into consideration conjoint absences (see Clifford & Stephenson 1975), leaves essentially three widely used and mathematically similar measures; the Jaccard, the Czekanowski, and the Kulczinski coefficients. These may be expressed as follows:

\[
\text{Jaccard} = \frac{a}{a+b+c} \tag{1}
\]

\[
\text{Czekanowski} = \frac{a}{\frac{1}{2}[(a+b)+(a+c)]} \tag{2}
\]

\[
\text{Kulczinski} = \frac{1}{2} \left[ \frac{a}{(a+b)} + \frac{a}{(a+c)} \right] \tag{3}
\]

where, \(a\) = number of attributes shared by both entities; \(b\) = number of attributes possessed by the first entity but not the second; and \(c\) = number of attributes possessed by the second entity but not the first. Whereas the Jaccard coefficient is, in effect, a simple proportional measure of the number of attributes shared by two entities, the other two coefficients take into consideration the number of attributes possessed by each entity as well. Using the 235 species x 194 sites data matrix described previously, a comparison of resulting dendrograms produced by these respective coefficients is given for the seven group level in Fig. 8 and Table 3. In each case fusion is by the UPGMA strategy, with results expressed in relation to the Jaccard analysis.

It is evident that, when used in conjunction with this particular data set, these coefficients yield very similar results, with the Jaccard and Czekanowski analyses being almost identical. For the purposes of this study however, the Jaccard coefficient is used since, of the three, it provides the simplest
Fig. 8: Comparison of dendrograms of 235 species x 194 sites data, at the seven-group level, using three similarity coefficients (see text). All fusions by UPGMA. Group numbers in analyses (B) and (C) refer to equivalent groups in the Jaccard analysis (see table 3). Note that fusion level is given as dissimilarity (i.e. 1-similarity).
Table 3: Comparison of site groups in Fig. 4, with reference to the Jaccard analysis. Values in parentheses indicate the number of sites in addition to (+), or absent from (-), the Jaccard grouping.

<table>
<thead>
<tr>
<th>Group No.</th>
<th>No. sites in Group</th>
<th>(a) Jaccard</th>
<th>(b) Czekanowski</th>
<th>(c) Kulczinski</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(p)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>47</td>
<td>47 (0)</td>
<td>46 (-2,+1)</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>74</td>
<td>72 (-2)</td>
<td>67 (-10,+3)</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>14</td>
<td>14 (0)</td>
<td>18 (-5,+9)</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>5 (+2)</td>
<td>4 (+1)</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>51</td>
<td>51 (0)</td>
<td>54 (-1,+4)</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>4</td>
<td>4 (0)</td>
<td>4 (-1,+1)</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>1</td>
<td>1 (0)</td>
<td></td>
<td>1 (0)</td>
</tr>
</tbody>
</table>

Percentage net difference: 1.03 (2) 9.79 (19)
(and thus most readily comprehensible) measure of inter-site similarity. Moreover, when the neighbourhood location of each site in the dendrogram was compared with an analysis of the five closest neighbours of each site in the Association Matrix, no blatant misclassifications were evident (see results). As W.T. Williams (1976) pointedly remarks, however, the choice of a numerical classificatory strategy depends ultimately on one essential criterion - its utility.

In conjunction with the description of Top End MVF habitat types given previously in Russell-Smith & Dunlop (1984), the results of this analysis provide a useful ecological framework for exploring patterns of distribution, population abundance, and the dispersal capacities of different MVF floristic elements.

3.2 Dispersal Studies.

The relative capacities of different plant species to disperse from parents has obvious implications for our understanding of biogeographical and ecological pattern. In order to assess the role of dispersal in the expression of extant MVF vegetation pattern in western Arnhem Land, three studies are reported here which explore dispersal-in-action in contrasting ecological situations. The first study examines the occurrence of MVF vegetation on Holocene substrates such as beach dunes, slumping coastal cliffs, and coastal/subcoastal floodplain sediments. The data used in this analysis are derived from the ecological survey outlined previously. The second study entails an assessment of the role of dispersal at three small MVF patches associated with springs in the western Arnhem Land escarpment. The third study examines the dispersal capacity of the escarpment MVF dominant, Allosyncarpia ternata S.T. Blake. These latter two studies are described below.

3.2.1 Dispersal at springs.

In the course of other field studies reported in this paper,
it was observed that MVF vegetation associated with perennial springs and seepages in the Arnhem Land escarpment commonly contain immature individuals of woody species which otherwise are not present as sexually mature forms (see Table 1 in Russell-Smith and Dunlop 1984). In order to examine this phenomenon more closely, three small seepage sites were selected for study.

The study was initiated in the late dry season (September) of 1983, and extended through the 1983/84 wet season. In the late dry season these seepages provide important sources of water for birds and other animals. Given that this time is also the major fruiting period for many MVF species, it was anticipated that such situations would be readily amenable for a study of bird dispersal of vine-forest fruits. The locations of these sites are given Table 4(a). The essential components of this study are as follows:

1. All woody individuals >5cm DBH occurring within (at least) 20m of the seepages were recorded. The occurrence of all other species present was recorded also. In the cases of the Nangaloar and Anbangbang sites, this effectively sampled all the MVF trees associated with the seepages. The Oenpelli site however, occurs within an extensive MVF patch. A detailed inventory of all species occurring in this patch was undertaken, however, in the course of the ecological survey (3.1.1).

2. At least 10 permanent sampling quadrats, each 1X1m², were established immediately adjacent to each seepage. All seedlings and saplings occurring in these quadrats were noted at the commencement of the study and again at the end of the wet season.

3. At each site two large plastic sheets, each 2X1m², were suspended above-ground beneath canopy trees. At various times during the late dry and early wet seasons, the plastic sheets were emptied of their contents. The contents were sorted into three classes. Conspicuous, large seeds which had been voided by birds were separated from those where the fruit ‘flesh’ was still intact; these latter fruits
Table 4: Location of Dispersal Study Sites.

<table>
<thead>
<tr>
<th>Site Name</th>
<th>1:100 000 Map Sheet No.*</th>
<th>Grid reference x</th>
<th>Grid reference y</th>
<th>Long.</th>
<th>Lat.</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Spring Study</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anbangbang spring</td>
<td>5472</td>
<td>628 729</td>
<td></td>
<td>132°49</td>
<td>12°52</td>
</tr>
<tr>
<td>Nangaloar spring</td>
<td>5472</td>
<td>625 783</td>
<td></td>
<td>132°48</td>
<td>12°51</td>
</tr>
<tr>
<td>Oenpelli Forest spring</td>
<td>5573</td>
<td>865 298</td>
<td></td>
<td>133°02</td>
<td>12°23</td>
</tr>
<tr>
<td>(b) <em>Allosyncarpia ternata</em> study</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Djirrinbal Ch.</td>
<td>5473</td>
<td>748 176</td>
<td></td>
<td>132°56</td>
<td>12°30</td>
</tr>
<tr>
<td>Lightning Dreaming</td>
<td>5572</td>
<td>853 707</td>
<td></td>
<td>133°02</td>
<td>12°56</td>
</tr>
<tr>
<td>Mt. Howship</td>
<td>5572</td>
<td>005 087</td>
<td></td>
<td>133°10</td>
<td>12°35</td>
</tr>
<tr>
<td>Oenpelli Forest</td>
<td>5573</td>
<td>868 298</td>
<td></td>
<td>133°02</td>
<td>12°23</td>
</tr>
</tbody>
</table>

* Division of National Mapping, Commonw. Australia.
originating from canopies immediately above the suspended traps. The large voided seeds were set aside for specific identification. The third category was the remaining 'fines'. These fines, comprising mainly leaf litter, were added to a sand/peat mixture, laid out in shallow trays, and watered daily in green-house facilities kindly supplied by the N.T. Herbarium. All germinants were identified and recorded. The plastic sheets were removed at the beginning of the wet season since access to none of these sites was possible during the wet.

4. Three surface soil samples, each of 1x1m² and to 5cm depth, were collected at each site immediately adjacent seepages at the commencement of the study. These were laid out in shallow trays and watered as for the trap fines. The germinants were identified and recorded.

3.2.2 Dispersal in Allosyncarpia ternata.

Allosyncarpia ternata is a myrtaceous, sclerophyllous, evergreen tree species which is restricted in its distribution to sandstone habitats of the Arnhem Land escarpment and plateau (Blake 1977). It is ecologically significant, however, in that it is often the sole canopy species present in much escarpment MVF vegetation. As such, it exerts a controlling influence on the subcanopy microclimate (Russell-Smith & Dunlop 1984). Although Allosyncarpia regenerates successfully from lignotuberous coppice when young, expansion of patch boundaries is effected only through the recruitment of new individuals at the margin (Russell-Smith 1984).

Following a short flowering period in late October-November, fully-developed dry seeds are shed from capsules in the ensuing wet season, generally from late January onwards. To assess the dispersal capacity of Allosyncarpia, counts of germinants were made using continuous transects extending across patch margins in four escarpment vine-forests. This study was undertaken in March, 1984. The location of the study sites is given in Table 4(b).
3.3 Biogeographical relationships.

The third study component explores the extra-regional biogeographical affinities of the Top End MVF flora. While having relevance to past and on-going debate concerning the significance of the "Indo-Malesian element" in the evolution of the Australian flora, rainforests especially (e.g., Barlow 1981; Beadle 1981; Burbidge 1960; Herbert 1960, 1967; Hooker 1860; Raven & Axelrod 1972; Schuster 1972; Specht 1958, 1981; van Steenis 1979; Talent 1984; Walker 1972; Webb & Tracey 1981a, b; Webb et al. 1984; Werren & Sluiter 1984), this analysis also provides a further opportunity for exploring the complementary themes of distribution and dispersal.

Biogeographical analysis is undertaken here at the species level. This level is selected since it may be anticipated that species distributions afford a less ambiguous avenue for exploring patterns of dispersal than do distributions of taxa at higher taxonomic levels (cf. van Balgooy 1976:3). Distributional data are derived from taxonomic revisions, regional floras, and communications with taxonomic specialists. As such these data represent taxonomic species concepts currently in usage as of early 1986. However, as Whiffin & Hyland (1984) indicate in their recent review of the status of taxonomic knowledge of the Australian rainforest flora, the flora is imperfectly known and little study of natural taxonomic relationships between and within species has as yet been undertaken. The extra-regional distributions of all taxa (so far as are known), as well as full acknowledgement to data sources, are given in Appendix 1.

In presenting this analysis a qualification is required since concepts of what constitute species (and other rankings of the taxonomic hierarchy) vary with different groups and the predilections of individual taxonomists (cf. van Balgooy 1971). For example, in his authoritative "Essays on Ficus", Corner (1985) first describes the taxon 'Ficus' as constituting a "natural
genus" (p. 128); he then goes on to suggest (p. 139) that, "the specialist can, if he wishes, treat all the subgeneric names in *Ficus* as genera and *Ficus* itself as a family". Clearly, given the current state of the taxonomic art, the plant species is simply "a utilitarian mental construct which in practice does not comply with sets of prescribed rules" (Levin 1979:381; see also Raven 1980). For the purposes of this analysis however, it will be assumed, however wrongly, that taxonomic species concepts adequately describe, or at least approximate, "groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1970:12). For further discussion of the plurality of the species concept, see Kitcher (1984) and references therein.
4.0 RESULTS

4.1 Ecological Survey

4.1.1 Classification

The numerical classification of the MVP floristic-site data set is considered here firstly at the 7 group level. This level is selected as it is readily interpretable ecologically. As indicated in Fig. 8(a), this group level represents the last six fusions in the dendrogram; the first of which, between groups 2 and 3, occurs at a dissimilarity level of 0.8228. At slightly lower levels of dissimilarity (e.g. between 0.7 - 0.8) the number of groups increases markedly (Fig. 9).

Of these seven groups four are relatively large, comprising 74, 51, 47 and 14 site-members, respectively. The remaining three groups comprise 8 members between them (Table 3). Examination of these latter groups reveals that they comprise sites representative of diverse marginal situations, and/or contain very small species assemblages. As such, these groups clearly represent outlying sites which have been difficult to place in the classificatory procedure. For the sake of simplicity, these sites have been reallocated amongst the four major groups on the basis of their affinities as indicated by the Nearest Neighbours Algorithm of the NTP package (Belbin et al. 1984). Using the same procedure, the robustness of the classification of the four large groups was checked also. This analysis revealed that, for the 186 sites considered (i.e. 194-8), 158 (85%) were classified in the same group as their five closest neighbours, with a further 22 sites (12%) classified in the same group as the majority of their neighbours. Six sites, however, were indicated as being better placed in another group and hence have been reallocated accordingly. Taking these reallocations into account, the revised classification is summarised in Table 5.

4.1.2 Floristic Groups
Fig. 9: Frequency distribution of the number of fusions in each 0.1 dissimilarity level interval of the Jaccard-UPGMA classification. The last six fusions used as the basis for classification occur at levels of dissimilarity to the right of the broken vertical line as indicated. (n=193).
Table 5: Floristic-site data classification after reallocation of sites (see text). Values in parentheses indicate the number of sites in addition to (+), or absent from (-), the original classification.

(a) **Original classification**

<table>
<thead>
<tr>
<th>Group No.</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. Sites in Group</td>
<td>47</td>
<td>74</td>
<td>14</td>
<td>3</td>
<td>51</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>

(b) **Classification after reallocation:**

<table>
<thead>
<tr>
<th>Group No.</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. Sites in Group</td>
<td>49</td>
<td>79</td>
<td>13</td>
<td>53</td>
<td>(+4,-2)</td>
<td>(+7,-2)</td>
<td>(-1)</td>
</tr>
</tbody>
</table>
The four floristic groups defined by the classification are characterised by the species assemblages listed in Table 6. As perusal of this Table (and Table 8) indicates, there is a high degree of floristic continuity in this flora as a whole. This is reinforced by the observation that 78 species, of a total of 367 recorded in the site survey, occur in all four groups.

4.1.3 Habitat Relationships

The habitat relationships of the four floristic groups are as follows:

Group 1: All 49 sites in this group are associated with seasonally dry sandstone habitats in the Arnhem Land escarpment. Habitats range from scree and bare pavements associated with deeply dissected sandstone terrain, through boulder-strewn seasonal watercourses, to sites of shallow sand accumulation at the bottom of escarpment gorges. While the great majority of sites occupy situations topographically protected from fire (e.g. rugged, broken terrain) (Fig. 10), one of the sites occurs in the middle of sandy plain where augering indicated the sandy mantle to be ca. 1.5m deep. On the basis of fieldwork undertaken, however, MVF patches occupying such situations are rare (Fig. 11).

Group 2: This large group of 79 sites typifies MVF vegetation associated with seasonally dry habitats of the coastal and subcoastal lowlands. Substrates are heterogenous, and include coastal calcareous and siliceous sediments (Fig. 12), seasonally inundated riverine floodplain alluvium (Fig. 13), well-drained lateritic landforms of the Koolpinyah Surface (Fig. 14), and excessively drained rock outcrops (Fig. 15). These last substrates comprise a variety of rock types which, in this survey, included limestone, dolerite, granite, sandstone and skeletal laterite. MVF vegetation was not observed to occur, however, on seasonally waterlogged, fine-textured soils which dry to considerable depth during the dry season.
Table 6: Species characteristic of, and exclusive to, each floristic group of the classification. Numbers in parentheses refer to frequency of occurrence of a species over all sites in each Group. Exotic species excluded.

(a) Characteristic species - the 25 most commonly occurring taxa in each Group.

<table>
<thead>
<tr>
<th>Group No.</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. 201</td>
<td>Vitex acuminata (0.96), Pouteria sericea (0.85), Flagellaria indica (0.85), Parsonsia velutina (0.79), Antidesma parvifolia (0.77), Alyxia ruscifolia (0.77), Smilax australis (0.77), Memecylon pauciflorum (0.77), Drynaria quercifolia (0.72), Acacia aulacocarpa (0.70), Ficus scobina (0.70), Rauwenhoffia leichhardtii (0.68), Canarium australianum (0.68), Cryptocarya exfoliata (0.68), Diospyros calycantha (0.66), Bridelia tomentosa (0.66), Strychnos lucida (0.64), Dioscorea transversa (0.62), Polyalthia holtzeana (0.62), Canthium sp. JHS 920 (0.60), Tinospora smilacina (0.60), Allosyncarpia ternata (0.57), Ficus leucotricha (0.57), Sterculia quadrifida (0.55).</td>
</tr>
<tr>
<td>2. 273</td>
<td>Litsea glutinosa (0.85), Strychnos lucida (0.85), Canarium australianum (0.78), Cupaniopsis anacardioides (0.77), Abrus precatorius (0.75), Jasminum simplicifolium (0.72), Capparis sulpharia (0.72), Smilax australis (0.70), Dioscorea transversa (0.70), Flagellaria indica (0.70), Opifya amentacea (0.68), Celtis philippensis (0.68), Ficus scobina (0.67), Wrightia pubescens (0.67), Bridelia tomentosa (0.66), Malaisia scandens (0.65), Passiflora foetida (0.63), Breynia cernua (0.63), Sterculia quadrifida (0.63), Drypetes lasiogyna (0.63), Glycosmis pentaphylla (0.61), Securinega melanthesioides (0.61), Exocarpus latifolius (0.59), Ichnocarpus frutescens (0.58), Terminalia sericocarpa (0.58).</td>
</tr>
<tr>
<td>3. 182</td>
<td>Carpentaria acuminata (1.00), Carallia brachiata (1.00), Breynia cernua (1.00), Gmelina schlechteri (1.00), Myristica insipida (1.00), Sterculia aff. quadrifida (0.92), Flagellaria indica (0.92), Stenochlaena palustris (0.92), Horsfieldia australiana (0.85), Polyalthia holtzeana (0.85), Ficus virens (0.85), Smilax australis (0.85), Embilia sp. GW 306 (0.85), Litsea glutinosa (0.85), Acacia auriculiformis (0.85), Terminalia sericocarpa (0.77), Ficus racemosa (0.77), Calophyllum soulattri (0.77), Macaranga involucrata (0.77), Ficus scobina (0.77), Euodia elleryana (0.77), Oplismenus burmannii (0.77), Stephania japonica (0.77), Timonius timon (0.77), Livistona benthamii (0.69).</td>
</tr>
</tbody>
</table>
4. 208 Flagellaria indica (0.92), Carallia brachiaata (0.81), Xanthostemon eucalyptoides (0.79), Melastoma malabathricum (0.77), Ilex arnhamicus (0.75), Lindsaea ensifolia ssp. ensifolia (0.70), Scleria polycarpa (0.70), Smilax australis (0.68), Helicia australasica (0.66), Planchnella aff. xerocarpa (0.64), Rapanea benthamiana (0.64), Syzygium angophoroides (0.62), Carpentaria acuminata (0.57), Calophyllum sill (0.57), Syzygium minutuliflorum (0.57), Euodia elleryana (0.53), Myristica insipida (0.53), Dendrobium dicuphum (0.51), Blechnum orientale (0.49), Allosyncarpia ternata (0.47), Fagraea racemosa (0.43), Coelospermum NB 1523 (0.42), Diospyros calycanthis (0.42), Dicranopteris linearis (0.42), Gmelina schlechteri (0.42).

(b) Exclusive species - taxa restricted to one Group, occurring at 5 or more sites.  
1. Capparis jacobson (0.11), Hoya sp. aff. australis (0.26), Xanthostemon umbrosus (0.11).
2. Abutilon indicum (0.08), Aglaia elaeagnoides (0.09), Antiaris toxicaria (0.10), Bidens bipinnata (0.23), Caesalpinia bondoc (0.10), Cansjera leptostachya (0.08), Caanthormion umbellatum (0.24), Cordia dichotoma (0.13), Croton armstrongii (0.28), Diospyros ferrea var. humilis (0.30), Diospyros maritima (0.19), Grewia CRD 6477 (0.18), Guettarda speciosa (0.08), Helicteres isora (0.08), Jasminum didymum (0.32), Marsdenia velutina (0.14), Mimusops elengi (0.19), Murraya paniculata (0.13), Paramignya trimera (0.09), Pilostigma malabaricum (0.09), Plumbago zeylanica (0.11), Premna serratifolia (0.11), Salacia chinensis (0.06), Santalum album (0.09), Terminalia muelleri (0.08), Zizyphus oenoplia (0.05), Rubiaceae JRS 718 (0.09).
3. Piper novae-hollandiae (0.62).
4. Ternstroemia cherryi (0.09), Xanthostemon eucalyptoides (0.79).
Fig. 10: MVF vegetation (dark canopy), dominated by Allosyncarpia ternata, associated with deeply dissected, rugged escarpment terrain.

Fig. 11: An isolated patch of MVF vegetation, dominated by Allosyncarpia ternata, in open terrain on the Arnhem Land plateau.
Fig. 12: MVF on coastal beach sediments abutting mangrove vegetation at the left of the illustration (Photo: Ian Morris).

Fig. 13: MVF occurring along drainage channels of the East Alligator River floodplain (Photo: Ian Morris).
Fig. 14: MVF on a deep sandy loam of the Koolpinyah Surface.

Fig. 15: MVF on granite boulder flow at the left, with eucalypt-dominated woodland savanna on skeletal loams at the right of the illustration.
Only one of the sites included in this group is located in the Arnhem Land escarpment. The status of this site is considered in later discussion.

Group 3: This small group of 13 members describes floristically diverse, and structurally complex MVF vegetation associated with sites of perennial water availability (Fig. 16). All these sites occur in relatively high rainfall areas of the north-western coastal/subcoastal region. These sites are associated with perennial springs in undulating sandstone terrain. The other ten sites are associated either with lowland springs, or sites of evident favourable year-round water status such as occurs at the margins of some floodplains.

Group 4: In common with the preceding group, this group of 53 members is associated likewise with sites of perennial/moisture availability (Fig. 17). In contrast, however, this MVF vegetation is relatively floristically and structurally attenuated, and is associated mainly with small springs in sandstone terrain. All the Arnhem Land spring sites, for example, are included in this group.

In outline, these habitat relationships match closely with the description of regional MVF Habitat Types given by Russell-Smith & Dunlop (1984). In the latter study, however, MVF associated with seasonal lowland situations is described as comprising three more-or-less floristically continuous habitat types; namely, MVF vegetation associated with coastal, subcoastal and rock outcrop landforms. While the numerical classification presented here indicates similarly, that MVF vegetation occupying the range of seasonal lowland habitats comprises essentially one floristic grouping, for the purposes of succeeding analyses (Sects. 4.2, 4.3) it is useful to consider coastal, subcoastal and rock outcrop components separately. Taking this refinement into consideration, Table 7 summarises the relationship between MVF vegetation structural components and habitat. This Table is derived largely from data given in Russell-Smith & Dunlop (1984). Structural terminology follows Webb (1968, 1978; Webb & Tracey
Fig. 16: MVF associated with a perennial spring in undulating terrain on Melville Island. Both the Melaleuca-dominated vegetation to the left of the MVF patch, as well as the open herbaceous vegetation in the foreground, occur on similar hydromorphic soils to those described as supporting wet campo vegetation in South American studies (e.g. Bieten 1978; Sarmiento 1983).

Fig. 17: MVF associated with a perennial stream in an Arnhem Land escarpment gorge. Note the surface root mat. Such a rooting habit is characteristic of woody MVF species occupying perennially moist substrates in the absence of soils. In this instance the roots are those of *Syzygium minutuliflorum*. (Photo: Ian Morris).
<table>
<thead>
<tr>
<th>Group. No.</th>
<th>Habitat</th>
<th>Vegetation Structural Type</th>
<th>Canopy Height (m)</th>
<th>Patch Size (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Seasonally dry, rugged sandstone terrain of the Arnhem Land escarpment. Probably other sandstone regions also. Habitats include scree, bare rock pavements, seasonal rocky watercourses, sand plains, and gorges. Soils, where present, are typically skeletal sands.</td>
<td>Evergreen Notophyll Vine Forest (ENVF) or Simple Evergreen Notophyll Vine Forest (SSENVF)</td>
<td>35 - &lt;10</td>
<td>&gt;500 - &lt;1.0</td>
</tr>
<tr>
<td>2</td>
<td>Seasonally dry lowland types:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2(a)</td>
<td>Rock outcrops. A variety of rock types including limestone, granite, dolerite, sandstone, siliceous metamorphics; and massive or concretionary laterite. Soils, where present, are skeletal and excessively drained.</td>
<td>Semi-Deciduous Notophyll Vine Forest (SDNVF), through to Deciduous Vine Thicket (DVT).</td>
<td>12 - 2</td>
<td>&gt;100 - &lt;0.1</td>
</tr>
<tr>
<td>2(b)</td>
<td>Coastal landforms. Siliceous and calcareous sediments, slumping coastal cliffs, and lateritic landforms of flat to gently sloping terrain. Soils, where present, range from skeletal types through to deep, well drained (&gt;2m) siliceous/calcareous facies, or red loamy lateritic soils.</td>
<td>ENVF (with/without palms), SDNVF, DVT.</td>
<td>20 - 2</td>
<td>&gt;1500 - &lt;0.1</td>
</tr>
<tr>
<td>2(c)</td>
<td>Subcoastal landforms. Elevated landform features (e.g. levees) and lateritic margins of riverine floodplains, and riparian strips associated with seasonal watercourses. Soils are thus highly variable, ranging from sandy to sandy-clay alluvial facies, to skeletal or deep loamy soils of lateritic red earths.</td>
<td>SDNVF, DVT. Riparian strips associated with more inland watercourses may comprise bamboo (Ambua arnhemica) thicket, or Vine Forest types may be overtopped by sclerophyll emergents (e.g. Melaleuca spp.).</td>
<td>20 - 2</td>
<td>&gt;1500 - &lt;0.1</td>
</tr>
</tbody>
</table>
Perennial springs of high rainfall, coastal regions, typically in the lowlands. Soils are waterlogged year-round, comprising shallow (20-50cm) loamy organic horizons over gleyed clays.

Perennial springs associated typically with rugged sandstone terrain. Where relief is steep, soils are skeletal or absent. Where relief is subdued, organic sands to sandy loams overlay either rock or gleyed clays.

Complex Notophyll Vine Forest (CNVF) or ENVF (with palms).  
25 - 20 >100 - <1.0

ENVF (with/without palms).  
35 - 20 >10 - <0.1
Table 8: Inter-Group Similarities (Jaccard) using full ecological survey floristic data set

(a) Floristic Groups

<table>
<thead>
<tr>
<th>GROUPS</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>0.382</td>
<td>0.277</td>
<td>0.549</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>0.497</td>
<td>0.471</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>0.472</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>

(b) Community Types

<table>
<thead>
<tr>
<th>GROUPS</th>
<th>1</th>
<th>2(a)</th>
<th>2(b)</th>
<th>2(c)</th>
<th>(sub-coastal)</th>
<th>(coastal)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>0.427</td>
<td>0.387</td>
<td>0.435</td>
<td>0.277</td>
<td>0.549</td>
</tr>
<tr>
<td>2(a)</td>
<td>1</td>
<td>0.531</td>
<td>0.597</td>
<td>0.382</td>
<td>0.391</td>
<td></td>
</tr>
<tr>
<td>2(b)</td>
<td>1</td>
<td>0.680</td>
<td>0.481</td>
<td>0.401</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2(c)</td>
<td>1</td>
<td>0.461</td>
<td>0.491</td>
<td>0.491</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.472</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>
Given that the floristic basis of the classificatory procedure used in this paper is essentially different from the definition, a priori, of Habitat Types described by Russell-Smith & Dunlop (1984), the term 'Community Type' is used here to describe the six MVF vegetation types defined above. Using the full data set of 367 species recorded in the ecological survey, measures of similarity between each of these Community Types are presented in Table 8. The values of similarity given are those as measured by the Jaccard coefficient.

4.1.4 The distribution of MVF in the western Arnhem Land region

The distributions of these defined MVF Community Types in the western Arnhem Land region are given in Fig. 18. This Figure is compiled from a complete coverage of 1:25 000 colour aerial photographs available for the area as indicated. In presenting this map a number of points require mention. Firstly, given both the relatively large scale of the photographic record, and that all photographs were taken in the dry season, it is probable that some very small MVF patches are not represented in Fig. 18. This applies particularly to small patches comprising mainly seasonally deciduous elements (e.g. MVF associated with rock outcrops). However, for patches generally greater than 0.1ha, and/or comprising conspicuous evergreen components, such qualifications are unlikely to be significant. Secondly, the only Community Type occurring in the greater region not present in western Arnhem Land concerns floristically diverse MVF vegetation associated typically with lowland springs (Group 3). Thirdly, seasonal coastal and subcoastal Community Types (Groups 2b, 2c) are distinguished only by a dotted line given their evident geographical continuity (Fig. 18). As well, seasonal subcoastal MVF vegetation is indicated on the map by two colour keys. That keyed as brown-green comprises subcoastal MVF vegetation occurring on or immediately adjacent lowland riverine and estuarine floodplains. That associated with seasonal watercourses further inland is keyed as blue-green. The
Fig. 18: Distribution of MVF vegetation in the western Arnhem Land region. See text for details.
significance of this distinction is considered in later discussion. And fourthly, for the most part it has not been possible to differentiate between MVF vegetation associated with seasonally dry and perennially moist escarpment habitats given the widespread canopy dominance of Allosyncarpia ternata in both Community Types. In Fig. 18 only those escarpment spring forests in which Allosyncarpia does not occur are indicated as such.

While the patterns of distribution expressed in Fig. 18 are considered more fully in later discussion (5.4.2), at this juncture the map serves simply to illustrate that the over-riding feature in the distribution of MVF in western Arnhem Land is its evident disjunction.

4.1.5 Species-Area Relationships

The species-area relationships of the four floristic groups defined in Table 5 are given in Fig. 19. The model used is the species/logarea (exponential) relationship (Connor & McCoy 1979), where Area is the area actually sampled. While it may be observed from this Figure that the number of species tends to increase concomitantly with the area sampled, there is large variation in species numbers at any one patch/site size (e.g. Figs. 19(a), (b), (d)). Of special significance however, is the occurrence of relatively large numbers of species in small patches, for example, all sites occurring to the left of the broken vertical line in Fig. 19 comprise patches approximately 2ha and less in extent. It follows that the individual population sizes of many component taxa are likely to be small.

The maximum number of species recorded at any one site is 96. This number was recorded at each of two seasonally dry lowland sites over areas of 6ha and 10ha, respectively. The smallest number recorded is 11 species, in a patch approximately 0.1ha in extent.

4.1.6 Population Sizes
Fig. 19: Species-Area relationships of the four floristic groups described in Section 4.1.3. Explanatory notes are as follows: 1. $s =$ number of species, $A =$ area sampled; 2. significance of the correlation coefficient ($r$) is given as $** = p < 0.01$, $*** = p < 0.001$; 3. the vertical broken line indicates a sampled area approximately 2ha in extent (see text).

(A) Floristic group No.1 ($n=49$)
$s = 23.66 (1 + \log A) + 21.30$
$r = 0.56***$

(B) Floristic group No.2 ($n=79$)
$s = 25.26 (1 + \log A) + 22.23$
$r = 0.55***$
Fig. 19 (continued).

(C) Floristic group No.3 (n=13)
\[ s = 27.97 \log A + 48.48 \]
\[ r = 0.71 \]

(D) Floristic group No.4 (n=53)
\[ s = 14.27 (1+\log A) + 21.23 \]
\[ r = 0.51 \]
Considering only discrete patches which were sampled effectively in their entirety, the proportion of species with populations of 50 or less mature individuals at each of 90 sites is given in Fig. 20. The patches range in size from approximately 0.1-3.0 ha and comprise representatives of all Community Types. Fig. 20(a) describes the frequency distribution of the proportion of all species at each of these sites represented by <50 mature individuals. Fig. 20(b) describes the frequency distribution of the proportion of shrub and tree species at each of these sites represented by <50 mature individuals. Fig. 20(c) describes the frequency distribution of the proportion of shrubs and tree species at each of these sites represented by 1-6 mature individuals. A total of 302 species were recorded at these 90 sites, of which 213 comprise shrubs and trees.

While it is necessary to stress that errors undoubtedly exist in the estimation of some population sizes, especially herbaceous and geophytic taxa included in Fig. 20(a), these Figures strikingly demonstrate that the sizes of individual breeding populations are commonly very small. In Fig. 20(b), for example, it may be observed that at 81 of the 90 sites considered, the majority of the woody species are represented by populations of 50 or less mature individuals. Similarly, at 16 of the sites, the majority of woody species are represented by from 1-6 mature individuals. Fig. 20(c). Such small population sizes may be considered doubly significant, moreover, for obligately exogamous species (e.g., Euphorbiaceae, Ebenaceae, Myristicaceae, Menispermaceae).

In Fig. 21 the relationship between the number of woody species with populations > 50 mature individuals is plotted against logarea, for each of these 90 sites. As expected, the number of populations of woody species with > 50 individuals tends to increase concomitantly with area \(r = 0.48; p < 0.01\). This significant correlation notwithstanding, the variability in the number of populations with > 50 individuals evidently increases
Fig. 20: Population sizes of mature individuals at each of 90 effectively-sampled, discrete patches (see text for details).
Fig. 21: Relationship between patch size \( A \) and the number of shrub and tree species with populations > 50 mature individuals \( P_w \), at each of 90 effectively-sampled, discrete patches.
with patch size (Fig. 21).

4.1.7 Summary

The main points arising from analysis presented in Section 4.1 may be summarised as follows. Numerical classification of the site-floristics data set reveals that regional MVF vegetation may be described with reference to essentially four floristic groups. These groups correspond generally with MVF occupying seasonally dry sandstone and lowland habitats, and perennially wet sandstone and lowland springs. For the purposes of subsequent analyses, however, the seasonally dry lowland group may be considered as comprising three more-or-less floristically continuous sub-Types. These correspond to MVF occupying rock outcrop, coastal and subcoastal landforms.

Species numbers range from 11 to 96 over the 194 sites sampled. While species numbers tend to increase with area, relatively large numbers of species commonly occur in very small sites. The latter observation suggests that breeding populations occurring in many patches are likely to be small. This is demonstrated in analyses of population sizes occurring at 90 discrete patches.

4.2 Dispersal Studies

4.2.1 Occurrence of species on Holocene landforms

The occurrence of MVF vegetation on recently evolved Holocene substrates such as coastal beach and chenier ridges, actively
slumping coastal cliffs, and coastal/subcoastal floodplain alluvia, provides a ready-made, natural opportunity for assessing the capacities of MVF species to disperse with effect. In the course of the ecological survey of MVF vegetation, 28 discrete patches occurring entirely on Holocene substrates were sampled. Of these 28 patches, 23 are classified with seasonally dry lowland Types (Groups 2(b), 2(c)), 2 with lowland springs (Group 3), and 3 with sandstone springs (Group 4). A further 44 patches occurring either partly on, or immediately adjacent to such landforms, were sampled also. Considering only those patches occurring entirely on Holocene landforms, supplemented by data given in Russell-Smith & Dunlop (1984), the Northern Territory MVF taxa known to occur on such substrates are indicated in Appendix 1.

For each Community Type, the proportion of species known to occur on Holocene landforms is given in Table 9. In this Table it may be observed that the proportion of species occurring on such substrates is consistently high over all Community Types. Indeed, on the basis of a relatively limited number of observations, 70% of the entire flora is known to occur on Holocene landforms. Such figures illustrate clearly that, taken as a whole, the flora is composed largely of species with a demonstrated capacity to exploit ecological opportunities as these arise through time. Such dispersal capacity provides a ready explanation for many of the small population sizes characteristic of this vegetation. Furthermore, the widespread occurrence of MVF on Holocene substrates is, in itself, a demonstration that the extant disjunction of MVF in western Arnhem Land is not simply an expression of fragmentation.

4.2.2 Dispersal in other situations

While the widespread occurrence of certain recently introduced (exotic) species (e.g. Passiflora spp. in Appendix 1) and the establishment de novo of floristically diverse MVF at the site of the abandoned British garrison of Victoria (Figs. 22, 23), provide further evidence of the general significance of
Table 9: Proportion of species in each Community Type occurring on Holocene landforms (data derived from Appendix 1).

<table>
<thead>
<tr>
<th>Community Type</th>
<th>1</th>
<th>2(a)</th>
<th>2(b)</th>
<th>2(c)</th>
<th>3</th>
<th>4</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. species occurring on Holocene landforms</td>
<td>131</td>
<td>154</td>
<td>215</td>
<td>187</td>
<td>170</td>
<td>153</td>
<td>273</td>
</tr>
<tr>
<td>Total No. species</td>
<td>186</td>
<td>173</td>
<td>233</td>
<td>209</td>
<td>204</td>
<td>212</td>
<td>388</td>
</tr>
<tr>
<td>Occurrence on Holocene landforms (%)</td>
<td>70.4</td>
<td>89.0</td>
<td>92.3</td>
<td>89.5</td>
<td>83.3</td>
<td>72.2</td>
<td>70.0</td>
</tr>
</tbody>
</table>
Fig. 22: Victoria Settlement in the mid-1840's showing the parade ground and vegetable garden (beyond the line of cottages in the centre of the illustration). The surrounding vegetation is evidently tall eucalypt forest, dominated by Eucalyptus miniata and E. tetrodonta, such as occurs widely in the region at the present day. The building with stairs on the right is the Quartermaster's Store. (From an original engraving by H.T. Melville, in Jukes 1847).

Fig. 23: Abandoned in 1849, that area cleared for the parade ground and vegetable garden is now under MVF. The stonework in the illustration is part of the surviving foundations of the Quartermaster's Store. (Photo taken in 1982).
dispersal, the results of two other studies are presented here to illustrate contrasting dispersal situations. These concern studies of dispersal at three escarpment springs, and a study of the dispersal capacity of the Arnhem Land escarpment dominant, *Allosyncarpia ternata*, respectively.

4.2.2.1 Dispersal at springs

This study focuses on three small springs in the Arnhem Land escarpment. At two of these springs, Anbangbang and Nangaloar, the MVF patches associated with them are very small (ca. 0.025ha and 0.03ha, respectively). The third spring, near Oenpelli, is also very small but is contained within a relatively large patch of seasonally dry MVF, some 8ha in extent. In each case however, the spring comprises perennial seepage from near-vertical sandstone cliffs. The locations of these springs, and study methods, have been outlined previously in Section 3.2.1.

Detailed results of the various components of this study are given in Appendix 2. The main points are summarised here in Table 10. In Table 10(a) it may be observed that at the two small patches, approximately half of the tree and shrub species present are not represented by sexually mature individuals. At the Oenpelli site, however, all species present either as seedlings or saplings in sampling quadrats occur also as sexually mature forms either in the immediate vicinity of the spring, or elsewhere in the extended patch. In the instances of Anbangbang and Nangaloar therefore, the occurrences of species in the absence of mature individuals can be derived in only two ways: from reserves of seed stored in the soil; or by transport of propagules from seed sources outside the patch.

In Table 10(b) is given the number of germinants recorded from three dry-soil samples collected immediately adjacent each seepage. These soil samples were collected at the commencement of the study (September 1983), in the late dry season. Thus the watering given these soils when laid out in the greenhouse would
Table 10: Summary of results of spring dispersal study.
(All data derived from Appendix 2).
Where given, figures in parentheses refer to numbers of species.

(a) Numbers of MVF tree and shrub species represented by mature individuals, or immature individuals only.

<table>
<thead>
<tr>
<th>Spring site</th>
<th>No. species represented by at least 1 mature individual</th>
<th>No. species recorded in sampling quadrats not represented by adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sept. 1983</td>
<td>May 1984</td>
</tr>
<tr>
<td>Anbangbang</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Nangaloar</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Oenpelli</td>
<td>21</td>
<td></td>
</tr>
</tbody>
</table>

(b) Number of germinants recorded from soil samples at commencement of study (Sept. 1983)

<table>
<thead>
<tr>
<th>Spring site</th>
<th>Mature individuals present</th>
<th>Mature individuals absent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anbangbang</td>
<td>16(2)</td>
<td>2(1)</td>
</tr>
<tr>
<td>Nangaloar</td>
<td>4(2)</td>
<td>-</td>
</tr>
<tr>
<td>Oenpelli</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

(c) Numbers of evacuated seeds and/or germinants from fine materials collected in seed traps

<table>
<thead>
<tr>
<th>Spring site</th>
<th>Mature individuals present</th>
<th>Mature individuals absent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anbangbang</td>
<td>66(4)</td>
<td>101(9)</td>
</tr>
<tr>
<td>Nangaloar</td>
<td>127(3)</td>
<td>112(6)</td>
</tr>
<tr>
<td>Oenpelli</td>
<td>246(13)</td>
<td>2(1)</td>
</tr>
</tbody>
</table>
have been the first substantial rain they had received since the end of the preceding wet season, in May. In this Table it will be observed that a total of only 19 germinants were recorded; these being representative of a total of three species (Acacia aulacocarpa, Melastoma malabathricum and Ficus virens).

At only one site, Anbangbang, were germinants recorded (both Ficus) in the absence of adults of the same species. Although open to other interpretation, these seeds were probably transported in. Moreover, while it is feasible that the germinants of these three species were derived from soil reserves of seed carried over from the preceding wet season, individuals of all three species occurring elsewhere in the general region were observed to carry mature fruits at the time soils were collected.

By way of summary, therefore, these results provide little evidence to suggest that the soils of these seepages contain significant seed reservoirs of many MVF species. Rather, the seeds of most MVF species occurring at these seepages would appear to germinate in the wet season and possess little capacity for longevity.

In Table 10(c) is given the number of seeds evacuated by birds, and/or germinants recorded from fine materials collected in seed traps. This Table speaks for itself; clearly many of the species recorded at the Anbangbang and Nangaloar springs may be derived from seed sources existing outside these patches. For example, in Table 10(a) it is indicated that in sampling seedling quadrats at the end of the 1983/84 wet season, three species were recorded at Anbangbang which otherwise were not present in the preceding dry season sampling. That the occurrence of each of these species (Diospyros calyacantha, Cryptocarya cunninghamii and Canarium australianum) is probably attributable to transport by birds is indicated by the presence of their evacuated seeds in seed trap collections (see Appendix 2(a)).

4.2.2.2 Dispersal capacity of Allosyncarpia ternata

As described previously (Sect. 3.2.2), the myrtaceous
evergreen species *Allosyncarpia ternata* is the major canopy dominant in much Arnhem Land escarpment MVF vegetation and, as such, exerts a controlling influence on the subcanopy microclimate. A study of the dispersal capacity of *Allosyncarpia* was undertaken in the late wet season of 1983/84 at four patches dominated by this species. Site locations are given in Section 3.2.2.

In Table 11 it may be observed that *Allosyncarpia* germinants are profuse under parent canopies, much reduced in number at the canopy margin, and absent at distances greater than 2m from the parent canopy. Such a distribution is explained simply by the fact that the dry seeds of *Allosyncarpia* are relatively heavy and thus are dispersed only within the immediate vicinity of parents (Fig. 24). Birds were not observed feeding on seeds or unopened dry capsules. Of note in this Table however, is the occurrence of 2 *Allosyncarpia* saplings in the open (transect 2, Lightning Dreaming). These individuals were clearly remnants of a former closed canopy given their location beside a recently fire-gutted, large *Allosyncarpia* trunk.

### 4.2.3 Summary

Dispersal data presented in Section 4.2 indicate that the regional MVF flora comprises essentially two elements. Firstly, on the basis of a relatively limited number of observations concerning the occurrence of MVF vegetation on recently evolved Holocene landforms, it is shown that the great majority of MVF species possess the capacity to disperse widely from parental plants (Sect. 4.2.1). By Community Type, the proportion of such species ranges from 70.4% in seasonally dry sandstone habitats, to 92.3% in seasonally dry coastal situations. Furthermore, as illustrated by the study of dispersal-in-action at three small escarpment springs (Sect. 4.2.2.1), the widespread phenomenon of small population sizes in this vegetation may be accounted for, at least in part, by such dispersal capacity. By contrast, only a relatively small number of species exhibit very restricted
Table 11: Dispersal capacity of *Allosyncarpia ternata*.
All data presented here collected in 1983/84 wet season. Data based on consecutive quadrats (1x2m²) along transects at right angles to patch margins.

<table>
<thead>
<tr>
<th>Site</th>
<th>Under <em>Allosyncarpia</em> canopy</th>
<th>Canopy edge</th>
<th>In open</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of germinants</td>
<td>Seedlings/ saplings</td>
<td>No. of germinants</td>
</tr>
<tr>
<td></td>
<td>(0-5m)</td>
<td>(5-7m)</td>
<td>(7-50m)</td>
</tr>
<tr>
<td></td>
<td>&lt;3cm DBH</td>
<td>&lt;3cm DBH</td>
<td>&lt;3cm DBH</td>
</tr>
<tr>
<td>(i) Mt. Howship</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>transect 1</td>
<td>239</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>transect 2</td>
<td>129</td>
<td>6</td>
<td>9</td>
</tr>
<tr>
<td>(ii) Lightning Dreaming</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>transect 1</td>
<td>111</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>transect 2</td>
<td>141</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>(iii) Oenpelli</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>transect 1</td>
<td>53</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>transect 2</td>
<td>13</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>(iv) Djirrinbal Creek</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>transect 1</td>
<td>153</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>transect 2</td>
<td>78</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>
Fig. 24: Germinating seeds of Allosyncarpia ternata.
dispersal capacities. This element is exemplified by the Arnhem Land escarpment dominant, *Allosyncarpia ternata* (Sect. 4.2.2.2).
4.3 Biogeographical Relationships

The biogeographical affinities of the Northern Territory MVF flora with other regional floras are explored here at the species level. Five Australian, and ten extra-Australian regions are considered (Table 12). Brief palaeogeographical and climatic notes are provided also in Table 12. The extra-regional distributions of Northern Territory Top End MVF species are outlined in Appendix 1, along with full acknowledgement to data sources. These data are summarised in Fig. 25 and Table 13.

As indicated in Fig. 25 and Table 13, much of the Top End MVF flora occurs also in other coastal Australian regions, in northern Australia especially. These data thus provide a further illustration of the relative floristic continuity of the north Australian MVF flora noted elsewhere by Byrnes et al. (1977), Kikkawa et al. (1981), Specht (1958), Specht et al. (1977) and Webb et al. (1984). Only 5.2% of Top End MVF species are shared with the contiguous Central Australian region, however; this low level of correspondence reflecting the marked gradient of increasing aridity away from the coast (Fig. 2).

Relatively high levels of floristic similarity are expressed also with extra-Australian regions, through Malesia especially, but declining generally with increasing distance. These data thus support earlier observations made by Specht (1958:Table 4) concerning the extra-Australian distributions of 81 MVF species recorded by him from Arnhem Land. The degree of similarity manifest with the far-flung regions of Africa, Tropical America, India, and indeed South-east Asia and Malesia generally, is at first perhaps surprising. Thus, although similarities between northern Australian floristic components with the floras of these regions have been noted many times previously, and their significance much debated (see references in 3.3), the degree to which many of these same patterns reflect on-going processes of dispersal generally has been overlooked. The MVF floristic connections with Africa and Madagascar, Tropical (South) America,
Table 12: Definition of regions for analysis of biogeographical affinities of the MVF flora
(see also Fig. 25).

<table>
<thead>
<tr>
<th>Region</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Australian</td>
<td></td>
</tr>
<tr>
<td>1. Western Australia - northern regions, excluding that area covered by Central Australia.</td>
<td>Cl.: mean annual rainfall decreasing sharply from 1500-1000mm in north to &lt;500mm southwards. Strongly summer rainfall regime. Mean annual air temperature &gt;24°C. Pg.: Landform relief dominated by the Kimberleys, comprising siliceous sedimentary lithology in the main, and of similar age (Precambrian) to the Arnhem Land Plateau. These two blocks separated by the late Proterozoic Victoria River Basin. Whereas the Kimberleys have been emergent through the Cretaceous, the Top End of the Northern Territory was submerged beneath a widespread Late Cretaceous sea. Marine incursion possibly separated these regions also in the Miocene. (Refs: Lloyd 1968a,b; Skwarko 1966,1994; Veevers 1984).</td>
</tr>
<tr>
<td>2. Northern Queensland - as defined by the Pastoral Districts of Cook, Burke, North Kennedy (Anonymous 1977)</td>
<td>Cl.: predominantly strongly seasonal summer rainfall, from 1500-1000mm on Cape York Peninsula to 1000-500mm south and east of the Gulf of Carpentaria. Pockets of high to very high rainfall on east coast with relatively aseasonal distribution. Mean annual air temperature &gt;24°C, except in high rainfall Atherton Tablelands region (22-24°C). Pg.: The Arnhem Land Plateau is separated from the coastal ranges along the northeast of Northern Queensland by the wide expanse of the Gulf of Carpentaria and the Tertiary Karumba Basin of which the Gulf is a part. The Karumba Basin in turn overlies the Mesozoic Carpentaria Basin. In the Late Cretaceous all of the Top End of the Northern Territory and most of Northern Queensland was submerged. Following marine regression a late Cretaceous, deeply weathered planation surface was developed. Through the Tertiary the Karumba Basin has witnessed three major cycles of</td>
</tr>
</tbody>
</table>
3. Southern Queensland - all other Queensland Pastoral Districts (see 2), excluding Central Australia.

4. South-eastern Australia - New South Wales and Victoria, excluding Central Australia.

5. Central Australia - as defined in Jessop (1981: Fig. 1) - see Fig. 25.

deposition associated with periodic orogenic uplift of the eastern highlands. Deeply weathered lateritic surfaces are known to be associated with the first two cycles, from the late Eocene to early Miocene, and Miocene-Pliocene, respectively. Arnhem Land was separated also from the east coast by the incursion of a widespread shallow Miocene sea. In the late Pleistocene, the Gulf of Carpentaria is considered to have been dry at the last Glacial Maximum ca. 18 000 BP. (Refs. : Grimes 1980; Idnurm & Senior 1978; Lloyd 1968a,b; Skwarko 1966; Smart 1977; Smart & Senior 1980; Veevers 1984).

Cl. : Summer-dominant rainfall, generally 1500-1000mm on the coastal fringe to <500mm inland. Mean annual temperature range between >24-18°C. Pg. : In late Cretaceous much of western Queensland and New South Wales inundated. With regression a deeply weathered planation surface formed. Through the Tertiary similar cycles of erosion of uplifted coastal ranges and deposited in inland basins as occurring in North Queensland. (Refs. : Idnurm & Senior 1978; Veevers 1984).

Cl. : Aseasonal, unpredictable precipitation <500-<100mm annually. Mean annual air temperature >24°C in the north to 18°C in the south. Pg. : As with much of the Australian platform, Central Australia has been tectonically relatively stable from Cretaceous time. Much of the region was inundated by the widespread late Cretaceous sea. In the Northern Territory, a number of deeply weathered planation surfaces are described; these probably corresponding with similar surfaces to the east ranging from early to late Tertiary in age (see 2 above). The widespread occurrence of surficial aeolian dunes points to the development of marked aridity for the latter half of the Quaternary at least. (Refs. : Hays 1967; Veevers 1984;
(b) Extra-Australian

6. Africa - Madagascar

Cl. : various. Pg. : Africa separated from South America from the mid Cretaceous (ca. 125 my BP), with separation complete by 90 my BP. Madagascar-India was gained with Africa prior to 90 my BP. Around 65 my BP Madagascar separated from India and subsequently moved southwards relative to Africa to occupy its present position. From 148-80 my BP Africa converged on Eurasia, and subsequently on Europe until, by the Palaeocene (65 my BP), Africa was connected. From the early Palaeocene to 53 my BP Africa and Europe temporarily separated, followed by subsequent convergence resulting in direct connection in the Miocene, ca. 17 my BP. (Refs.: Axelrod & Raven 1978; Raven 1979).

7. India - India, Sri Lanka, Pakistan


8. South-east Asia - Andaman and Nicobar Islands, continental S.E. Asia north of the Kra Isthmus, Hainan, Hong Kong, Taiwan.

Cl. : various. Pg. : S.E. Asia, of Laurasian lithology, has occupied its present location since 85 my BP at least, but has undergone a net 40°-50° anticlockwise rotation. Through this time the Indo-Australian plate has converged on S.E. Asia, firstly India and then subsequently Australia in the Miocene. (Refs. : Audley-Charles et al. 1981; Powell et al. 1984).

9. Western Malesia - Malay Peninsula, Sumatera, Jawa, Kalimantan.

Cl. : Predominantly perhumid or slightly seasonal rainfall generally much greater than 2000mm annually. Western Jawa however, and a few other localised pockets, are under the influence of a strongly seasonal/seasonal rainfall distribution generally in the range of 2000-1500mm annually. Pg. : This

region covers the southern extension of Sundaland with a plate tectonic history as with 8. above. Much of the region currently submerged occupies a shallow shelf area subject to episodic emergence/submergence associated with Quaternary glacio-eustatic sea level fluctuations. (Refs.: Audley-Charles 1981; Verstappen 1975; Whitmore 1981).

Cl.: various, but strongly seasonal rainfall distribution in the south and other pockets scattered through the Celebes and the Philippines. Similarly, mean annual rainfall tends to increase from 1500-1000 mm in the south to >3000 mm northwards.

Pg.: The northward rafting Australian (Sahul) platform collided with westwards-rotating trailing portions of Sundaland at or near the eastern Celebes in the mid Miocene (ca. 15 my BP). The islands of the Moluccas (which are underlain by Gondwanic lithosphere) are likely to have been emergent only from the early Pliocene (ca. 5 my BP). Emergence of the volcanic islands of the Inner Banda Arc is likely to have commenced from the late Miocene associated with the collision of Sunda and Sahul in the vicinity of Timor by the mid Pliocene. Colonisation of these volcanic islands could have begun in the early Pliocene, but more likely by the late Pliocene following rapid uplift. The palaeogeography of the Philippines is uncertain but may comprise eastwards moving fragments rifted from continental S.E. Asia in the late Mesozoic, which collided with an intraoceanic westwards moving volcanic arc in the Oligocene. (Refs.: Audley-Charles 1981; Bowin et al. 1980; Hamilton 1979; Veevers 1984).


Cl.: various, but strongly seasonal rainfall in the south tending less seasonal northwards. Similarly, rainfall trends from 1500-1000 mm in the south 3000-2000 mm northwards. Pg.: See 10. above. By contrast with Western Wallacea, however, all these islands are underlain by Gondwanic continental lithosphere. The Outer Banda Arc islands however comprise an allochthon of arc-trench sediments.
tamped onto the Indo-Australian plate associated with its subduction beneath the Eurasian plate. Emergence of the Indo-Australian plate associated with its subduction beneath the Eurasian plate commenced in the mid-Pliocene, the extensive shallow continental shelf that has been subject to episodic emergence/submergence through the Tertiary (refs. Audley-Charles 1981; Carter et al. 1976; Hamilton 1979; Pigram et al. 1984; Veevers et al. 1979).

13. New Caledonia

Typically seasonal rainfall distribution. Ca. 2000mm annually. P. New Caledonia has the northern occupant of the Norfolk Ridge, together with the contiguous Lord Howe Rise, as its northern limit.
rifted from the eastern continental margin of Australia-Antarctica in the late Cretaceous (ca. 89 my BP) with the development of the Tasman Basin. Separation of the Norfolk Ridge from the Lord Howe Rise through the creation of the New Caledonia Basin commenced ca. 75 my BP and was completed by the early Palaeocene; the spreading of the Tasman Basin was not completed until the Eocene. While marine transgressive facies of late Cretaceous and Eocene age occurring along the axial region of New Caledonia are indicative of early submergence, the biotic complement of extant New Caledonia is such as to suggest that at least some part of New Caledonia has always been emergent. Raven (1979), for example, describes the flora of New Caledonia as a virtual Gondwanic museum. (Refs.: Coleman 1980; Crook 1981; Crook & Belbin 1978; Kroenke 1985).

Cl. : various. Pg. : Fringing the eastern convergence zone between the Pacific and Indo-Australian plates, the islands of Tonga, Fiji, and the New Hebrides have been derived as volcanic arc systems (as with the Bismarcks and Solomons), associated with subduction of the north-westerly moving Pacific Plate beneath the eastern spreading margin of the Indo-Australian plate from the early Tertiary. On the other hand, island chains occupying mid-plate positions on the Pacific plate (e.g. Hawaiian, Marguessa, Society, Austral islands) have developed through volcanogenesis associated with the passage of oceanic crust over relatively fixed hot spots in the underlying mantle. Given that sea-floor spreading into the western Pacific generally describes a north-westerly direction, the ages of seamounts in any one island chain progressively increase from the southeast to the northwest. For example, dated volcanoes in the Hawaiian chain range from the presently active Kilauea volcano in the southeast to 27 my old seamounts located 2800 km to the northwest. (Refs.: Coleman 1980; Crook 1981; Crough 1984; Jarrard & Clague 1977; Kroenke 1985; McDougall & Duncan 1980).
15. Tropical America

Cl. : various. Pg. : Following the final separation of Africa from South America ca. 90 my BP, direct overland connection between South America and Antarctica-Australia existed until ca. 80 my BP, and then more tenuously until the end of the Eocene (ca. 40 my BP). From the Eocene onwards South America began to close on North America until, in the Pliocene (ca. 6 my BP), an isthmian link between these continental masses was forged. (Refs. : Crook 1981; Raven 1979).
Fig. 25: Distribution of 380 MVF taxa occurring in the 'Top End' of the Northern Territory, in other regions as defined in Table 12. Seventeen species are considered as being Top End endemics. Exotic species are excluded.
Table 13: Extra-regional distribution of the Northern Territory (Top End) MVF flora. Numbers given without parentheses refer to species numbers. Numbers in parentheses give the number of species in each row cell as a percentage of the total number of species occurring in respective columns. All data derived from Appendix J; exotic species are excluded.

<table>
<thead>
<tr>
<th>Region</th>
<th>Community Type</th>
<th>Numbers in brackets refer to species numbers</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2a</td>
</tr>
<tr>
<td>(a) Australian</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Western Australia</td>
<td>120 (65)</td>
<td>123 (73)</td>
<td>148 (63)</td>
</tr>
<tr>
<td>2. North Queensland</td>
<td>151 (81)</td>
<td>143 (85)</td>
<td>185 (78)</td>
</tr>
<tr>
<td>3. Southern Queensland</td>
<td>88 (41)</td>
<td>79 (47)</td>
<td>102 (43)</td>
</tr>
<tr>
<td>4. South-eastern Australia</td>
<td>40 (22)</td>
<td>29 (17)</td>
<td>35 (15)</td>
</tr>
<tr>
<td>5. Central Australia</td>
<td>13 (7)</td>
<td>14 (8)</td>
<td>12 (5)</td>
</tr>
<tr>
<td>(b) Extra-Australian</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Africa, Madagascar</td>
<td>25 (14)</td>
<td>25 (15)</td>
<td>36 (15)</td>
</tr>
<tr>
<td>7. Indian subcontinent</td>
<td>53 (29)</td>
<td>54 (32)</td>
<td>76 (32)</td>
</tr>
<tr>
<td>8. South-east Asia</td>
<td>60 (31)</td>
<td>67 (38)</td>
<td>92 (38)</td>
</tr>
<tr>
<td>9. Western Malesia</td>
<td>78 (42)</td>
<td>72 (42)</td>
<td>103 (43)</td>
</tr>
<tr>
<td>10. Western Wallacea</td>
<td>76 (41)</td>
<td>86 (51)</td>
<td>119 (50)</td>
</tr>
<tr>
<td>11. Eastern Wallacea</td>
<td>79 (43)</td>
<td>92 (5)</td>
<td>124 (52)</td>
</tr>
<tr>
<td>12. Eastern Malesia</td>
<td>105 (56)</td>
<td>109 (64)</td>
<td>154 (65)</td>
</tr>
<tr>
<td>13. New Caledonia</td>
<td>36 (20)</td>
<td>34 (20)</td>
<td>58 (24)</td>
</tr>
<tr>
<td>14. Oceania</td>
<td>42 (23)</td>
<td>38 (23)</td>
<td>59 (25)</td>
</tr>
<tr>
<td>15. Tropical America</td>
<td>7 (3)</td>
<td>10 (5)</td>
<td>15 (6)</td>
</tr>
</tbody>
</table>
and India, for example, are instructive here given that these regions share with Australia a Gondwanic heritage (Table 12). From the listing of eleven distribution patterns given at the end of this Section it may be observed that, contrary to the expectation that MVF species shared between the Top End and these aforementioned regions might, to some degree at least, represent text-book examples of palaeogeographical isolates, consideration of the wide distributions of the species concerned reveals them to be, without exception, a motley collection of opportunists. However, as is taken up in later discussion (5.2), more tangible Gondwanic connections are illustrated by the extra-regional distributions of a small number of taxa with restricted dispersal capacities.

Similarly, if one considers the complement of Top End MVF species which occurs also in the Laurasian regions of Western Malesia and Western Wallacea, as well as on the relatively recent emergent island landmasses of Gondwanic Eastern Wallacea (Table 12), it is observed that 195 species (51%) must have dispersed either away from or towards the Sahul platform to occur in their present locations (data derived from Appendix 1). As such, these data provide a further illustration of the dispersal capacity of the regional MVF flora as a whole. Moreover, while it is impracticable here to consider the ultimate origins of Top End MVF species occurring also, for example, in Laurasian Malesia and Eastern Wallacea, it is observed in passing that the relatively large number of such vagile species indicates that Top End MVF vegetation constitutes, at least in part, a satellite of a greater regional vegetation (Fig. 26).

In conclusion to this section, 11 generalised distribution patterns are illustrated from data given in Appendix 1. For the sake of brevity, occurrences in South-east Asia, New Caledonia, and Oceania have been omitted (unless otherwise noted), given that no distribution patterns are expressed exclusively between these and Australian regions.
Fig. 26: Distribution of evergreen rainforest and monsoon forest (sensu lat) vegetation in Malesia (from Whitmore 1984b), and evergreen rainforest and MVF in northern Australia (after Kahn & Lawrie 1984; Kenneally & Beard 1984; Lavarack & Godwin 1984; Russell-Smith & Dunlop 1984; Winter et al. 1984). It is to be noted that the distribution of Australian MVF vegetation as given, is schematic only. Even where maps are available (i.e. Cape York Peninsula), the small size and diffuse occurrence of MVF patches precludes their being mapped individually here.
1. Northern Territory Endemics (n=17): Allosyncarpia ternata, Bambusa arnhemica, Blainvillea dubia, Blepharocarya depauperata, Canthium sp. aff. lucidum, Carpentaria acuminata, Croton armstrongii, Croton bynesii, Diospyros bundeyana, Flacourtia territorialis, Lophopetalum arnhemicum, Nervilia sp. (DJ 1339), Popowia australis, Ptychosperma bleeseri, Rauwenhoffia sp. (NB 2829), Syzygium minutuliflorum, Terminalia erythrocarpa.

2. Northern Territory and Western Australia only (n=14): Adansonia gregorii, Alstonia ophioxyloides, Aristolochia sp. (CRD 6392), Capparis jacobii, Denhamia obscura, Ficus coronulata, Ficus scobina, Maytenus ferdinandi, Stenocarpus sp. (CRD 3938), Syzygium armstrongii, Typhonium sp. (DJ 1380), Vitex glabrata, Xanthostemon eucalyptoides, Xanthostemon psidioides.


4. Northern Territory and Central Australia only (n=0).
5. Australia only (n=28): Amorphophallus galbra, Bursaria spinosa, Cassine melanocarpa, Dioscorea transversa, Dipodium stenochilum, Dodonaea lanceolata, Dodonaea platypeta, Erythroxylum australe, Ficus leucotricha, Mallotus nesophilus, Marsdenia cinerascens, Marsdenia velutina, Miliusa sp. (NB 940), Parsonsia velutina, Polyalthia holtzeana, Pouteria sericea, Premna acuminata, Psychotria nesophila, Saccopetalum brahei, Sarcostemma australe, Sesbania formosa, Smilax australis, Syzygium angophoroides, Terminalia sericocarpa, Thunbergia arnhemica, Tinospora smilacina, Trichosanthes holtzei, Vitex acuminata.

6. Northern Territory (in Australia) only, with other regions as given (n=7): Artocarpus glautus (W. Malesia, W. & E. Wallacea), Calophyllum soulattri (S.E. Asia to Oceania), Elaeocarpus culminicola (E. Malesia), Gmelina schlechteri (E. Malesia), Mallotus didymochryseus (E. Malesia), Ophioglossum intermedium (W. Malesia, W. Wallacea), Tröpidia curculigoides (S.E. Asia, W. Malesia, W. Wallacea).

7. Australia and Eastern Malesia (± New Caledonia and Oceania) only (n=58): Acacia aulacocarpa, Acacia auriculiformis, Acmena hemilampra, Actéphila latifolia, Aglaia sapindina, Alstonia actinophylla, Alyxia spicata, Ampellocissus acetosa, Arthroclis irritabilis, Anacardium australianum, Canavalia sp. aff. papuana, Capparis quiniflora, Cayratia acri, Choriceras tricorne, Clerodendrum cunninghamii, Clerodendrum floribundum, Cryptocarya cunninghamii, Cryptocarya exfoliata, Cupaniopsis anacardioidea, Curcuma australasica, Dillenia alata, Diospyros ferrea var. reticulatus, Dysoxylum oppositifolium, Elaeocarpus arnhemicus, Emmenosperma cunninghamii,
Endospermum medullosum, Glochidion disparipes, Helicia australasica, Horsfieldia australiana, Ilex arnhemensis, Jasminum didymum, Jasminum simplicifolium, Lindsaea ensifolia spp. agathii, Livistona benthamii, Mackinlaya macrosciadia, Muehlenbeckia zippro, Neolitsea australiensis, Nervilia holochila, Ophelia brownii, Pavetta brownii, Phyllanthus coccoides, Phymatosorus grossus, Planchonella sp. aff. xerocarpa, Polyalthia ridgetissima, Polyscias australianum, Rhaphidophora australasica, Securinega melanthesoides, Semecarpus australiensis, Stenocarpus salignus, Syzygium forte, Tarenna dallathiana, Terminalia subacroptera, Ternstroemia cherryi, Thrixspermum congestum, Triumfetta microcantha, Uvaria holtzei, Zanthoxylum parviflorum.

8. Australia and Malesia (+ S.E. Asia, New Caledonia, and the Oceania) (n=70): Aidia conchinchinensis, Alphitonia excelsa, Alyxia ruscifolia (-W. Malesia, W. Wallacea), Atalaya salicifolia (-W. Malesia, W. Wallacea, E. Malesia), Blechnum indicum, Buchanania arborescens, Calophyllum sie (-W. Malesia, W. Wallacea), Cansjera leptostachya (-W. Malesia), Cassia surattensis, Cayratia maritima, Claxoyxylon tenerifolium (-W. Malesia), Clematis pickeringii, Cordyline cannifolia, Crataeva religiosa, Croton argyraus (-E. Malesia), Croton tomentellus (-W. & E. Malesia), Cyathostemma micranthum, Dendrobium dicuphum (-W. Malesia, W. Wallacea, E. Malesia), Dendrobium lobii (-E. Wallacea), Diospyros ferrea var. humilis (-W. Malesia, W. Wallacea), Diospyros maritima, Drypetes lasiocynna (-W. Malesia, E. Wallacea), Euodia elleryana (-W. Malesia, W. Wallacea), Exocarpus latifolius (-W. Malesia), Fagraea racemosa (-Sahul), Ficus adenopserma (-W. Malesia), Ficus congesta (-W. Malesia), Ficus opposita (-W. Malesia), Ficus
platypoda (-W. & E. Malesia), Geodorum neocaledonicum, Glochidion sumatranum, Glochidion xerocarpum, Glycosmis pentaphylla, Gymnanthera nitida, Harrisonia browii (-W. Malesia), Homalanthus novo-quinaensis (-W. Malesia), Hypoestes floribunda (-W. Malesia), Ixora klanderana (-W. Malesia, W. Wallacea), Jasminum aemulun, Litsea ferriginea, Luśia terretifolia, Macaranga involucrata (-W. Malesia), Malāsia scandens, Malaxia acuminata (-E. Malesia), Maranthes corymbosa (+Tropical America), Melastoma malabathricum, Memecylon pauciflorum, Mitromelum minutum, Myristica insipida (-W. Malesia), Nephelepis hirsutula (-W. Malesia, W. Wallacea, E. Wallacea), Nervilia aragoana (-E. Wallacea), Paramignya recurva (-W. & E. Malesia), Phaleria octandra (-W. Malesia), Pittosporum ferrugineum, Pittosporum moluccanum (-W. & E. Malesia), Pleomele angustifolia, Polyaulax cilindrocarpa (-W. Malesia, E. Wallacea), Schefflera actinophylla (-W. Malesia, W. Wallacea), Scleria polycarpa (-W. Malesia, W. Wallacea), Secamone elliptica (-W. Malesia), Selenodesmium obscurum (-W. Wallacea, E. Wallacea), Stenochlaena palustris, Sterculia quadrifida, Strychnos lucida (-W. & E. Malesia), Suregada glomerulata, Syzygium fibrosum (-W. Malesia, W. Wallacea), Tabernamontana orientalis, Taenitië blechnoides (-W. Wallacea, E. Wallacea), Vavaea amicorum, Vittaria ensiformis (-W. Wallacea, E. Wallacea).

9. Australia to India (+ New Caledonia and Oceania) (n=62)
Acmenaspasma claviflorum, Adenanthera pàvonina, Achiu num n., Aglaia subulata, Amorphophallus paeoniifolius, Antidesma quaesembilla, Arringtonia acutangula, Blechnum orientale, Bombax ceiba, Bridelia tomentosa, Brucea javanica, Callicarpa candicans, Cassia timorensis, Cathormion umbellatum, Cayratia trifolia, Cheilanthes
tenuifolia, Cissus adnata, Coleus scutellarioides, Cordia dichotoma, Cyperus diffusus (-W. Wallacea, E. Wallacea), Dalbergia candidatensis, Drynaria quercifolia, Elaeocarpus angustifolius, Entada phaseoloides, Ficus benjamina, Ficus hispida, Ficus racemosa, Ficus virens, Hanguana malayana, Harpullia cupanioides, Helminthostachys zeylanica, Ichnocarpus frutescens, Leea rubra, Litsea glutinosa, Lygodium flexuosum, Lygodium japonicum (-W. Wallacea), Macaranga tanarius, Mallotus philippensis, Melia azederach, Mimusops elengi, Mucuna gigantea, Murraya paniculata, Nauclea orientalis, Nephrolepis acutifolia (-W. Wallacea, E. Wallacea), Pachygone ovata (-S.E. Asia), Peltophorum pterocarpum, Piliostigma malabaricum, Pongamia pinnata, Salacia chinensis, Santalum album, Schizaea dichotoma (-W. Wallacea, E. Wallacea), Scleria terrestris, Selaginella ciliaris (-W. Malesia), Sphenoclea zeylanica, Stephania japonica, Strychnos psilosperma (-W. Wallacea, E. Wallacea), Syzygium operculatum (-E. Wallacea, E. Malesia), Timonius timon, Trema aspera, Trichosanthes sp. aff. ovigera, Wrightia pubescens, Zizyphus oenoplia.

10. Australia to Africa (+ New Caledonia and Oceania) (n=35):
Cembrus precatorius, Adiantum hispidulum, Allophyllum cobbe, Antiaris toxicaria, Aspafagus racemosus (-E. Malesia), Capparis sepiaria, Carallia brachiata, Celtis philippensis, Cyperus javanicus, Cyperus zollingeri (-India, S.E. Asia, W. Malesia), Derris trifoliata, Dicranopterus linearis, Dioscorea bulbifera, Diplocyclos palmatus, Flagellaria indica, Ganophyllum falcatum, Helicostegia isora, Hypholytrum nemorum (-W. Wallacea, E. Wallacea), Jacquemontia paniculata, Laportea interrupta, Lindsaea ensifolia ssp. ensifolia, Luffa cylindrica, Lygodium microphyllum, Opilia
amentacea, Pisonia grandis (-India, S.E. Asia), Plumbago zeylanica, Premna serratifolia, Remusatia vivipara, Schizaea digitata (-W. Wallacea, E. Wallacea), Scleria lithosperma, Tacca leontopetaloides, Tamarindus indica, Trichosanthes cucumerina, Triumfetta rhomboidea, Vernonia cinerea.

5.0 DISCUSSION

The results of various studies have been presented in preceding sections which, collectively, explore the complementary themes of MVF distribution and dispersal. In concluding Sections of this paper, these results are first reviewed, dispersal mechanisms are discussed and finally, the status of MVF vegetation in western Arnhem Land is assessed.

5.1 Classification

Numerical classification of a data set comprising 194 sites X 235 common MVF species (3.1.2) reveals that MVF vegetation in the Top End of the Northern Territory can be considered as comprising essentially four floristic Groups. These Groups correspond generally with MVF occurring both in seasonally dry, and perennially moist, escarpment and lowland habitats, respectively. While this classification corresponds closely with the definition, a priori, of Habitat Types defined by Russell-Smith & Dunlop (1984), a number of significant differences are evident also.

Firstly, whereas these latter authors describe all MVF vegetation associated with springs and seepages in sandstone terrain as being of the 'one Type, the numerical classification places three sandstone spring assemblages occurring in relatively high rainfall areas of the north-west of the Northern Territory with similarly-located species-diverse assemblages associated with moist coastal/subcoastal lowland situations. Conversely, the numerical classification places a small number of relatively species-poor lowland spring assemblages with the escarpment springs. While it is thus evident that the Association Measure used in classification, the Jaccard, differentiates between these assemblages largely on the basis of floristic abundance, the analysis suggests also that the MVF flora associated with perennially moist habitats is relatively continuous, and that the arbitrary distinction between lowland and escarpment types is not necessarily supportable. These observations notwithstanding, it
may be stated confidently that sandstone spring habitats do provide a specialised niche for a small number of species at least. For example, only one filmy fern, Selenodesmium obscurum (Family Hymenophyllaceae), is known from the region; this occurring in widely disjunct, ever-humid microenvironments associated with sheltered rock faces only provided in broken sandstone terrain.

Secondly, included with the 79 sites comprising the seasonal lowland Group, is one small MVF patch occurring in the Arnhem Land escarpment. This site exhibits interesting dynamic relationships, however, since it comprises a complement of widespread, vagile MVF species beneath a mature stocking of typical woodland types (e.g. Erythrophloeum chlorostachys, Eucalyptus spp., Pandanus spiralis). As such, this patch is evidently in an establishment phase. Of note, moreover, is the occurrence there of two individuals of the recently introduced custard apple, Annona reticulata; the nearest fruiting source of which is probably 5 km distant, at the township of Qenpelli.

And thirdly, Russell-Smith & Dunlop (1984), describe seasonal lowland MVF vegetation with respect to three Habitat Types; namely, MVF associated with coastal, subcoastal and rock outcrop landforms. As indicated in their Table 5, however, these three Habitat Types are more-or-less floristically continuous. As a basis for mapping MVF vegetation in the western Arnhem Land region (4.1.4), these Types have been retained. In order to distinguish between the Types employed by Russell-Smith and Dunlop (1984) and those defined here, the term Community Type is used.

Before proceeding to other discussion it is necessary to indicate the limitations of this classification. The ecological survey on which it is based was focused on the north-western sector of the Northern Territory, especially the western Arnhem Land region. The relatively high rainfall and floristically diverse areas of the coastal far north-west (e.g. Melville and Bathurst Islands; Fig. 8) are probably under-sampled, and eastern
Arnhem Land and much of the hinterland were not sampled at all. While the MVF vegetation of eastern Arnhem Land is probably similar to that as described here for western coastal and subcoastal regions, floristic similarities with Cape York (north Queensland) are likely to be greater. With regards inland regions, MVF vegetation becomes increasingly scattered and attenuated, both structurally and floristically, away from the coast (Russell-Smith & Dunlop 1984). However, as well as occupying spring, riparian and rock outcrop landforms, MVF species are associated also with closed thicket communities, dominated by Acacia spp. Such vegetation was not sampled in the course of this survey.

5.2 Distribution and Dispersal

It is a generally accepted thesis that the scattered occurrence of small patches or tracts of MVF across monsoonal northern Australia are relictual remnants representing the fragmentation of a former, more-or-less continuous expanse of closed forest vegetation (e.g. Hnatiuk & Kenneally 1981; Specht 1958; Specht et al. 1977; Stocker & Mott 1981). On the other hand, Kikkawa et al. (1981) and Russell-Smith & Dunlop (1984) suggest that this extant distribution represents processes of both fragmentation and colonisation. While Beard (1976) has previously suggested likewise, that MVF on the Mitchell Plateau, Western Australia, probably represents recent colonisation following the last post-glacial rise in sea-level, he has more recently abandoned this view in favour of fragmentation (Beard et al. 1984; Clayton-Greene & Beard 1985). In preceding Sections of this paper (4.2, 4.3) evidence has been presented which indicates that the presumed relictual status of much MVF vegetation in the Top End of the Northern Territory is not sustainable.

In Section 4.1.4 it is shown that the broad pattern of MVF distribution in the western Arnhem Land is highly disjunctive (Fig. 19). In Section 4.1.5 it is shown that the number of species occurring in small patches is commonly relatively large;
thus suggesting that population sizes of many component species must be small. This observation is demonstrated in Section 4.1.6 where, in Fig. 20(b), for example, it is shown that, at 81 of 90 effectively sampled, discrete patches, the majority of woody species present are represented by populations of 50 or less mature individuals. Similarly, in Fig. 20(c), it is shown that at 16 of these 90 patches, the majority of woody species are represented by populations of from 1 to 6 mature individuals. That the disjunction manifest in the regional distribution of this vegetation, as well as the small sizes of many breeding populations may be explained, in part, as an expression of the high vagility of the flora as a whole is indicated by a number of lines of evidence.

Firstly, on the basis of a relatively small number of observations concerning the occurrence of patches (in their entirety) on Holocene landforms, 70% of the entire Top End MVF flora of nearly 400 species is known to occur on recently evolved substrates such as calcareous and siliceous beach ridges, actively slumping coastal cliffs, and coastal and subcoastal riverine floodplain alluvia (4.2.1). By Community Type, the proportion of such species ranges from 70% in seasonal sandstone habitats, to 92% in seasonal coastal situations (Table 9). Such proportions would doubtless increase, furthermore, with more observations.

A second illustration of dispersal-in-action is provided by the study of dispersal at three small escarpment springs (4.2.2.1). This study demonstrates that the occurrence of sexually immature individuals in the absence of adults is, at two of the springs (Anbangbang and Nangaloar), more reasonably attributed to transport of diasporas from seed sources existing outside these patches, than to reserves of seed in the soil (Table 10). Dispersal distances were not ascertained however.

In passing, it is pertinent to note that in addition to those species given in Appendix 2 whose seeds evidently possess a significant capacity for longevity (i.e. Acacia dulantocarpa,
Coleus scutellarioides, Ficus vires, Melastoma malabathricum and Panicum trichoide, the following MVP germinants were recorded from a further 19 dry season soil samples collected in a variety of escarpment and lowland situations: Alphitonia excelsa, Alyxia spicata, Ficus leucotricha, Ficus platypoda, Ficus racemosa, Ficus scobiná, Hibiscus tiliaceus, Morinda citrifolia, Muehlenbeckia zippellii, Passiflora foetida, Tinospora smilacina, Trema aspera and Triumfetta micracantha. Considering that a total of 28 soil samples, each 1.0 X 1.0 X 0.05 m³, were tested for dry season seed reserves, the total number of MVP species recorded (18) is low in comparison with species numbers reported from other tropical closed forest soils (Cheke et al. 1979; Gnevara & Gomez-Pompa 1972; Hall & Swaine 1980; Hopkins & Graham 1983; Keay 1960; Liew 1973; Symington 1933). In common with these studies, however, all germinants recorded here are essentially secondary forest species.

A third illustration of marked dispersal capacity is provided by the widespread occurrence of Northern Territory MVP species in certain other extra-Australian regions. In Section 4.3, two examples are given. The first concerns those species which occur also in the Gondwanic regions of Africa and Madagascar, India, and Tropical (South) America. Rather than providing text-book examples of palaeogeographic isolates, the distributions of 100 or so species indicate them as being widespread opportunists. Similarly, the occurrence of a further suite of species in the regions of Western Malesia, Western and Eastern Wallacea (as defined in Table 12), indicates that at least 5% of the Top End flora must have dispersed either from, or towards the Australian platform in order to account for their present distributions.

A final example is provided by Figs. 22 and 23. These figures illustrate the establishment of a small patch of MVP in the ruins of the British garrison of Victoria, on the Coibour Peninsula, following its abandonment in 1849 (Spillett 1972). Atherton and Greeves (1985) describe an analogous situation from
Green Island, off north-eastern Queensland. Following total clearance of this island by the 1880s at the hands of beche-de-mer fishermen, closed canopy vine-forest has reestablished within 100 years. Krakatau affords a further well known example (Whittaker et al. 1984 and references therein). These examples illustrate the rapidity and facility with which many vine-forest species are dispersed and can establish themselves. As well, these examples, together with others given previously concerning the colonisation of Holocene landforms, demonstrates that many patches themselves are of recent origin.

By contrast with these situations, however, in Section 4.2.2.2 is presented the results of a study exploring the dispersal capacity of the Arnhem Land MVF dominant, Allosyncarpia ternata. Other than in situations where the dry seeds of Allosyncarpia are transported by slope wash etc., dispersal in this species is evidently restricted to within 2m of the edge of parent canopies. Such restricted dispersal capacity is probably shared by less than a handful of Top End MVF species; but including, significantly, other similarly dry-seeded myrtaceous species such as Xanthostemon psidioides and X. umbrosus. The third Xanthostemon species occurring in the Top End, X. eucalyptoides, has winged seeds, and this, together with its typically riparian habit, probably confers a degree of vagility; it is observed on Holocene landforms, for example. In common, however, all these species are restricted to sandstone landforms or their near vicinity.

By contrast with many of the previously discussed, more vagile species; moreover, these myrtaceous taxa provide a tangible link with Gondwanaland. Allosyncarpia, for example, is one of four monotypic genera of the Arilastrum alliance, which exhibits a "fairly definite relationship" with the eucalypts (Johnson & Briggs 1984:751). The three other genera, Eucalyptopsis, Arillastrum, and an as yet undescribed genus, occur in New Guinea, New Caledonia, and North Queensland, respectively (L.A.S. Johnson pers.comm.). Xanthostemon species
exhibit a somewhat similar distribution. However, while represented in northern Australia and New Guinea, and having radiated extensively in New Caledonia, Xanthostemon occurs also in the Philippines (i.e. Western Wallacea), the Moluccas (i.e. Eastern Wallacea), and the Solomon Islands (P.G. Wilson pers. comm.). As such, Xanthostemon evidently disperses more readily than do members of the Arillastrum alliance.

Stenocarpus (Proteaceae) exhibits a similar Gondwanic distribution pattern (Johnson & Briggs 1975); but in the Northern Territory, S. salignus at least, is evidently relatively vagile (Appendix 1). However, with the exception of a small number of genera centred on the Australian region (e.g. Dodonaea, Exocarpos, Santalum), or which are endemic to Australia and New Guinea (e.g. Blepharocarya, Bursaria, Carpentaria, Choriceras, Denhamia, Hydriastele and Notelaea), the great majority of Top End MVF taxa belong to groups widespread in other regions (Webb & Tracey 1981a: Appendix 1).

Collectively, therefore, these examples indicate that the regional MVF flora is characterised by essentially two dispersal elements. On the one hand, the great majority of species exhibit a demonstrated capacity to disperse widely from parental canopies, and an ability to exploit ecological opportunities as these arise through time. These species thus conform to the definition of biological nomads as described by van Steenis (1958). On the other hand, the flora comprises but a small number of species whose dispersal capacity is severely limited. This element is exemplified by dry-seeded myrtaceous species associated typically with sandstone terrain. Disjunctions in the distributions of these latter elements, therefore, can reasonably be attributed only to processes of fragmentation.

5.3 Dispersal Mechanisms:

While much attention has been given in preceding Sections to the relative dispersal capacities of various elements of the regional MVF flora and vegetation, the means by which species
Dispersal have, for the most part, not been considered. In this Section, following discussion of such means, the implications of dispersal for patch dynamics are briefly explored.

5.3.1 Dispersal Spectra

Discussion of the means by which MVF species disperse is undertaken here with reference to dispersal spectra presented as Tables 14 and 15. In presenting these Tables a general qualification is required since, as Berg (1983:13) pointedly remarks, "a traditional dispersal spectrum of a flora, based on specialized dispersal alone, does not necessarily reflect the dispersal capabilities of that flora, nor the actual means of dispersal by which the individual species arrived to that particular area."

In Table 14 is given the frequency of occurrence of ten propagule types in each of the six Community Types defined previously (4.1.3). The categories of propagule type are those as recognised by Russell-Smith & Dunlop (1984). The formalised system of Dansereau & Lems (1957) is not followed here since, with some categories, finer distinctions are warranted. While the categories used here are mostly self-explanatory, a number require additional comment. Firstly, the fleshy fruited types are given as two size classes; greater than, and less than, 2.5cm width, respectively. This distinction is based on the assumption that the largest avian frugivore in the region, the Torresian Imperial Pigeon (Ducula spilorrhoa), probably ingests fruits up to a maximum size of 2.5cm width. For example, in a study of fruit dispersal by D. spilorrhoa in north-eastern Queensland, the widest fruit recorded as being transported by these pigeons was 1.85cm width (Crome 1975:Table IV). Secondly, the category 'presented' includes dry seeds or seeds with an insignificant sarcotesta which are displayed in open fruits held on the plant. This type corresponds with the mimetic class of van der Pijl (1972:33). And thirdly, 'bouyant', although more strictly a dispersal mechanism than a propagule type, describes those
Table 14: Frequency of occurrence of propagule types within each Community Type and the flora as a whole. (data derived from Appendix 1).
Note that columns sum to greater than 100%. This reflects simply that some species exhibit more than 1 propagule type.

<table>
<thead>
<tr>
<th>Propagule Type</th>
<th>Community Types</th>
<th>Total species (n=388)</th>
<th>Species on Holocene landforms (n=273)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 (%)</td>
<td>2a (%)</td>
<td>2b (%)</td>
</tr>
<tr>
<td>Fleshy fruit (&gt;2.5 wide)</td>
<td>2.1</td>
<td>1.7</td>
<td>2.9</td>
</tr>
<tr>
<td>Fleshy fruit (&lt;2.5cm wide)</td>
<td>53.5</td>
<td>57.0</td>
<td>51.9</td>
</tr>
<tr>
<td>Arillate, funiculate</td>
<td>4.3</td>
<td>4.1</td>
<td>2.9</td>
</tr>
<tr>
<td>Presented (mimetic)</td>
<td>9.6</td>
<td>10.5</td>
<td>10.3</td>
</tr>
<tr>
<td>Dry (explosive, gravity)</td>
<td>12.3</td>
<td>14.0</td>
<td>11.7</td>
</tr>
<tr>
<td>Spores, dust-like seeds</td>
<td>9.1</td>
<td>3.5</td>
<td>6.3</td>
</tr>
<tr>
<td>Winged, plumed</td>
<td>11.2</td>
<td>11.6</td>
<td>9.2</td>
</tr>
<tr>
<td>Burred, sticky</td>
<td>1.6</td>
<td>4.1</td>
<td>3.3</td>
</tr>
<tr>
<td>Bulbils</td>
<td>1.6</td>
<td>1.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Bouyant</td>
<td>2.1</td>
<td>1.2</td>
<td>8.4</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>107.4</strong></td>
<td><strong>108.9</strong></td>
<td><strong>107.4</strong></td>
</tr>
</tbody>
</table>
propagules for which water is a known major dispersal agent (cf. Carlquist 1974; Gunn & Dennis 1976; Guppy 1906; Ridley 1930). It is noted however, that many contenders for this category are omitted given that they are not necessarily dependent on water transport explicitly (e.g. plumed seeds of Bombax, Apocynaceae and Asclepiadaceae; membranous, winged seeds; bulbils of Dioscorea).

Small fleshy fruits are clearly the most abundant propagule type in all Community Types and the flora as a whole (Table 14). The incidence of such a large proportion of species with small fleshy fruits, together with presented, and arillate and funiculate types, is, moreover, strongly suggestive of the importance of avian and/or chiropteran frugivory. In total, these three propagule types are representative of 58.8% of the entire flora and, by Community Type, range from 66.2% in sandstone spring communities (Type 4), to 71.6% in MVF associated with rock outcrops (Type 2a). The frugivorous avifauna on the other hand comprises only three obligate frugivores and a further 16 facultatively frugivorous species (Russell-Smith & Dunlop 1984). Of these species, the obligate frugivores, at least, may be identified as important dispersal vectors. These species, Ptilinopus cincta, P. regina, and Ducula spilorrima, are all fruit pigeons (Family Columbidae). In feeding, the fruit is swallowed whole and the seed, minus the pericarp, is excreted intact. None of these species possesses a muscular gizzard (Frith 1982).

Twelve species have large fleshy fruits. To this group, however, is added the indehiscent legume of Tamarindus indica given that the seeds are surrounded by the bitter-sweet pulp of culinary fame. Of the twelve strictly fleshy types, only in one, Syzygium forte, does the pericarp surround a single large seed. The fruits of the rest are either composite types (e.g. Annona reticulata, Morinda citrifolia) or are many seeded fleshy types (i.e. berries, syconia). As such they need not be ingested whole to effect dispersal. Even in the absence of birds
with gapes of sufficient size to swallow these fruits whole, however, dispersal may be effected by water (e.g. Crataeva religiosa, Guettarda speciosa, Morinda citrifolius, Nauclea orientalis and Syzygium forte) or frugivorous bats of the Family Pteropodidae (Marshall 1983; van der Pijl 1957, 1972). In support of the latter contention, germinants of both Picus racemosa and Morinda citrifolius were recorded from excreta collected in traps laid beneath a camping roost of the Black Flying-Fox, Pteropus alecto, in a complementary study to that as outlined previously in Section 3.2.1. Moreover, while it is well known that fruit bats typically ingest only juice and pulp (including small seeds), they often carry heavy fruits short distances to roosts before feeding (e.g. Marshall 1983; van der Pijl 1972). Besides Pteropus alecto, only one other fruit bat occurs in the region, the Little Red Flying Fox, P. scapulatus.

In passing, it is salient to note that, as with many MVF plants, four of the five frugivorous species given above occur also outside Australia. Frith (1982) gives the following distribution notes for the fruit pigeons. Both Ptilinopus cinctus and P. regina occur in the Lesser Sunda Islands and the southern Moluccas. In Australia, whereas P. regina occurs from the Kimberleys through to eastern Australia, P. cinctus is restricted to the Arnhem Land escarpment. Ducula spilorrhoa ranges from the Kimberleys to eastern Australia, and then northwards through New Guinea and the Bismarck Archipelago and the Aru Islands. Frith, however, considers D. spilorrhoa to be conspecific with the other two Imperial Pigeons, D. bicolor and D. luctuosa, which range, collectively, from the Andaman and Nicobar Islands through to New Guinea. D. spilorrhoa, moreover, is migratory, and although it is known that eastern Australian populations migrate annually to and from New Guinea, the source(s) of north-western Australian populations is as yet unresolved. Of the fruit bats, Pteropus alecto ranges from the Kimberleys through to eastern Australia. Outside Australia it occurs from the Celebes, through the Lesser Sunda Islands, to New Guinea (Hall 1983). Pteropus scapulatus is the odd fox, being restricted
of the remaining propagule types listed in Table 14, it is observed that 15.5% of the flora possesses dry seeds with no apparent specialised dispersal function, followed by spores (ferns) and dust-like seeds (orchids) (11.9%), winged and plumed seeds (8.2%), and then buoyant types (6.4%), burred and sticky types (2.6%), and lastly, bulbils (1%). With respect to the main body of Table 14, it may be observed that proportions of individual propagule types are generally similar over all Community Types. Of note, however, are the relatively large
proportions of species with spores and dust-like seeds in
Community Types 3 (14.1%) and 4 (15.0%); typically, lowland and
sandstone spring vine-forests, respectively. This reflects,
simply, that relatively large numbers of epiphytic and terrestrial
ferns and orchids occur in these habitats, exploiting relatively
humid micro-environments therein prevailing. As well, 'bouyant'
propagules are evidently under-represented, as one might expect,
in Community Types 1 (2.1%) and 2 (1.2%); typically, seasonal
sandstone and rock outcrop MVF vegetation, respectively.

As a means of testing whether any one propagule type confers
a greater capacity for dispersal over other types, the proportions
of propagule types representative of the 273 species known from
Holocene landforms are given in the final column of Table 14. By
comparison with equivalent proportions for the flora as a whole
given in the penultimate column, it may be observed that the two
sets of figures are remarkably similar. These data are thus
strongly suggestive that no one category of propagule confers
greater dispersability than another, at least within the
geographical region considered. This is not to imply, however,
that the propagules of individual species within each category are
equally dispersed. As illustrated by the limited dispersal
capacity of the dry seeds of Allosyncarpia ternata (4.2.2.2),
all species with dry seeds clearly do not disperse equally.

To facilitate comparisons with other published dispersal
spectra, a summary of the apparent means by which this flora
disperses is presented as Table 15. Of the total flora, 64% of
the species possess propagules with characteristics traditionally
considered amenable to avian and/or mammalian transport. The
proportion of such species in all Community Types is over 70%. In
addition to the internal transport of propagules by birds and
fruit bats discussed previously, other types of animal-mediated
dispersal pertinent to this flora include: 1. the external
transport of viscid or barbed, burred, etc. seeds and fruits (e.g.
Pisonia), and; 2. transport by arboreal and ground-dwelling
mammals. In this latter case, however, the non-chiropteran mammal
Table 15: Means of dispersal in each Community Type and the flora as a whole.
(data derived from Table 14). Note that columns sum to greater than 100%. This reflects simply that some species exhibit more than one apparent means of dispersal.

<table>
<thead>
<tr>
<th>Means of dispersal</th>
<th>Propagule types</th>
<th>Community Types</th>
<th>Total Species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Animal transport</td>
<td>large and small fleshy fruits, arillate and funiculate, presented, burred and sticky</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>spores and dust-like seeds, winged and plumed.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Winged and plumed only)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gravity/no apparent specialised mechanism</td>
<td>dry seeds, bulbs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water</td>
<td>bouyant</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2a</th>
<th>2b</th>
<th>2c</th>
<th>3</th>
<th>4</th>
<th>Total Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Animal transport</td>
<td>71.1</td>
<td>77.4</td>
<td>71.0</td>
<td>71.6</td>
<td>72.3</td>
<td>70.4</td>
<td>63.7</td>
</tr>
<tr>
<td>Wind</td>
<td>20.3</td>
<td>15.1</td>
<td>15.5</td>
<td>15.6</td>
<td>19.5</td>
<td>23.0</td>
<td>20.1</td>
</tr>
<tr>
<td>Gravity/no apparent</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>specialised mechanism</td>
<td>13.9</td>
<td>15.2</td>
<td>12.5</td>
<td>12.7</td>
<td>9.8</td>
<td>11.7</td>
<td>16.5</td>
</tr>
<tr>
<td>Water</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.1</td>
<td>1.2</td>
<td>8.4</td>
<td>7.1</td>
<td>6.8</td>
<td>5.6</td>
<td>6.4</td>
</tr>
</tbody>
</table>

| Total                | 107.4 | 108.9 | 107.4 | 107.0 | 108.4 | 110.7 | 107.7          |
fauna is singularly depauperate, comprising no species obligately dependent on MVF habitats, and just three species which regularly frequent MVF (Russell-Smith & Dunlop 1984). These three species include two terrestrial rodents and an arboreal marsupial. Although one of the rodents, Zyzomys woodwardi, may be dependent on MVF fruits in the late dry/early wet season (Begg & Dunlop in press), none of these species is likely to be a dispersal agent of any consequence.

Of the remaining species, 20% may be wind dispersed, 16.5% dispersed by gravity alone (or exhibit no specialised dispersal mechanism), and 6.8% dispersed by water. As noted previously, however, the proportion of species with bouyant propagules is doubtlessly much underestimated. These dispersal spectra are somewhat similar to those reported by Webb and Tracey (1981a) for a variety of rainforest communities in North Queensland and Cape York Peninsula. The proportions of animal dispersed fruits reported here are consistently marginally smaller, however, and the proportions of wind and gravity dispersed propagules correspondingly greater; water-dispersed propagules are not considered by Webb and Tracey. It is not clear from their Table 2, however, whether the spectra are representative of all species present at their sample sites, or represent particular synusiae.

Dispersal spectra for equivalent closed forest vegetation occurring in other strongly seasonal tropical regions are scarce (cf. Howe & Smallwood 1982:Table 2). In a phenological study of 113 dry forest tree species in a markedly seasonal region of Costa Rica, Frankie et al. (1974) observed that approximately 50% of the species possessed fleshy fruits, about 30% were adapted for wind dispersal, and roughly 20% were neither fleshy nor wind-adapted. Gentry (1982:Table VIII; see also Gentry 1983) gives postulated dispersal vector data for 5 other neotropical dry forests, comprising 4 inventory plots and one local florula. Using dispersal vector data given in that Table for a total of 317 dry forest tree and liana species, the dispersal spectrum may be calculated thus: 57% animal (i.e. mammal and bird) dispersed, 32%
dispersed by wind, 9% by gravity alone (i.e. autochorous), and 1% water dispersed. Moreover, by comparison with other neotropical closed forest vegetation types occurring under higher, more equable rainfall regimes, Gentry observes that wind dispersed species tend to decrease proportionately with increasing precipitation, whereas animal dispersed species correspondingly increase. These characteristics are not overtly expressed in Northern Queensland closed forest vegetation (cf. Webb & Tracey 1981a:Table 2), nor in the gradient from seasonally dry to moister closed forests in the Northern Territory. In Table 15, for example, this gradient is expressed generally as from Community Type 1 through to 4 (i.e. from left to right across the Table). The proportion of animal dispersed species shows no tendency to increase with increasing moisture availability. To facilitate strict comparison between neotropical and Northern Territory wind dispersed species, however, only proportions of Northern Territory species with winged and plumed propagules (given in parentheses in Table 15) are considered since Gentry gives data for tree and liane species only; i.e. the spores and dust-like seeds (ferns and orchids) category is extraneous. In this instance there is indeed an apparent trend, if only slight, for the proportion of wind dispersed (mostly woody) species to decrease with increased moisture availability. Webb & Tracey (1981a) however, note that the largest proportions of wind dispersed species in northern Queensland rainforests occur in windy habitats (e.g. mountain summits and coastal sand dunes). Similarly, both Jones (1956) and Keay (1957) report that, in lowland rainforest in Nigeria, the greatest proportions of wind dispersed species occur in the upper canopy. While this is attributed, in part, to windier conditions in these strata, Keay notes that the majority of wind dispersed species are characteristic also of secondary forest vegetation. These few data, while admittedly scanty, suggest nevertheless a degree of parallelism in the dispersal ecologies of at least northern Australian and neotropical seasonal closed forest vegetations.

By way of conclusion to this discussion of dispersal
mechanisms, it is useful to return to Berg's qualification, quoted previously, that dispersal spectra do not necessarily "reflect the dispersal capabilities of that flora, nor the actual means of dispersal by which the individual species arrived to that particular area". A salient example of this concerns the agency of people in the dispersal of MVF species. Thus, although it is widely recognized that the original Aboriginal inhabitants of Australia practised no horticulture at the time of European colonization (e.g. Golson 1972; Harris 1977; White & O'Connell 1982), less well appreciated is their direct involvement in promoting the productivity of certain 'crops' through skilled application of burning techniques (cf. Beaton 1982; Gould 1971; Jones 1969; Latz & Griffin 1978), and, in northern Australia at least, their planting seeds and tubers of various food species (e.g. Hynes & Chase 1982; Jones 1975).

In coastal Arnhem Land, for example, Jones (1975:24-5) describes the apparent casual manner with which seeds of fruit species are discarded in the vicinity of camp sites; these subsequently germinating and developing into groves over which ownership rights are exercised. In the course of field studies reported here similar groves were encountered on Holocene dune facies, associated with former camps. Such groves comprised large numbers of individuals of the fruit-tree species Syzygium suborbiculare, Terminalia grandiflora, Sterculia quadrifida and Antidesma ghaesembilla; the latter two species being, typically, MVF constituents. A second example concerns the association of individuals of the large-fruiting 'white apple', Syzygium forte, with rock-shelter camps in the Arnhem Land escarpment. As indicated earlier in this Section, this species is typically a riparian MVF component. And, thirdly, as related to me by my Aboriginal teachers, in the past, yams, especially Dioscorea bulbifera, were planted in escarpment springs to ensure the availability of food supplies on subsequent visitations. Harris (1977) and Hynes and Chase (1982) report similar practices on off-shore islands in north-eastern Queensland. To these observations may be added the case of
Tamarindus indica, a species supposedly introduced by beche-de-mer fishermen from Macassar, Indonesia, within the last millennium (cf. MacKnight 1976). While this species is widespread in western coastal regions of the Northern Territory, in coastal Arnhem Land and the Gulf of Carpentaria this species is so faithfully associated with Macassan camp sites that its occurrence is used in archaeological surveys as an indicator species (R. Baker pers. comm.). As noted by Golson (1971), moreover, the widespread occurrence of Malesian food-plants in the floras of Arnhem Land and northern Queensland, and the degree of similarity in their usage between the two Australian regions and Malesia, is strongly suggestive that human-mediated plant dispersal in prehistorical times has been 'not insignificant'. Evidently species may disperse by means other than those for which they appear, at first sight, adapted.

5.3.2 Dispersal and patch dynamics

As has been described widely in studies concerning the occurrence of thickets or 'bush clumps' in tropical and subtropical savanna regions, the expansion of patches comprising vagile species occurs essentially as a two-stage succession (e.g. Aubreville 1966; Blydenstein 1967; Cowling 1983; Davidson & Morton 1984; Eggeling 1947; Eiten 1975, 1978; Frost 1984; Hamilton 1982; Hopkins 1974; Jones 1963; Kellman & Miyanishi 1982; Menaut & Cesar 1982; Myers 1936; Tinley 1982; Trollope 1983; Tupas & Sajise 1977; Walter 1971; Werger 1983). The first stage involves the dispersal of forest or thicket initials, commonly by birds, typically to sites which afford some protection from fire, and/or sites of nutrient enrichment or favourable water balance conditions (e.g. termitaria, rock outcrops, erosion gullies, beach dunes, islands, springs, the bases of roost trees). The successful establishment of initials provides a nucleus both towards which further dispersal may be directed (Howe & Smallwood 1982), and from which the developing patch may expand in the second stage of succession. By contrast, patches comprising species with very restricted dispersal capacities, or which are under the canopy dominance of
such species (e.g. *Allosyncarpia ternata*), can expand only through the progressive extension of the patch boundary.

As such it may be seen that the relative capacity of species to disperse has significant implications for biological conservation. For vagile species the persistence of populations in individual patches may not be so much dependent on the maintenance of viable population sizes and structures in each patch in isolation, as on the collective population scattered through a number of wide-spread patches. For less vagile species however, or for species whose habitat or microhabitat requirements are such that ecological opportunities are scarce, persistence is dependent on the maintenance of viable populations in each isolated patch, together with the preservation through time of sufficiently large areas of suitable habitat refugia. In the absence of data concerning the efficaciousness of pollination however, the extent to which disjunct populations may be genetically isolated is unknown.
5.4 Historical Implications

In preceding discussion it has been established that the regional MVF flora comprises many species with a demonstrated capacity to disperse widely from parent canopies. On the other hand, a small number of species are evidently not so vagile. In this final section it remains to consider how these observations may contribute usefully to an understanding of MVF vegetation pattern in the western Arnhem Land region. In presenting this discussion the known vegetation and climatic history of northern Australia is first reviewed, and then, on the basis of these and other data presented in this paper, the status of MVF vegetation in western Arnhem Land is assessed.

5.4.1 Northern Australian Vegetation and Climatic History

5.4.1.1 The Tertiary

The vegetation history of tropical, northern Australia is very inadequately known. Tertiary assemblages are known from only three widespread localities. At Goat Paddock in north-western Australia, an assemblage containing mainly rainforest proteaceous pollens and other taxa of temperate affinity is attributed to the Eocene (Harms et al. 1980). On Mélville Island in the Northern Territory, a macrofossil assemblage containing rainforest types is likewise attributed as being possibly Eocene or younger (White 1978). And on the Atherton Tablelands in north-eastern Queensland, a pollen assemblage containing many taxa still extant, as well as *Nothofagus* and a number of gymnosperm taxa now locally extinct, is attributed as being of Late Tertiary to Early Pleistocene age (Kershaw & Sluiter 1982). These few data, while of uncertain age, point to the likelihood that mesic rainforest vegetation containing elements now extant in more temperate bioclimates (Nix 1982), has, for unknown periods through the Tertiary, occurred more widely across northern Australia. While the decline and eventual decimation of such vegetation(s) is undocumented, it may be noted that grass pollens occur in
sufficient quantity in two central Australian assemblages, attributed to the Mid-to Late Miocene, as to suggest that rainforest vegetation was restricted there to mesic habitats by this time (Harris in Callan & Telford 1976; Kemp 1978; Truswell & Harris 1982). Similarly, Bonnefille (1984) reports that tropical forest in East Africa was fragmented also by this time.

In the plethora of recent reviews of Australian vegetation history, the decimation of rainforests from all but the wetter fringes of Australia by the end of the Tertiary is considered to reflect major changes in global circulation associated with the development of the circum-Antarctic current and the progressive build-up of the Antarctic ice sheet (Galloway & Kemp 1981; Kemp 1978, 1981; Kershaw et al. 1984; Lange 1982; Martin 1978, 1981, 1984; Truswell & Harris 1982; Walker & Singh 1981). While rafting of the Australian plate into lower latitudes is considered to have compensated somewhat for the general cooling trend of the mid-to late Tertiary (Kennett 1977; Shackleton & Kennett 1975), the steepening of the meridional temperature gradient is likely to have resulted in the intensification of global atmospheric and ocean current systems with the net effect of increasing seasonality. Of special significance would have been the strengthening and equatorwards displacement of seasonally oscillating southern Hemisphere, mid-latitude high pressure systems (e.g. Bowler 1982; Flohn 1982, 1984; Nix 1982). As well, in the approximately 100my interval between the development of the Antarctic ice cap in the mid-Miocene (Shackleton & Kennett 1975), and the development of Arctic ice in the Pliocene (Shackleton & Opdyke 1977), it is likely that a strong hemispheric circulation asymmetry would have pertained given the marked ocean temperature contrast between the polar regions (Flohn 1984). Flohn suggests this would have led to the further shift equatorwards of the Southern Hemisphere anticyclone, with the concomitant displacement of the rain-bearing ITCZ (2.2) into the Northern Hemisphere towards 5-15°N. The significance of the northwards displacement of these circulation systems for northern Australia is that, away from the eastern seaboard with its developing orogeny, the climate
of the late Tertiary is likely to have been one of marked seasonal aridity (Flohn 1984: Table 3).

The climatic evidence for monsoonal northern Australia, however, is minimal. In the Barkly Tablelands region of north-western Queensland, the existence of fresh, late Tertiary limestones over a strongly laterised surface, sets an upper age limit to that surface (Williams 1969b) and suggests that a seasonal water balance regime was already established by this time. In north-west Australia, palaeomagnetic dating of laterites suggests that seasonality was established by the Mid-Miocene (Luck, in Schmidt & Embleton 1976). In south-western Queensland, however, similar dating of weathered profiles suggests seasonality as early as the latest Cretaceous to early Eocene (Idnurm & Senior 1978). From the Karumba Basin in the Gulf of Carpentaria, Grimes (1980) describes a strongly laterised surface, the Aurukun Surface, which he suggests may be equivalent with both the palaeomagnetically dated Oligocene (late Eocene to early Miocene) Canaway Profile of Idnurm & Senior (1978), and the Tennant Creek surface described by Hays (1967) from the Northern Territory.

5.4.1.2 The Quaternary

Even for the Quaternary, relevant palaeorecords are scarce. In the Australian tropics the only studies which bear directly on long-term vegetation change are the palynological investigations of Kershaw (e.g. 1975, 1976, 1978, 1983, 1985; Kershaw et al. 1984; Singh et al. 1981); on the Atherton Tablelands in north-eastern Queensland. While this region is not strictly comparable with much of northern Australia given its possession of an aseasonal rainfall regime (cf. Nix 1982), these studies provide a relatively detailed history of the flux of rainforest vegetations from sediments deposited in Lynch's Crater, over a period attributed as encompassing the last two glacial/interglacial cycles (ca. 200 000 years). These studies suggest that mesic evergreen rainforest has expanded over the basaltic tablelands during relatively warmer and wetter
interglacial periods, with drier types of rainforest replacing them during glacial periods. However, within the radiocarbon dated part of the sequence (ca. 40,000 years), drier rainforest pollen types are shown to be replaced by sclerophyll pollen taxa, especially *Eucalyptus* and *Casuarina*, at around 38,000 BP, with the transition to sclerophyll pollen types virtually complete by 26,000 BP. These pollen taxa remain dominant until the Holocene. At the start of the transitional phase, moreover, there is a sharp increase in the concentration of charcoal particles. Kershaw interprets this increase in charcoal (which declines thereafter [e.g. Singh et al. 1981:Fig. 5]), and the replacement of dry rainforest by sclerophyll vegetation, as being attributable to the advent of Aboriginal burning impact. As argued by Horton (1982) and Clark (1983), however, these data are open to other interpretation. For example, while Kershaw (1985) notes that lake conditions apparently give way to swamp at some time prior to the dry, gymnosperm-dominated forest/sclerophyll transition, and that at the start of the transition itself the swamp sediments are markedly decomposed, he neglects to consider that these phenomena may not simply reflect a trend of diminishing annual precipitation, but the development of seasonal water balance conditions. In the same paper he observes that such gymnosperm dominated vegetation is less favoured by a seasonal climate (see also Nix 1982). Thus, the gradual replacement of dry forest pollen taxa might just as readily be explained by deteriorating water balance conditions leading to greater fire susceptibility, than to Aboriginal burning per se. In any event, mesic evergreen rainforest once again becomes the dominant vegetation type in the Early Holocene, the expansion of which Kershaw attributes as reflecting the resumption of favourable interglacial climatic conditions.

From the Arafura Sea, wood obtained at 99m depth and dated at 14,500 BP (Jongsma 1974) suggests that exposed portions of the Sahul shelf may have supported an extensive vegetation at the Last Glacial Maximum low sea-level. Such vegetation is likely to have been of a monsoonal type given the postulated climatic conditions.
prevailing at that time (see below). Also in the marine record, Zaklinaya (1978) describes a pollen sequence, attributed as being of Late Pliocene to Recent in age, from sediments in the Timor Trough. While of low resolution, this record indicates that gymnosperm-dominated rainforest pollen taxa of Laurasian affinity have been replaced by more monsoonal types of Gondwanic affinity on at least two occasions through this period. Collectively, these two marine records suggest that marked fluctuations in Quaternary glacio-eustatic sea-level (e.g. Chappell 1983a; Chappell & Veeh 1978; Fink & Kuikla 1977), and attendant climatic change, have exerted a profound influence on the relative extent of monsoonal (and other) vegetation occurring in the shelf region. While other direct evidence for this is unavailable, it has been noted elsewhere that wide disjunctions in the distributions of many monsoon forest species are suggestive that seasonal conditions have prevailed over extensive areas in the past (Burkill & Holtum 1923; van Meeuwen et al. 1961; van Steenis 1957, 1961, 1979; Verstappen 1975; Whitmore 1981, 1984a). For the balance of northern (monsoonal) Australia, however, fossil evidence for the nature of Quaternary dry-land vegetation change is singularly lacking.

A small body of imperfectly dated data is available, however, concerning late Quaternary climates in monsoonal northern Australia. Such evidence as is available points to the likelihood that regional climates were seasonally wetter at some period in the vicinity of, but previous to, 28 000 BP (Bowler 1983a; Jones & Bowler 1980). This is determined from dates of soil carbonate and limestone sampled from the floors of formerly expanded Lakes Wood and Gregory, in the Northern Territory and northern Western Australia, respectively. Kershaw (1985), however, suggests that these lakes were more likely to be full in the period 80 000 – 120 000 BP, when sea-level would have been sufficient to just cover the extensive northern continental Sahul shelf and thus provide higher levels of atmospheric moisture for monsoonal precipitation.

Following this wetter phase was a period of marked aridity
Fig. 27: Palaeogeographic features of the northern Australian region ca. 18000 BP, as described in the text. Sources: Last Ice Age coastline (150m bathymetric contour) from a map provided by Simon Wild (ANU); Lake Carpentaria as given in Torgeraen et al. 1983; "Lake Bonaparte" as given in van Andel & Veevers 1967; distribution and inclination of continental dunes based on an unpublished map provided by Keith Fitchett (ANU) and Bob Wasson (CSIRO).
Evidence for this is found in both the terrestrial and marine record. On land, the superimposition of longitudinal dunes on the calcareous soils of Lakes Wood and Gregory described above indicates a phase of dune mobilisation. While this phase is undated it is evidently younger than the ages of the soils upon which the dunes rest (Bowler 1983b; Bowler & Wasson 1984). Similar dunes are described by Jennings (1975) from the Fitzroy estuary in north-western Australia. There is even less time control in the dating of these dunes, but given that they lie unmodified directly beneath Holocene estuarine sedimentary facies, Jennings considers they probably date to the Last glacial low sea level. Also, given the inclination of these relict dunes (Fig. 27), Jennings considered that dry season easterlies were annually much more dominant than they are now; as well, such winds are likely to have been significantly stronger (e.g. Ash & Wasson 1983; Manabe & Hahn 1977; Newell et al. 1981; Wasson 1984). At Shelburne Bay, in the far north of Cape York Peninsula, well dated coastal dunefields are known to have been actively mobile at the height of the last ice age (Lees 1986). For Australia as a whole, it may be noted that the widespread occurrence of linear dunes is yet to be shown to be older than 500 000 - 700 000 years (Wasson 1982).

In the marine record, the studies of Jongsmá (1970) and van Andel & Veevers (1967) on the Sahul Shelf, and those of Chappell (1974, 1976, 1983) and Veeh & Veevers (1970) in New Guinea and northeastern Queensland, respectively, provide a relatively consistent pattern of sea-level in the vicinity of 150m below that of the present at the Last Glacial Maximum (ca. 18 000 BP) (Fig. 27). This marine regression had not only the effect of exposing the vast expanse of the epicontinental shelf, thus eliminating a major source of moisture for monsoonal and cyclonic precipitation, but cut off the passage of warm Pacific water influx through the Torres Strait. Without this influx there may have been no alleviation to the increased incursion of cold waters up the Western Australian coast generated by intensified and more equatorward Ice Age westerlies (van Andel & Veevers 1967; Mayr
1944; Nix & Kalma 1972; Webster & Streten 1972, 1978). However, as indicated in the maps of Last Glacial Maximum Sea surface temperature estimates for the Indian Ocean (CLIMAP 1976; Hutson 1978; but especially Prell 1982 and Prell et al. 1980), seasonal sea surface temperatures of the northern fringing seas are shown to be only 1-2°C less at 18,000 BP than now occurs. In contrast to these results, however, van Andel & Veevers (1967) indicate that cores from the Trough reveal that the frequency of tropical planktonic foraminifera diminishes, and more temperate types increases, in sediments below a dated level of 13,000 BP. It would thus appear that the capacity of the northern epicontinental sea to provide moisture for precipitation over northern Australia would have been much reduced, mostly as a consequence of diminished sea surface area, but also due to the reduction, if only slight, of sea surface temperature (cf. Torgersen et al. 1983).

Also in the marine record, van Andel & Veevers (1967) describe the occurrence of calcareous nodules dredged from the ocean floor which they consider to be kunkar, a soil limestone of pedogenic origin which forms under highly seasonal, low precipitation conditions. While undated, the surficial position of these nodules is taken to suggest they were formed during the most recent period of shelf exposure. As well, evidence from lagoonal sediments in the Bonaparte Depression on the edge of the north-west shelf indicates that, at the maximum eustatic sea-level lowering, the Depression was an almost landlocked embayment. Given both the absence of any evidence for brackish or freshwater conditions in these sediments, and that major rivers of north-western Australia drained into this lagoon at that time, van Andel & Veevers (1967) suggest that rainfall and runoff must have been considerably reduced at this time. Similarly, Smart (1977) indicates that, at maximum low sea level, the vast closed basin now encompassed by the Gulf of Carpentaria was dry.

On the basis of such observations, Nix & Kalma (1972) and Webster & Streten' (1972, 1978) suggest that rainfall across
northern Australia during this period of lowered sea-level may have been reduced by as much as a half present values, the climate of Arnhem Land being much as that endured 500km to the south (Fig. 2).

Accompanying the glacio-eustatic rise in sea-level to its termination around 6 000 BP (Chappell 1983b; Chappell et al. 1982), it is widely observed in the tropics that water balance conditions improved markedly (cf. Kutzbach 1980; Rognon & Williams 1977; Street 1981; Street & Grove 1976, 1979; Williams 1984). However, for monsoonal northern Australia little can be said save that the occurrence of stabilised dunes indicates that, relative to the Last Glacial, water balance conditions in the Holocene have evidently been more favourable for plant growth (Jennings 1975). There is the suggestion that regional climates were markedly wetter than at present in the period 5 000 - 8 000 BP (Clarke et al. 1979; Jennings 1975; Nix & Kalma 1972; Smart 1976; Stocker 1971), but this is not demonstrated unequivocably (Schrire 1981; Woodroffe et al. 1985a). Similarly, Kershaw (1983) interprets Holocene palynological sequences on the Atherton Tablelands as reflecting the advent of more seasonal conditions after 6 000 BP, but again, the general applicability of this evidence to monsoonal northern Australia requires verification.

The vegetation history of monsoonal northern Australia is thus poorly known. Such evidence as is available concerning Late Quaternary climates, however, expresses similar general features as are widely reported from other tropical regions (cf. Hamilton 1982; Rognon & Williams 1977; Sarntheim 1978; Street 1981; Street & Grove 1979; Thomas & Goudie 1984; van Zinderen Bakker 1982; Williams 1984): It is not unreasonable to suggest, therefore, that the marked climatic oscillations of the Late Quaternary (at least) have had as profound an influence on the distribution of closed forest vegetation in monsoonal northern Australia, as it has in equatorial regions generally (cf. Campbell & Frailey 1984; Flenley 1979; Hamilton 1982; Kershaw 1985; Street 1981; Talbot et al. 1984; Tricart 1975, 1977; Walker & Hope 1982; White
1983; and various contributions in France 1982).

5.4.2 The Status of MVF in western Arnhem Land

Given the dearth of relevant fossil evidence which bears directly on the nature of dry land vegetation change in the western Arnhem Land region, the attempt at historical reconstruction must necessarily be hypothetical. Having said this, however, it is considered here that on the basis of such evidence as is available concerning landform, sea-level and climatic change, and knowledge of the extant distribution patterns and dispersal capacities of regional MVF vegetation components, it is possible to make some general observations concerning the historical status of MVF vegetation occurring in the western Arnhem Land region.

5.4.2.1 Seasonal Escarpment MVF vegetation

Seasonal escarpment MVF vegetation is mostly restricted to actively eroding, rugged and deeply dissected terrain, but occurs also in a small number of open situations associated with relatively deep sandy mantles (4.1.3). In effect, this distribution reflects predominantly the distribution of Allosyncarpia ternata (3.2.2). Alternatively, in those relatively small number of situations where Allosyncarpia does not occur, such vegetation is dominated typically by other myrtaceous, sclerophyllous species of the genus Xanthostemon (i.e. X. psidioides and X. umbrosus). In previous sections of this paper it has been indicated that each of these species exhibits very restricted capacities for dispersal (5.2). The disjunct pattern of vegetation distribution expressed in Fig. 18 may thus be attributed to processes of fragmentation. Moreover, that such fragmentation has been an ongoing process from the Tertiary at least, is indicated by the widely disjunct distributions of these Xanthostemon species in other northern Australian sandstone regions, and the extant distribution of taxa closely related to Allosyncarpia in north Queensland, New Guinea
The disjunct occurrences of populations with such restricted dispersal capacities both in the Arnhem Land escarpment and in other sandstone regions is strongly suggestive, therefore, that dissection of landforms in geological time has been a significant contributive factor in the fragmentation of these populations at least. In the absence of any major Cainozoic tectonic upheaval in the Northern Territory, such dissection may be attributed to differential erosion, dominated by scarp retreat and pediplanation, of an extensive Cretaceous sandstone surface covering much of northern Australia following its uplift from at least the Miocene (Grimes 1980; Hayes 1967; Skwarko 1966, 1967; Veevers 1984; Williams 1969a,b). Extensive Miocene marine transgression in relatively low-lying basins both to the south-east and south-west of the Top End of the Northern Territory (Lloyd 1968a,b; Veevers 1984) is likely also to have been of significance.

Episodic periods of aridity such as pertained at the height of the last Ice Age have probably contributed also, although evidence for this is lacking. However, given the evident tolerance of Allosyncarpia to xeric substrates in the present day, bare rock pavements for example, harsh water balance conditions per se do not explain the disjunct distribution pattern of seasonal MVF vegetation in the Arnhem Land escarpment. The current confinement of this vegetation mostly to deeply dissected, rugged terrain may be a historical legacy of the influence of fire. Such vegetation is likely also to have provided a significant refugium for many populations during periods of marked aridity.

5.4.2.2 MVF vegetation associated with springs

By contrast with seasonal MVF vegetation types occurring in escarpment and lowland habitats respectively, numerical analysis reveals that MVF vegetation associated with situations of
perennial water availability is relatively floristically homogenous over the western Arnhem Land region as a whole (4.1.2). Despite such continuity however, the regional distribution of this Community Type is evidently highly disjunctive (Fig. 18).

To a large extent, this extant distribution pattern reflects simply the scarcity of available habitat at the present day. Furthermore, relative to the last glacial period it might be anticipated that such vegetation has expanded given both climatic amelioration and, as well, the rise in regional water tables, in lowland areas especially, concomitant with the rise in sea-level. While there is little substantive evidence to indicate the extent to which such expansion has in fact occurred, it may be noted that 7 MVF patches associated with well-watered sites were sampled on a variety of Holocene coastal/subcoastal substrates. For example, on Koolpinyah Station near Darwin two floristically diverse patches were sampled associated with springs actually intruding floodplain sediments. In Borneo, Anderson and Muller (1975) and Morley (1981) describe the similar Holocene development of swamp forest over coastal estuarine and freshwater facies, respectively. As may be observed in Fig. 18 a number of spring forests occur at floodplain margins in the western Arnhem Land region. It remains problematic, however, whether the rising sea drowned possible riparian vine-forests associated with former river valleys in the region.

That mesic vegetation has occurred more widely across monsoonal northern Australia than now occurs is indicated by two lines of evidence. Firstly, fossil evidence from sites in the Kimberleys and Melville Island points to the likelihood that mesic vegetation occurred more widely in the Tertiary. While no evidence is available concerning the demise of such vegetation, it may reasonably be assumed that the development of marked seasonal aridity by the Late Tertiary at least, was a significant contributory factor (5.4.1.1). A second line of evidence is provided by wide disjunctions in the distributions of extant taxa both within the Northern Territory, and with north-eastern
Queensland especially (e.g. Elaeocarpus angustifolius, Horsfieldia australiana, Ilex arnhemicus, Planchonella sp. aff. xerocarpa, Polyscias australianum, Ternstroemia cherryi). Even given that some of the above taxa are evidently vagile as indicated by their occurrences on Holocene substrates (Appendix 1), it is improbable that in the absence of linking populations dispersal of these fleshy fruited species would be effected directly over such large distances as that between the Northern Territory and north-eastern Queensland. As yet however, apart from geomorphological evidence which indicates that water balance conditions were presumably more favourable for the expansion of mesic vegetations at some time prior to 28 000 B.P., the Late Cainozoic climatic history of the region is too little known to hazard speculation as to when contact between the floras of these two regions may last have been facilitated. However, on the uniformitarian assumption that the occurrence of certain fossil taxa in the Eocene Goat Paddock assemblage are indicative of a more temperate climate prevailing at that time (e.g. Dacrydium, Microcachrys, Gunnera, Podocarpus [Truswell & Harris 1982]), the extant spring forest flora, comprising taxa with essentially mega- and mesothermal responses (Nix 1982), is improbably derived from such vegetation.

5.4.2.3 Seasonal lowland MVF vegetation

The distribution of seasonal coastal and subcoastal MVF Community Types given in Fig. 18 reveals two broad patterns.

Firstly, the great proportion of this vegetation occurs as patches on, or fringing, Holocene floodplain sediments associated with the lower reaches of all major river systems in the region. Recent geomorphological studies on the South Alligator River floodplains indicate that these are underlain by Holocene estuarine muds extending over a distance 80km inland from the present coastline (e.g. Hope et al. 1985; Woodroffe et al. 1985a,b). Even to the present day this river is tidal almost throughout this range. As may be observed in Fig. 18, patches of
seasonal lowland MVF occurring within the Holocene tidal range are
distributed discontinuously only in association with floodplain
margins and on recently evolved landform features of the South
Alligator River floodplain itself. With the possible exception of
a few patches (Russell-Smith 1984), this vegetation is composed
only of highly vagile species, many with typically maritime
distributions. As such it would thus appear that the great
majority of this MVF vegetation is of relatively recent origin;
the establishment of which being associated with, or post-dating,
the attainment of present sea-level in the Mid-Holocene.

Furthermore, indirect evidence indicates that the regional
extent of such vegetation is unlikely to have been significantly
greater in the Early to Mid-Holocene than that which occurs now.
Such evidence is provided by the distribution of large earthen
incubation mounds, often of huge dimension (e.g. 20m diameter and
5m high), built by the Megapode bird, the Orange-footed Scrubfowl,
Megapodius reinwardt (syn. M. freycinet). While this
widespread species exhibits great variability in its nesting
behaviour over its range (cf. Frith 1956), in northern Australia
M. reinwardt scrapes together `compost heaps' of earth and
vegetable matter, almost invariably in more-or-less closed canopy,
high litter producing, vine forest and thicket habitats. The
occurrence of abandoned mounds in vegetation types other than MVF
may be taken, therefore, as indicating that at some previous time
MVF would have occupied these sites (Harris 1977; Lavarack &
Godwin 1984; Russell-Smith 1984, 1985; Stocker 1971; Webb 1977)
(Fig. 28). That such mounds may exhibit considerable longevity
even where the closed canopy is removed, is indicated by the age
of a mound dated at ca. 8 000 BP from charcoal fragments
incorporated into the basal mound fabric by Stocker (1971) on
Melville Island. Given that Megapodius reinwardt is a highly
vagile species which has been widely observed nesting on coral
cays and other relatively ephemeral landforms (e.g. Bell 1969;
Frith 1956; Olson 1980; pers.obs.), it might be assumed that for
MVF to have been more extensive over coastal/subcoastal lowland
areas of western Arnhem Land in the Holocene at least, conspicuous
Fig. 28: Exposed incubation mound of the Yellow-footed Scrubfowl, *Megapodius reinwardt*, denoting the former occurrence of closed canopy MVP vegetation at this site (see text). In this instance the canopy has been destroyed within the living memory of local Aboriginal people (Bill Neiiji pers. comm.).
evidence in the form of remnant incubation mounds should be apparent. Such evidence is singularly lacking (Russell-Smith 1984).

Finally, the second pattern manifest in the distribution of seasonal subcoastal MVF vegetation concerns its occurrence as riparian communities associated with seasonally dry watercourses in the southern section of the western Arnhem Land region (Fig. 18). In this Figure it may be observed that such vegetation occurs as extensions of MVF associated with perennially wet spring habitats, or is associated with major rivers. While it is probable that improved water balance conditions relative to the last Glacial period have been conducive for expansion of seasonal MVF vegetation along these watercourses also, there is no evidence to indicate that this in fact has occurred. Similarly, no evidence is available concerning the status of MVF vegetation occupying rock outcrop habitats. Given the occurrences of both these Community Types in the Northern Territory hinterland, however, it is probable that, despite the evident vagility of most of the component species (4.2.1), at least some populations, and assemblages (Kikkawa et al. 1981), would have withstood the withering climatic conditions of the Last Glacial period. Given also that seasonal lowland MVF vegetation occurs on a variety of xeric substrates (e.g. rock outcrops), it is unlikely that the disjunct distribution of this vegetation can be attributed solely as a consequence of fluctuating water balance conditions. As with MVF occupying seasonally xeric escarpment habitats, the present distribution of seasonal lowland types is likely also to reflect the historical influence of fire.
6.0 SUMMARY

It has been suggested, on the one hand, that the extant disjunct distribution of MVF across northern Australia represents the fragmentation of a former, widespread, closed canopy vegetation. This fragmentation has been attributed as being a consequence of, essentially, deteriorating Late Cainozoic water balance conditions and/or more recent human burning impact (e.g. Beard et al. 1984; Clayton-Greene & Beard 1985; Gillison 1983; Nix & Kalma 1972; Specht 1958a; Stocker & Mott 1981). On the other hand, a number of authors have suggested that this extant pattern expresses elements of colonisation as well (Beard 1976; Gillison 1984; Kikkawa et al. 1981; Russell-Smith & Dunlop 1984). Given the paucity of relevant fossil evidence, this paper reports various ecological and biogeographical studies undertaken for the purpose of exploring the status of MVF vegetation in the western Arnhem Land region of the Northern Territory.

Following description of the Community Types of MVF vegetation occurring in the Top End of the Northern Territory, and their habitat relationships, the distribution of MVF vegetation occurring in the western Arnhem Land region is given in Fig. 18. This map reveals such distribution to be highly disjunctive. Furthermore, it is shown that breeding populations of individual species occurring in any one patch are commonly very small. That both this extant disjunct distribution pattern and the small population sizes characteristic of this vegetation are explainable, at least in part, as an expression of the facility with which most of this flora disperses, is demonstrated by the widespread occurrence of MVF on a variety of Holocene landforms (e.g. coastal beach dunes). This is illustrated also by dispersal studies conducted at three escarpment springs, and other observations (e.g. Figs. 22, 23). On the other hand, only a small number of species exhibit very restricted dispersal capacities; these being exemplified by dry seeded, myrtaceous species dominant in MVF vegetation occurring in the western Arnhem Land escarpment. These contrasting capacities for dispersal are expressed also in
the distributions of Top End MVF species occurring in other Australian and extra-Australian regions. The mechanisms whereby species disperse, and patches expand, are considered in discussion also.

On the basis of these observations and such palaeorecords as are available for the region, it is suggested, firstly, that the distribution of much MVF vegetation occurring in the Arnhem Land escarpment, and probably also in certain other inland situations, represents fragmentation. In part, such fragmentation may be attributed to landform dissection in geological time given the disjunct distributions of certain taxa associated with scattered occurrences of sandstone terrain. As well, the demonstration of mesic rainforest vegetation in northern Australia Tertiary fossil assemblages, together with wide disjunctions in the extant distributions of certain taxa associated with perennially moist habitats, strongly suggests that deteriorating Late Tertiary water balance conditions, and more recent fluctuations, have been contributive also. On the other hand, it is considered that the distribution of much coastal/subcoastal lowland MVF vegetation in western Arnhem Land is of Recent origin. This MVF vegetation, derived ostensibly from refugial populations and maritime sources, is exemplified by those patches occurring on, or closely associated with, Holocene estuarine and riverine floodplains. Such vegetation, moreover, has not been significantly more widespread in the Holocene at least, than occurs now.

Given the occurrences of both seasonal escarpment and lowland MVF vegetation types on xeric substrates at the present day, it is improbable that disjunctions manifest in the distributions of these respective vegetation can be attributed solely to processes of landform dissection and deteriorating Late Cenozoic water balance conditions. The present distribution of such vegetation is likely also to reflect the historical influence of fire. The significance of fire is explored in the second part of this study (Russell-Smith 1986a).
This study was undertaken with the generous support of the Australian National Parks and Wildlife Service, Canberra; the Kakadu National Park, Northern Territory; the Departments of Prehistory (Research School of Pacific Studies) and Geography (The Faculties), ANU, Canberra; the North Australia Research Unit, Darwin; a Commonwealth Post-graduate Research Scholarship; and Meg Russell-Smith. Access to numerical classificatory procedures contained in the Numerical Taxonomic Package was provided by Lee Belbin, Division of Water and Land Resources, CSIRO, Canberra. Taxonomic assistance was provided by Clyde Dunlop (Conservation Commission of the Northern Territory, Darwin), Lyn Craven (Australian National Herbarium, CSIRO, Canberra), and many other persons acknowledged in Appendix 1. Assistance in the field was provided by officers of Kakadu National Park, Joy Djolom, Clyde Dunlop, Billy Gunbunuka, Rhys Jones, Robyn and Ross Kaires, Nipper Kapirigi, Dave Lindner, Diane Lucas, Rob Muller, George Namingam, Bill Neiiji, Keith Taylor and Hélen Thomson. The use of unpublished information in the compilation of certain Figures, and the provision of certain photographs, is acknowledged in Figure captions. Keith Crook (Dept. Geology, ANU) provided information concerning recent plate tectonics literature cited in Table 12. Geoff Hope (Dept. Geography, ANU) and Garry Werren (Dept. Geography, Univ. N.S.W.) kindly read the manuscript. Figures were prepared by Val Lyon (Dept. Geography, ANU), and the manuscript was typed by Jan Watson (Computext, Canberra). Thank you.
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Appendix 1: Ecological relationships and extra-regional distributions of Northern Territory MVF species.

This Appendix is presented in two parts. In Appendix 1.1 is given data concerning the occurrence of MVF species both within Community Types in the Top End region of the Northern Territory, and their geographical occurrence elsewhere. In Appendix 1.2 is given a comprehensive listing of the sources consulted in compiling the extra-regional distribution data.

1.1 Distribution data: explanatory notes

(i) Species list. The species list is based on the checklist provided in Russell-Smith and Dunlop (1984), supplemented by additional records. Undescribed or unnamed taxa are listed by a collector's initials and numbered specimen. These reference specimens are lodged in the Darwin Herbarium (DNA). Collectors are as follows: N.B. (Byrnes); C.R.D. (Dunlop); D.J. (Jones); M.R. (Rankin); J.R.S. (Russell-Smith); G.W. (Wightman); W. & T. (L.J. Webb and J.G. Tracey).

Where known, the growth form(s) and propagule type(s) of each species listed is indicated with reference to the following keys:

<table>
<thead>
<tr>
<th>Growth Form</th>
<th>Propagule Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>T tree (&gt;8m tall)</td>
<td>1 fleshy fruit &gt;2.5cm wide</td>
</tr>
<tr>
<td>t small tree (&lt;8m)</td>
<td>2 fleshy fruit &lt;2.5cm wide</td>
</tr>
<tr>
<td>s shrub</td>
<td>3 arillate, funiculate</td>
</tr>
<tr>
<td>c climber</td>
<td>4 presented</td>
</tr>
<tr>
<td>c/s scandent shrub</td>
<td>5 dry (explosive or gravity dispersed)</td>
</tr>
<tr>
<td>p palm</td>
<td>6 spores, dust-like seeds</td>
</tr>
<tr>
<td>a herb</td>
<td>7 winged, plumed</td>
</tr>
<tr>
<td>e epiphyte</td>
<td>8 burred, sticky</td>
</tr>
<tr>
<td>g geophyte</td>
<td></td>
</tr>
</tbody>
</table>
Exotic species are indicated by a hash (#).

(ii) Community Types: The six Community Types occurring in the Top End of the Northern Territory are defined in Sect. 4.1.3, where MVF vegetation is associated with:

1. seasonally dry sandstone escarpment/plâteau landforms
2. seasonally dry lowland landforms
   (a) rock outcrops
   (b) coastal landforms
   (c) subcoastal landforms
3. perennially moist substrates in relatively high rainfall coastal regions, especially in the north-west corner of the Top End
4. perennially moist substrates, mostly in situations other than 3.

Where given, numbers express the sampled frequency of occurrence of a species in each Community Type. For example, in the main Table of this Appendix it may be observed that Adiantum philippense is ascribed a value of 0.09 in Community Type 4 (sandstone spring communities). This means that of the 53 representative sites sampled in the course of the ecological survey, this species occurs at 5; in other words, a frequency of occurrence of 0.09. Where a species was recorded at less than 5 sites representative of any one Community Type, its occurrence is indicated by a slash (/). Where a species was not recorded during sampling, data presented in Russell-Smith and Dunlop (1984) and/or herbarium records have been used. In this instance the occurrence of a species in a Community Type is indicated by an asterisk (*).

In summary, then:

numbers = frequency of occurrence of a species recorded at 5 or more sites representative of any one Community Type.
/ = recorded at less than 5 sites representative of any one Community Type.
* = not recorded in survey; occurrence based on data given in Russell-Smith and Dunlop (1984), and/or herbarium records.

As well, the occurrence of species on Holocene landforms is given in a separate column denoted by a + sign.

(iii) Extra-regional distribution: Distributional data are given for 15 geographical regions defined previously in Sect. 4.3. The geographical regions are as follows (see also Table 12):

1 Western Australia
2 North Queensland
3 Southern Queensland
4 South-eastern Australia
5 Central Australia
6 Africa, Madagascar
7 Indian subcontinent
8 South-east Asia
9 Western Malesia
10 Western Wallacea
11 Eastern Wallacea
12 Eastern Malesia
13 New Caledonia
14 Oceania
15 Tropical America

Endemic species are indicated in a separate column. Distributional data derived from published revisions and floras, and information provided through correspondence with taxonomic specialists, are indicated in the following Table by a dash (-). For each species, the source(s) of this distributional information is referenced numerically in the final column. Using these numerical references as a key, a full listing of the sources consulted may be found in Appendix 1.2, Table (a). Supplementary distributional data
provided by various herbaria, and individuals with expertise in certain regional floras, are indicated alpha-numerically in the main body of Appendix 1. Using these alpha-numeric references as a key, a listing of these sources is given in Appendix 1.2, Table (b). The extra-Australian distributions of exotic species are not given.
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<td>(b)</td>
<td>(c)</td>
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<td>B. pristentale L.</td>
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<td>Stenochlaena palustris (Burm.) Hedw.</td>
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<td>a</td>
<td>6</td>
<td>/</td>
<td>/</td>
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<tr>
<td></td>
<td>Hymenophyllaceae</td>
<td>Taenitis blechnoides (Willd.) Sw.</td>
<td>a</td>
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<tr>
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<td>Selenodesarium obscursum (Bl.) Copel.</td>
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<td>N. biserrata (Sw.) Schott.</td>
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<td>Helminthostachys zeylanica (L.) Hook.</td>
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<td>Ophioglossum intermedium Hook.</td>
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<td>Drynaria quercifolia (L.) J. Sm.</td>
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<td>(Langsd. &amp; Fisch.) Brownie</td>
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<td>Psilotum nudum (L.) Fries</td>
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<td>Lycopodium flexuosum (L.) Sw.</td>
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<td>L. japonicum (Thurb.) Sw.</td>
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<td>L. microphyllum (Cav.) R. Br.</td>
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<td>S. digitata (L.) Sm.</td>
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<td>Cyclosorus interruptus (Willd.) Ching</td>
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**ANGIOSPERMIA**

| Acanthaceae |          |          |                           |               |            |
| Hypoestes floribunda R. Br. | s | 5 | 0.49 | 0.30 | 0.33 | 0.46 | 0.19 | / | - | - | - | - | - | 75 |
| Thunbergia arnhemica F. Muell. | c | 5 | / | / | / | / | / | / | - | - | - | - | - | 75 |
| Agavaceae |          |          |                           |               |            |
| Cordyline carnifolia R. Br. | s | 2 | / | - | - | - | - | - | - | - | - | - | - | 61 |
| Pleomele angustifolia (Ramb.) N. E. Br. | t | 2 | 0.24 | / | 0.54 | / | 0.54 | / | + | - | - | - | - | 81 |
| Awaranthaceae |          |          |                           |               |            |
| Me yranthes aspera L. | s | 8 | / | 0.10 | / | / | / | / | a | b | b | - | - | 102 |
| Anacardiaceae |          |          |                           |               |            |
| Blepharocarya depauperata Specht | T | 7 | 0.32 | / | - | - | - | - | - | - | - | - | - | 103,121 |
| Buchanania arborescens (Bl.) Bl. | T | 2 | 0.36 | 0.20 | / | 0.24 | 0.49 | 0.40 | + | - | - | - | - | 4,121 |
| Semecarpus australiensis Engl. | T | 2 | / | / | / | / | / | / | - | - | - | - | - | 4 |
| Amentaceae |          |          |                           |               |            |
| Vannona reticulata L. | t | 1 | / | / | / | / | / | / | b | b | - | - | - | 4 |
| Growth Prop. | Community Type | Type 1 | 2 | 2(a) | 2(b) | 2(c) | 3 | 4 | Landforms 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | Reference |
|--------------|----------------|--------|----|------|------|------|----|----|--------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Cyathodium micranthum (A. DC.) J. Sinclair | c | 2 | * | * | * | * | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Mililua sp. | T | 2 | 0.16 / | 0.46 / | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Polyalthia holsteeana F. Muell. | T | 2 | 0.42 / 0.42 / 0.33 / 0.46 / 0.41 / 0.85 | 0.15 | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| P. nitidissima (Oxalid) Benth. | t | 2 | 0.47 / 0.33 / | 0.54 / 0.30 | / | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Polylepis tilindrocarpa (Burck) Backer | s | 2 | * | | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Poponia australis Benth. | T | 2 | / | / | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Rauwenhoffia sp. | c/s | 2 | 0.68 | / | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Sacopeptalum brahei F. Muell. | T | 2 | 0.51 / 0.46 / 0.67 / 0.42 / 0.59 | 0.09 | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Umbellwardiana F. M. Bailey | c/s | 2 | 0.55 / | / | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Ubria holzii F. Muell. | c | 2 | 0.15 / 0.33 / | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Zerosos sp. | c/s | 2 | / | / | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |

**Nyctaginaceae**

| Alstophyia azchnophylla (A.Dunn.) K. Schum. | T | 7 | 0.46 / 0.39 / 0.21 / 0.65 | 0.09 | + | a | b | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| A. ophiolylodes F. Muell. | T | 7 | / | / | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | d |
| Alyxia rusci folia R. Br. | s | 2 | 0.77 / | / | 0.11 | + | a | b | c | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| A. spicata R. Br. | c | 2 | 0.46 / 0.06 | 0.21 | / | 0.23 | + | a | b | b | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Ichnocalyx frutescens (L.) R. Br. | c | 7 | 0.23 / 0.38 / 0.67 / 0.58 / 0.54 / 0.62 | / | + | a | b | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Parsonia velutina R. Br. | c | 7 | 0.39 / 0.32 / 0.39 / 0.46 / 0.19 | / | 0.32 | + | a | b | b | c | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Tabernaemontana orientalis R. Br. | t | 2 | 0.45 / 0.20 / | 0.38 | / | / | + | a | b | b | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Tabernaemontana pubescens R. Br. | t | 2 | 0.11 / | / | / | + | a | b | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Wrightia pubescens R. Br. | t | 7 | 0.21 / 0.67 / 0.67 / 0.63 / 0.70 | / | - | + | a | b | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |

**Acanthaceae**

| Ilex arnhemensis (F. Muell.) Loes. | t | 2 | / | 0.75 | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |

**Araceae**

| Anarthropous galbra F. M. Bailey | g | 2 | / | 0.28 / 0.33 | 0.30 | / | + | a | b | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| A. paemiioldus (Dennst.) Nielson | g | 2 | / | 0.14 / 0.33 | / | / | + | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Rhazopsis vivipara (Ramb.) Schott | g | 9 | / | / | / | / | / | / | / | / | / | - | - | - | - | - | - | - | - | - | - | - | 85 |
| Rhaphidophora australis R. Br. | c | 2 | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | - | 85 |
| Rhaphidophora sp. | C/ | 5632 | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | - | 85 |
| Tymbrophus sp. | D | 1380 | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | - | 85 |

**Anacardiaceae**

| Mackinlaya macrocledia (F. Muell.) F. Muell. | s | 5 | 0.15 | / | / | / | / | / | / | / | / | - | - | - | - | - | - | - | - | - | - | - | - | 85 |
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Schefflera actinophylla !Endl.l Har•s
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Carpf1!1taria acuninata
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Hoya sp. aff. australi's R. Br.
Marsdenia cine:rascens R. Br.
11. velutina R.\ Br.
1'1arsdenia sp. DJ J540
ttarsdenia :sp. }RS 940
Marsdeni a sp. JRS 894
Sarcosteuia austral e ti!', Br.
Secaaone elliptica R. ~.
Tylophora creb~iflora S. T., Blake
T. fl ex uosa R. Br.
Tylophora ~· CRD 6642
Vincetoxicua elegans Benth.
Asteraceae
Bidens bipinnata L.
Blainvillea dubia Specht
Vernonia cinerea u:. l Less.
Barringtooiaceae
BarringtQnia acutangula !L. l 6aertn.

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### Holocene geographic distribution

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#### Ebenaceae

- **Ebenaceae**
- **Diospyros**
  - **D. bundeyana Kostermans**
  - **D. calycantha D. Schwarz**
  - **D. ferrea (Mill.) Bakh. var. humilis (R. Br.) Bakh.**
  - **D. ferrea var. reticulata R. Br.**
  - **D. maritima Bl.**

#### Elaeocarpaceae

- **Elaeocarpus angustifolius Bl.**
- **E. arnhemiacus F. Muell.**
- **E. culminicola Warb.**

#### Euphorbiaceae

- **Actepila latifolia Benth.**
- **Antidesma ghaesebiita Gaertn.**
- **Az. parvifolius F. Muell.**
- **Brennia cornua (Poir.) Muell. - Arg.**
- **B. rhyndocharca Benth.**
- **Bridelia tomentosa Bl.**
- **Choriceras tricorne (Benth.) Airy Shaw**
- **Claoxylon tenebfoliua (Baill.)f. Muell.**
- **Croton argyratus Bl.**
- **Croton arnotioli S. Moore**
- **Croton arnhemiacus Muell. - Arg.**
- **Croton bynesii Airy Shaw**
- **Croton tomentillus F. Muell.**
- **Croton sp. CRB 6650**
- **Croton sp. EM 1333**
- **Drypetes lasiodyna (F. Muell.) Fox & Hoffm.**
- **Endosperum medullosum L. S. Smith**
- **Glochidion disparipes Airy Shaw**
- **Glochidion sumatrana (Benth.) Airy Shaw**
- **Glochidion vescocarpum (D. Schwarz) Airy Shaw**
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**Hernandiaceae**
- *Gyrocarpus americanus* Jacq.
  - T 7 0.13 0.15 0.28 / / + -

**Lamiaceae**
- *Coleus scutellarioides* (L.) Benth.
  - a 5 0.36 0.11 0.28 / / + a -

**Rubiaceae**
- *Rhytidostegia vaudaisiana* (L.) Poir.
  - a 5,8 / 0.38 0.61 0.21 0.81 / 0.38 +

**Lauraceae**
- *Cassutha filiformis* L.
  - c 2 0.11 0.10 / 0.29 / + a b b -
- *Cryptocarya cunninghamii* Meissn.
  - T 2 0.36 0.29 / 0.21 0.41 0.46 0.23 + a -
- *Cryptocarya exfoliata* Allen
  - t 2 0.18 / 0.11 -
- *Endiandra sp.* N 12573
  - t 2 / / +
- *Litsea ferruginea* Bl.
  - t 2 / / / e i -
- *Litsea glutinosa* (Lour.) C.B. Robinson
  - T 2 0.53 0.05 0.76 0.96 0.81 0.85 0.25 + a -
- *Neoitsea australiensis* Kostermans
  - t 2 0.06 / / / + - c d

**Leeaceae**
- *Leea rubra* Bl. ex Spreng.
  - g 2 0.39 0.28 0.46 0.41 0.69 / + b -

**Liliaceae**
- *Asparagus racemosus* W.Jlid.
  - c 2 / 0.48 0.39 0.46 0.54 / + -

**Linaceae**
- *Diandra caerulea* Sims
  - gr 2 0.32 / / 0.24 + b c

**Erythroxylaceae**
- *Erythroxylon australis* R. Br.
  - t 2 / / / / a b b c

**Loganiaceae**
- *Fagraea racemosa* Jack
  - t 2 / / 0.43 +
- *Strychnos jacea* R. Br.
  - t 2 0.64 0.85 0.85 0.75 0.87 0.38 / + -
- *Strychnos psilopus* F. Muell.
  - c 2 / / +

**Malvaceae**
- *Abutilon indicum* (L.) Sweet
  - s 5 0.08 / / + a -
- *Hibiscus tiliaceus* L.
  - T 5,10 0.25 0.63 0.14 / + + c
  - t 5,10 / / + -
- *Hibiscus sp.* CRO 6395
  - t 5 / / +

**Melastomataceae**
- *Melastoma malabathricum* L.
  - s 2 / / / / / 0.77 + -
- *Melanthera pauciflora* Bl.
  - t 2 0.77 0.28 / 0.50 0.22 / 0.32 +

**Meliaceae**
- *Aglaia elaeagnoides* (A. Juss.) Benth.
  - T 2 + -
- *Aglaia sp.* aff. *rufa* Miquel
  - T 2 0.09 0.21 / +
- *Aglaia sapindina* (F. Muell.) Harms
  - T 2 / / + -
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<th>Growth Prop.</th>
<th>Community Type</th>
<th>Holocene</th>
<th>geographical distribution</th>
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**Orchidaceae**

- *Cansjera leptostachya Benth.*
  - Opilia aeminent A.Berb.
  - Opilia arenacea Romb.
  - Opilia arenacea Romb.

**Plumbaginaceae**

- *Opilia arenacea Romb.*
  - Opilia arenacea Romb.
  - Opilia arenacea Romb.

**Piperaceae**

- *Adenia heterophylla (Bl.) Koord.*
  - Adenia heterophylla (Bl.) Koord.
  - Adenia heterophylla (Bl.) Koord.

**Pittosporaceae**

- *Bursaria incana Lindl.*
  - Pittosporum ferrugineum Ait.
  - Pittosporum ferrugineum Ait.

**Plumbaginaceae**

- *Plumbago zeylanica L.*
  - Plumbago zeylanica L.
  - Plumbago zeylanica L.

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<td>geographical distribution</td>
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<td>2(b)</td>
<td>2(c)</td>
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<tr>
<td>Scleria schlechteri H.J. Lam.</td>
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<td>Planta camara L.</td>
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<tr>
<td>Cayratia acris (F. Muell.) Domin</td>
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<tr>
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<td>(= C. maritima n.c.)</td>
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### 1.2 Extra-regional distribution data sources: explanatory notes

Sources of information concerning the extra-regional distributions of Top-End MVF taxa are given in three Tables as follows:

(a) Published revisions and floras, and information provided through correspondence with taxonomic specialists. This Table is arranged in numerical order; the numbers correspond with those given as a key in the column headed, 'References' in Appendix 1.1. Certain references are abbreviated as follows.

<table>
<thead>
<tr>
<th>Source</th>
<th>Description</th>
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(b) Supplementary distributional information provided in checklists, herbarium records, and information provided by individuals with expertise in certain regional floras. This Table is arranged in alpha-numeric order; the letters correspond with those given in the main body of Appendix 1.1.

(c) This Table acknowledges all those people who generously
provided distributional information, or clues as to where it might be obtained. Where given, numbers and letters following people's names indicate references in preceding Tables.
### Appendix 1.2, Table (a): Numerical References

   Note: David Jones is currently revising Northern Territory fern and orchid collections.
21. AIRY SHAW, H.K., F.C.A., p. 188.
   Note: Strychnos psilosperma F. Muell. is considered by the author as a race of S. axillaria Colebr.
45 DRENTH, E., F.M. I., vol. 7:806-819.
48 SOEPADMO, E., F.M. I., vol. 8:31-76.

Note: *Trema aspera* (Brongn.) Bl. is considered by this author as a synonym of *T. cannabina* Lour.

49 WOMERSLEY, J.S., F.C.A., p. 16.

Note: The widespread Malayan species "*Vitex glabrata*" is in fact the closely related *V. helogiton*. *Vitex glabrata* R. Br. is probably endemic to north-west Australia.


Note: *Coleus scutellarioides* (L.) Benth. is considered as a synonym of *Plectranthus scutellarioides* (L.) R. Br.

52 AIRY SHAW, H.K., F.M. I., vol. 4:27.
54 BURKILL, I.H., F.M. I., vol. 4:293-335.

Note: *Breynia rhynchocarpa* Benth. is given as a
synonym of B. cernua (Poir.) Muell.-Arg.


   Note: The author regards Vavaea australiana S.T. Blake as a synonym of V. amicorum Benth. As two distinct ecotypes occur in the N.T. region both names are retained here for practical purposes.


   Note: Aglaia elaeagnoides (A. Juss.) Benth. is regarded as being conspecific with A. roxburghiana (Wight & Arn.) Miguel. In recent correspondence (1986), Dr Pannell advises that specimens referred here to Aglaia sp. aff. rufa require further consideration.


   Notes: Sterculia sp. CRD 3661 is regarded as conspecific with S. quadrifida R. Br.; Helicteres sp. JRS 692 is possibly endemic to the Northern Territory.


   These taxa are under revision at the present time; correct nomenclature is uncertain.


   Note: The taxon listed as Cissus maritima (n.c.) is to be described in a forthcoming publication.


Note: Jasminum aemulum R. Br. is otherwise known in Malesia as J. bifarium Wall.

Note: New combinations of various of the Annonaceae taxa listed are to be described in a forthcoming revision.

Note: Muehlenbeckia zippelii (Meissn.) Danser is given as M. rhyticarya F. Muell. in many collections.


Note: Aidia conchinchinensis Lour. is to be described under a new combination.


Note: Taxonomic status of Ixora, Pavetta and Tarenna spp. is uncertain.


Notes: Taxonomic status of Rapanea benthamiana Mez. is uncertain. Canthium sp. aff. lucidum is probably a Northern territory endemic.

Notes: Ichnocarpus frutescens (L.) R. Br. is more strictly, I. volubilis (Lour.) Merr. Similarly, Alphitonia excelsa (Fenzl.) Benth. is otherwise known as A. zizyphoides (Spreng.) A. Gray, and Triumfetta rhomboidea Jacq. is equivalent to T. bartramia L.


Note: Tabernaemontana pubescens R. Br. is considered as a synonym of T. orientalis R. Br.


117 de JONCHEERE, G.J., pers. comm. (1986).
Note: Dr. de Joncheere relates that the taxon Adiantum pubescens Schkur. (listed by David Jones - see ref. 3
- as occurring in the N.T.) is better considered as a synonym of the more widely occurring A. pispidulum Swartz.

118 SOHMER, S.H., pers. comm. (1986).

Note: The taxonomic status of N.T. Psychotria spp. require critical evaluation.


### Appendix 1.2, Table (b): Alpha-numeric References

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<td>b. Queensland</td>
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<td>e. Malaysia</td>
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<td>f. Thailand</td>
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### Appendix 1 Table (c): Acknowledgements

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(Melbourne, Vic.); G. Wightman (Darwin, N.T.); K.L. Wilson, 96 (Sydney, N.S.W.); P.G. Wilson, 95 (Sydney, N.S.W.).
Appendix 2: Dispersal at springs.

This Appendix summarises data collected in a study assessing dispersal at three small spring sites in the Arnhem Land escarpment (see Sect. 3.2). The first column of figures indicates the number of mature individuals occurring at each site. Columns 2 and 3 give the number of immature individuals sampled in permanent quadrats both at the start of the study (Sept. 1983) and at the end (May 1984), respectively. Ten quadrats (1x1m²) were established at the Anbangbang and Nangafoar sites, whereas quadrats (1x1m²) at the Oenpelli site. Column 4 gives the number of seeds evacuated by birds which were collected in traps, and/or the number germinants recorded after the fine in the traps had been laid out in shallow germination trays in the greenhouse. Column 5 gives the number of germinants recorded from three dry soil samples (1x1x0.05m³) collected immediately adjacent each seepage at the start of the study. Only MVF trees, shrubs and herbs are considered here.
(a) Anbangbang (ca. 0.025ha).

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<th>Immature individuals (&lt;5cm DBH)</th>
<th>Dispersed Seeds</th>
<th>Soil germinants (Sept 1983)</th>
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(b) Nangaloar (ca. 0.03ha)

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<tr>
<td>Coleus scutellarroides (Lam.)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Panicum trichoides (Poa.)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3</td>
</tr>
</tbody>
</table>

Soil = Seeds germinated from seeds present in the soil

Immat. Individuals = Dispersed, Seeds and Soil germinants
(G) Oenpelli (small seepage area in large tract of MVF ca. 8ha)

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Mature individuals</th>
<th>Immature individuals</th>
<th>Dispersed Seeds</th>
<th>Soil germinants</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(&gt;5cm DBH)</td>
<td>Sept 1983</td>
<td>May 1984</td>
<td></td>
</tr>
<tr>
<td><em>Carpentaria acuminata (Arec.)</em></td>
<td>20</td>
<td>3</td>
<td>7</td>
<td>36</td>
</tr>
<tr>
<td><em>Calophyllum sil (Clus.)</em></td>
<td>11</td>
<td>40</td>
<td>58</td>
<td>6</td>
</tr>
<tr>
<td><em>Horsfieldia australiana (Myristic.)</em></td>
<td>6</td>
<td>5</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Cryptocarya cunninghamii (Laur.)</td>
<td>5</td>
<td>2</td>
<td>14</td>
<td>25</td>
</tr>
<tr>
<td><em>Allosyncarpia ternata (Myrt.)</em></td>
<td>4</td>
<td>0</td>
<td>14</td>
<td>25</td>
</tr>
<tr>
<td><em>Syzygium minutuliforum (Myrt.)</em></td>
<td>4</td>
<td>67</td>
<td>154</td>
<td>85</td>
</tr>
<tr>
<td><em>Buchanania arborescens (Anácard.)</em></td>
<td>2</td>
<td>0</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td><em>Myristica insipida (Myristic.)</em></td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Helicia australiana (Prot.)</em></td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Blepharocarya depauperata (Bleph.)</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Dysoxylum oppositifolium (Mel.)</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td><em>Maranthes corymbosa (Chrysobalan.)</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Rapanea benthamiana (Myršín.)</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Strychnos lucida (Logah.)</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>36</td>
</tr>
<tr>
<td><em>Polyalthia holtzeana (Annon.)</em></td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td><em>Ixora klanderana (Rub.)</em></td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td><em>Diospyros calycantha (Ebén.)</em></td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td><em>Pouteria sericée (Sapot.)</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td><em>Ficus scobina (Mor.)</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>Planchonella aff. xerocarpa (Sapot.)*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Acacia auricocarpa (Mimos.)</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>12</td>
</tr>
<tr>
<td><em>Acacia auriculiformis (Mimos.)</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
</tbody>
</table>

* mature individuals of these species were recorded elsewhere in this patch.
ADDITIONAL APPENDICES CONCERNING (1) DATA COLLECTED IN THE ECOLOGICAL SURVEY OF MVF VEGETATION AND (2) NUMERICAL CLASSIFICATION ANALYSES

A1. SITE DATA FOR 194 SITES USED IN THE NUMERICAL ANALYSIS OF SITES X FLORISTICS

A2. FLORISTICS DATA FOR 194 SITES

A3. FUSION TABLE FOR CLASSIFICATION OF 194 SITES X 235 MVF FLORISTIC ATTRIBUTES USING THE JACCARD ASSOCIATION MEASURE AND WITH FUSION BY THE UPGMA SORTING STRATEGY

A4. DENDROGRAM OF CLASSIFICATION OF 194 SITES X 235 MVF FLORISTIC ATTRIBUTES USING THE JACCARD ASSOCIATION MEASURE AND WITH FUSION BY THE UPGMA SORTING STRATEGY: ALL GROUPS

A5. DENDROGRAM AND SITE COMPOSITION OF CLASSIFICATION OF 194 SITES X 235 MVF FLORISTIC ATTRIBUTES USING THE JACCARD ASSOCIATION MEASURE AND WITH FUSION BY THE UPGMA SORTING STRATEGY: 7 GROUP LEVEL

A6. THE FIVE NEAREST NEIGHBOURS TO EACH OF THE 194 SITES

A7. FINAL 4 GROUP CLASSIFICATION AFTER SITE REALLOCATIONS

A8. SITE COMPOSITION AND SPECIES ATTRIBUTES OCCURRING AT 90 EFFECTIVELY SAMPLED, DISCRETE PATCHES

A9. SITES AND SPECIES OCCUPYING HOLOCENE LANDFORMS
APPENDIX 1: SITE DATA FOR 194 SITES USED IN THE NUMERICAL ANALYSIS OF SITES X FLORISTICS

This appendix provides a listing of data summarising the characteristics of monsoon vine-forest (MVF) patches sampled in the course of an ecological survey of MVF vegetation in the Top End of the Northern Territory. Data are given here for the 194 sites used in numerical analyses of sites x floristics data, described elsewhere in this thesis. All sites were sampled 1981-4.

Data for each site are given on three lines. The site number and its geographical location are given on the first line. Thirty-nine other attributes (e.g., number of species, buffalo impact, geology) are given on the next two lines as follows:

**LINE 1:**
- **SITE NUMBER** (COLUMNS 1-3)
- **LOCATION:**
  - **LATITUDE** (DEGREES AND MINUTES) (COLUMNS 5-8)
  - **LONGITUDE** (COLUMNS 10-14)

**LINE 2:**
1. **SAMPLING EFFECTIVENESS** (COLUMN 1)
   - 0 = whole patch sampled
   - 1 = only part of patch sampled
2. **AREA SAMPLLED** (ha) (COLUMNS 3-7)
3. **NUMBER OF MVF SPECIES** (COLUMNS 9, 10)
4. **PROPORTION OF MVF SPECIES WITH 6 OR LESS MATURE INDIVIDUALS PRESENT (%)** (COLUMNS 12, 13)
5. **PROPORTION OF MVF SPECIES WITH 50 OR LESS MATURE INDIVIDUALS PRESENT (%)** (COLUMNS 15, 16)
6. **PROPORTION OF MVF SPECIES WITH GREATER THAN 50 MATURE INDIVIDUALS (%)** (COLUMNS 17, 18)
7. **GENERAL CANOPY HEIGHT, EXCLUDING EMERGENTS (m)** (COLUMNS 21, 22)
8. **SEEDLING ABUNDANCE** (COLUMN 24)
   - 1 = very rare
   - 2 = few per (10x10) square metres
   - 3 = few per (3x3) square metres
   - 4 = few per 1 square metre
   - 5 = abundant
9. **PATCH CONFIGURATION** (COLUMN 26)
   - 1 = discrete patch with sharp/diffuse boundary
   - 2 = discrete patch with open canopy inlets
   - 3 = main patch with minor outliers
   - 4 = segmented patch arrangement
   - 5 = more-or-less diffuse scattering of MVF individuals
10. **SCRUB-FOWL MOUNDS IN MVF PATCH** (COLUMN 28)
   - 0 = absent
   - 1 = present
11. **SCRUB-FOWL MOUNDS EXTERNAL TO PATCH MARGIN** (COLUMN 30)
   - 0 = absent
   - 1 = present
12. **FIRE IMPACT** (COLUMN 32)
   - 0 = absent
   - 1 = localised impact due lightning strike
   - 2 = minor impact on exposed patch boundaries
   - 3 = severe impact (e.g., tree death) on patch boundaries only
   - 4 = severe impact on patch margins and internal vegetation
13. **BUFFALO IMPACT** (COLUMN 34)
   - 0 = absent
   - 1 = present, but minor
   - 2 = localised and severe (e.g., tree death)
   - 3 = widespread and severe
14. **PIG IMPACT** (COLUMN 36)
    - as for 13 above
15. **FLOOD-WATER IMPACT** (COLUMN 38)
    - as for 13 above
16. **STORM/WIND IMPACT** (COLUMN 40)
    - as for 13 above
17. **CULTURAL IMPACT** (COLUMN 42)
    - as for 13 above
18. **FUEL LOAD AT EXPOSED PATCH MARGINS** (COLUMN 44)
    - 0 = absent/inapplicable
    - 1 = diffuse short grass-cover
    - 2 = patchy cover of dense tall-grass/shrubs
    - 3 = continuous cover of dense tall-grass/shrubs
19. **ABUNDANCE OF SAVANNA GRASSES IN MVF PATCH** (COLUMN 46)
    - 0 = absent
    - 1 = rare
    - 2 = common in localised situations
ABUNDANCE OF WOODY WEEDY SPECIES (NATIVES, EXOTICS) IN MVF PATCH (COLUMN 48) as for 19 above

ABUNDANCE OF Acacia Species IN PATCH:
21. INDIVIDUALS GREATER THAN 10cm DBH (COLUMN 50) --- as for 19 above
22. SHRUBS (COLUMN 52) --- as for 19 above
23. INDIVIDUALS LESS THAN 1m HEIGHT (COLUMN 54) --- as for 19 above

ABUNDANCE OF Eucalyptus spp./Erythrophloeum chlorostachys IN PATCH:
24. MATURE INDIVIDUALS (COLUMN 56) --- as for 19 above
25. SHRUBS/REGENERATION (COLUMN 58) --- as for 19 above

ABUNDANCE OF PAPERBARKS (ie. Melaleuca/Lophostemon lactiflora) IN PATCH:
26. MATURE INDIVIDUALS (COLUMN 60) --- as for 19 above
27. SHRUBS/REGENERATION (COLUMN 62) --- as for 19 above

SUBSTRATE PARENT MATERIAL:
0 - absent
1 - present
LIMESTONE (COLUMN 64)
BASIC IGNEOUS ROCK (eg. DOLERITE) (COLUMN 66)
ACID IGNEOUS ROCK (eg. GRANITE) (COLUMN 68)
SANDSTONE ETC. (COLUMN 70)
LATERITIC SUBSTRATES (COLUMN 72)
COASTAL SILICIOUS/CALCAREOUS FACIES (COLUMN 74)
SILICIOUS ALLUVIUM/COLLUVIUM (COLUMN 76)
FLOODPLAIN ALLUVIUM (COLUMN 78)

DEPTH OF SOIL (COLUMN 80)
1 - mostly bare rock
2 - skeletal
3 - shallow (less than 40cm)
4 - moderate (less than 100cm)
5 - deep (greater than 100cm)

GENERAL TEXTURE CLASS OF TOPSOIL (0-10cm) (COLUMN 2)
0 - absent
1 - sand
2 - sandy loam
3 - loam
4 - clay loam
5 - clay

GENERAL TEXTURE CLASS OF SUBSOIL (50-60cm) (COLUMN 4)
as for 30 above

FIELD pH (COLUMNS 6-8)

DEPTH OF OBSERVABLE SOIL ORGANIC STAINING (cm) (COLUMNS 10, 11)

SUBSTRATE DRAINAGE CHARACTERISTICS (COLUMN 13)
1 - excessive/free
2 - impeded
3 - waterlogged

SUBSTRATE INUNDATION (COLUMN 15)
0 - absent
1 - seasonally inundated
2 - perennially wet/inundated

DRY-SEASON FREE WATER AVAILABILITY (COLUMN 17)
0 - absent
1 - present

DOMINANT TERRAIN TYPE (COLUMN 19)
1 - rugged, broken country
2 - rolling, outcropping country
3 - gentle relief, flat country

DOMINANT SLOPE ANGLE (COLUMN 21)
1 - flat (0-2%)
2 - gentle (3-8%)
3 - moderate (9-20%)
4 - steep (21-35%)
5 - very steep (greater than 35%)

DISTANCE TO NEAREST HOLOCENE MARITIME LANDFORM (COLUMN 23)
1 - occurrence of MVF patch directly and exclusively on such a landform
2 - partly on such a landform
3 - immediately adjacent (eg. at edge of coastal floodplain)
4 - within 5km
5 - within 20km
6 - within 100km
7 - at a distance greater than 100km
<table>
<thead>
<tr>
<th>Column 1</th>
<th>Column 2</th>
<th>Column 3</th>
<th>Column 4</th>
</tr>
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</tr>
<tr>
<td>02</td>
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<td>50</td>
<td>0.2</td>
</tr>
<tr>
<td>03</td>
<td>3.0</td>
<td>01</td>
<td>0.3</td>
</tr>
<tr>
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<td>30</td>
<td>0.4</td>
</tr>
<tr>
<td>05</td>
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<td>05</td>
<td>0.5</td>
</tr>
<tr>
<td>06</td>
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</tr>
</tbody>
</table>

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<thead>
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<th>Number</th>
<th>Code</th>
<th>Value</th>
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</thead>
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<tr>
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<tr>
<td>10</td>
<td>8.54</td>
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</table>

**Note:** The table continues with similar entries, each representing a different number with its associated value.
APPENDIX 2: FLORISTICS DATA FOR 194 SITES.

This appendix provides a listing of floristics data for each of 194 sites described in Appendix I. In total, each site is described by the presence or absence of 426 floristic attributes (species).

The floristics data comprises three groups of species as follows:

1. **Savanna taxa** (Columns 1–57)
   - Fifty-seven floristic attributes describing the occurrence of typically savanna taxa are given in the first fifty-seven column cells.

2. **Common MVF taxa** (Columns 58–292)
   - Two hundred and thirty-five floristic attributes occurring at at least 5 sites, are coded in columns 58–292. As well, only species which were readily identifiable throughout the year (e.g., perennial evergreen taxa) are listed here, since this block of attributes constitutes the basic data set used in numerical analyses.

3. **Other MVF taxa** (Columns 293–426)
   - One hundred and thirty-four other MVF taxa are coded in columns 293–426. These taxa were either sampled at fewer than five sites or, due to their growth habit, were not readily identifiable/conspicuous at all sampling times through the seasonal cycle (e.g., geophytes, annuals).

A listing of the 426 floristic attributes is given immediately below, on each line the attribute (column) number is given first, then the alpha-numeric label used as an identifier in numerical classification analyses, and lastly, the species comprising the attribute concerned.

1. **Acacia** various Acacia spp. other than A. auriculiformis, A. aulacocarpa
2. **Legumes** Acylics, Burtonia, Crotalaria, Dianella, Flemingia, Jacksonsia, and Tephrosia spp.
3. **Banksia** Banksia dentata
4. **Boronia** Boronia lanceolata
5. **Brachychiton** Brachychiton diversifolius
6. **Brachydon** Brachydon paradoxus
7. **Buchanania** Buchanania obovata
8. **Casuaria** Casuaria phyphylla spp.
9. **Poaceae** Chrysochis, Cowleria, Cymbopogon, Eriachne, Imperata, Isopogon, Muriarita, Panicum (except F. tricholoides), Plectranthus, Phragmites, Schizachyrium, *Sorghum*, Sporobolus, Themeda, Triodia
10. **Cleome** Cleome spp.
11. **Cochlospermum** Cochlospermum spp.
12. **Cordyline** Cordyline ensete var.
13. **Corchorus** Corchorus spp.
14. **Crescentia** Crescentia aspaticum
15. **Cycas** Cycas spp.
16. **Dicrastylis** Dicrastylis spp.
17. **Erythrina** Erythrina spp.
18. **Eucalyptus** Eucalyptus spp.
19. **Grevillea** Grevillea spp.
20. **Gardenia** Gardenia megasperma sens lat.
21. **Hibiscus** Hibiscus spp.
22. **Hibiscus** Hibiscus spp.
23. **Hibiscus** Hibiscus spp.
24. **Hibiscus** Hibiscus spp.
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64. **Hibiscus** Hibiscus spp.
65. **Hibiscus** Hibiscus spp.
66. **Hibiscus** Hibiscus spp.

...
The abundance of a species/attribute at a site is coded with respect to the following scale:

0 = absent
1 = 1 mature individual present
2 = 2-6 mature individuals present
3 = 7-20
4 = 21-50
5 = >50

The last three column cells after the full-stop indicate the site number.
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APPENDIX': FUSION TABLE FOR CLASSIFICATION OF 194 SITES X 235 MVF FLORISTIC ATTRIBUTES
USING THE
.
JACCARD ASSOCIATION MEASURE AND WITH FUSION BY THE UPGMA SORTING STRATEGY
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The fus~?n table presented below sununarises the classific~tion of the 194 sites on the basis of
235 MVF floristic attributes 11iven in APPENDIX 2. Classification was undertaken usinQ the Jacc:ird
association measure with fusion by the UPGMA sortinq strateqy. The ~irst column qives the
4
?rder of fusio~. The second column qives the number.oit remaininq qroups. The column entitled
FUSION GROUPS indicates the qroups beinq fused; note that each site is considered a separate
11roup until fused with another qroup. The descriptors after the site number (eq. CML/l( 47) after
site rfumber 47 on the first row) ·are site labels used for aidinq interpretation. The column
entitled •ASSOCIATION'. Qives the level of dissimiJ-arity (-1-sinunilatity) at which qroups have been
fused.
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FUSION GROUPS

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FUSION GROUPS

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193 47 CML/l ( 47)
192 64 MOL/l ( 64)
191 · 190 GP/2 ( 190)
190 100 TF/2 ( 100)
189 120 CASB ( 120)
188 82 BIGJL ( 82)
187 107 MTBl( 107)
186 '13 RG/1 ( l;l)
185 78 BPNT ( 78)
• 184 114 JC/l ( 114)
183 77 MAW.CC 77)
182 64 MOL/1 ( 64)
181 l KNG/1 (
1)
180 17 KUM/l ( 17)
179 82 BIGJL( 82)
178 16 RG/4 ( 16)
177 94 JAJ/l ( 94)
. 176 11 NL/2 ( 11)
175 109 DPT ( 109)
174 176 MTHl( 176)
173 49 SAI/1 ( 49)
172 119 HJ
( 119)
171 114 JC/1 ( 114)
170 1S2 ST.H( 152)
169 6 BS/2
(
6)
168 78 BPNT ( 78)
167 77 MAW.CC 77)
166 14 RG/2 ( 14)
165 100 TF/2 ( 100)
164 86 ESTPT ( 86)
163 SS YB/S ( SS)
162 49 SAI/1( 49)
161 72 OR
(
72)
160 ·92 NG/2 ( 92)
1S9 62 KG/l ( 62)
158 44 MAL/1 ( '14)
1S7 27 DA/4 ( 27)
1S6 86 ESTPT ( 86)
lSS 82 BIGJL( 82)
1S4 114 JC/l ( 114)
1S3 64 ~/1 ( 64)
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152 t; B /2
7)
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lSO 1S2 ST.H( 1S2)
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(
148 72 ·O
72)
147 8 NL/1
(
8)
(
20)
146 20 JJ./2
14S 86 ESTPT( 86)
144 17 KUM/l ( 17)
143 11 NL/2 ( 11)
142 16 RG/4 ( 16)
141 26 DA/3 ( 26)
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5)
140 s 85/l
139 106 NPT ( 106)
138 29 DA/6 ( 29)
"137 19 JJ/1 -( 19)
S6)
136~ S6 NGil. (
13S 76 V.SET(. 76)
134 96 YAW/1 ( 96)
69)
• 133 69 C.HIL(
17)
13.2 17 KUM/1(
131 61 EVELN ( 61)
7)
130 7 NLROCK(
129 l i NL/2 ( 11)
'l.28 82 BIGJL"l" 82)
127 114 JC/1 ( 114)
126 166 CHFI ( 166)
125 87 DPSPK( 87)
124 55 YB/5 ' ( 55)
123 77 MAW.CC 77)
122 88 PETH ( 88)
7)
121 7 NLROCK(
58)
120 58 BC/2 (
119 167 HDMG( 167)
\i&.18 23 GC/2 ( 23)
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108 MTB2 ( 108)
15 RG/3 ( 15)
79 C.DUN( 79)
122 BJ/2 ( 122)
89 CASCA ( 89)
65 MOL/2 ( 65)
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22 GCJi ( 22)
144 CVD ( 144)
180 LD/1 ( 180)
95 JAJ/2 ( 95)
12 NL/3 ( 12)
111 INJC ( 111)
189 MF/3( 189)
101 BB/l ( 101)
126HWDS( 126)
121 BJ/1 ( 121)
15S CP/l ( 155)
13 RG/1 ( 13)
81 SMPNT ( 81)
147 ARTH ( 147)
41 BS/4 ( 41)
179 MTH4 ( 179)
120 CASB ( 120)
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136 CUTT ( 136)
14 RG/2 ( 14)
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86 ESTPT ( 86)
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168 MUNA ( 168)
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64 MOL/l ( 64)
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156 CP/2 ( 156)
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0.4107 0.0081
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0.4211, 0. 0017
0.4222 o. 0011
0.42SO 0.0028
0.4262 0. 0012
0.4355 o. 0093
0.4421 0. 00 66
0.4487 0. 00 67
o. 44 97 0.0009
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0.461S 0.007S
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0.4737 0.0020.
0.4762 0.002S
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0.5083 0.0002
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0,5143 0.0004
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0.5165 0.0005
0. 5167 0.0002
0.5208 o. 0041
0.5218 0.0010
0. 52 63 0.0045
o. 5265 0.0002
0.5288 0.0024
o. S293 O.Q005
o. 5303 0.0009
0.5306 0.0003
0.5325 0.0019
0.5343 0.0017
0.5379 0.0037
o. 5394 o. 0014
0.5404 0.0010
0.5405 0.0001
0. 54 29 o. Q024
0.5435 0.0006
0.5439 0.0004
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<tbody>
<tr>
<td>188</td>
<td>6</td>
<td>3 F.ISL (3)</td>
<td>+</td>
<td>88 FETH (88)</td>
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<td>3 F.ISL (3)</td>
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<td>189</td>
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<td>3</td>
<td>1 KNG/1 (1)</td>
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<td>54 KNG/2 (74)</td>
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<td>2</td>
<td>1 KNG/1 (1)</td>
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<td>+</td>
<td>57 KNG/1 (57)</td>
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<tr>
<td>192</td>
<td>1</td>
<td>1 KNG/1 (1)</td>
<td></td>
<td>+</td>
<td>149 KNG/1 (149)</td>
<td>-</td>
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</tbody>
</table>
APPENDIX 5: DENDROGRAM AND SITE COMPOSITION OF CLASSIFICATION OF 194 SITES X 235 MWF FLORISTIC ATTRIBUTES USING THE JACCARD ASSOCIATION MEASURE AND WITH FUSION BY THE 6.4 SORTING STRATEGY: 7 GROUP LEVEL

This appendix first reproduces the 194 sites X 235 floristic attributes classification dendrogram as given in the fourth paper of the thesis, showing the fusion of the last seven groups. The site composition of these groups is given below.

<table>
<thead>
<tr>
<th>LEVEL OF DIS SIMILARITY</th>
<th>0.8228</th>
<th>0.8369</th>
<th>0.8509</th>
<th>0.8650</th>
<th>0.8790</th>
<th>0.8931</th>
<th>0.9071</th>
<th>0.9212</th>
<th>0.9352</th>
<th>0.9493</th>
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The site composition of the seven groups illustrated in the above dendrogram is given below. The descriptors following each site number (e.g. KNG/1 (1) after site number 1 on the first row of group 4) are simply site labels used to help in interpretation. It is to be noted that Groups 4, 6 and 7 comprise eight site members between them. As described in the fourth paper of the thesis these groups comprise outlying sites. For example, site 149, the sole member of group 7, contains only 11 MWF species—see data in APPENDIX 1. The three members of group 4 are each ecotonal sites on seasonally dryer lateritic loamy substrates. Similarly, the four members of group 6 are ecotonal sites in sandstone terrain.

For simplicity, these eight sites were reallocated amongst the four major site groups on the basis of their floristic affinities with other sites as indicated in the diagnostic program, "NEAREST NEIGHBOURS"—see APPENDIX 6.

GROUP 1: 47 MWF/3/S

<table>
<thead>
<tr>
<th>1 KNG/1 (1)</th>
<th>12 KNG/2 (2)</th>
<th>7 NROCK (7)</th>
<th>51 Y/1 (51)</th>
<th>14 BG/1 (14)</th>
<th>41 BS/1 (41)</th>
<th>54 Y/4 (54)</th>
<th>16 2G/4 (16)</th>
</tr>
</thead>
<tbody>
<tr>
<td>180 LD/1 (80)</td>
<td>72 OR/1 (72)</td>
<td>169 M/1 (169)</td>
<td>189 MP/1 (189)</td>
<td>100 TF/1 (100)</td>
<td>182 O/EI (182)</td>
<td>179 M/1 (179)</td>
<td>32 DN/1 (32)</td>
</tr>
<tr>
<td>56 NG/1 (56)</td>
<td>92 NG/2 (92)</td>
<td>94 M/2 (94)</td>
<td>94 NG/2 (94)</td>
<td>92 EA/1 (92)</td>
<td>71 EA/1 (71)</td>
<td>69 C/1 (69)</td>
<td>144 DJ/1 (144)</td>
</tr>
<tr>
<td>21 DJ/1 (21)</td>
<td>66 M/2 (66)</td>
<td>134 G/5 (134)</td>
<td>20 G/1 (20)</td>
<td>62 KG/1 (62)</td>
<td>63 KG/2 (63)</td>
<td>174 DU/1 (174)</td>
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</tr>
<tr>
<td>161 DJ/1 (161)</td>
<td>161 DJ/2 (161)</td>
<td>194 M/2 (194)</td>
<td>91 EA/2 (91)</td>
<td>93 NG/3 (93)</td>
<td>173 M/1 (173)</td>
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<td></td>
</tr>
</tbody>
</table>

GROUP 2: 74 MWF/5/S

<table>
<thead>
<tr>
<th>2 F/3 (2)</th>
<th>11 NL/2 (11)</th>
<th>12 NL/3 (12)</th>
<th>49 SA/1 (49)</th>
<th>101 BB/1 (101)</th>
<th>70 Y/2/1 (70)</th>
<th>325 X/1 (325)</th>
<th>17 XT/1 (17)</th>
</tr>
</thead>
<tbody>
<tr>
<td>22 GC/2 (22)</td>
<td>47 HL/1 (47)</td>
<td>48 CH/2 (48)</td>
<td>18 NUM/1 (18)</td>
<td>39 CO/1 (39)</td>
<td>113 HN/1 (113)</td>
<td>23 GC/2 (23)</td>
<td>50 SA/1 (50)</td>
</tr>
<tr>
<td>44 ML/1 (44)</td>
<td>45 ML/2 (45)</td>
<td>103 M/1 (103)</td>
<td>108 M/2 (108)</td>
<td>70 V/1 (70)</td>
<td>79 C/1 (79)</td>
<td>81 SM/1 (81)</td>
<td></td>
</tr>
<tr>
<td>82 BG/1 (82)</td>
<td>83 BL/1 (83)</td>
<td>144 C/1 (144)</td>
<td>137 S/1 (137)</td>
<td>84 ES/1 (84)</td>
<td>120 GA/1 (120)</td>
<td>123 GA/2 (123)</td>
<td>116 PI/1 (116)</td>
</tr>
<tr>
<td>190 GP/2 (190)</td>
<td>191 GP/3 (191)</td>
<td>109 DP/1 (109)</td>
<td>111 IN/1 (111)</td>
<td>110 IN/1 (110)</td>
<td>139 YH/1 (139)</td>
<td>85 H/1/2 (85)</td>
<td>10 UB/1 (10)</td>
</tr>
<tr>
<td>194 NP/1 (194)</td>
<td>195 NP/2 (195)</td>
<td>196 NP/3 (196)</td>
<td>153 C/1 (153)</td>
<td>152 C/2 (152)</td>
<td>158 TH/1 (158)</td>
<td>154 CP/1 (154)</td>
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<tr>
<td>145 IU/1 (145)</td>
<td>98 IN/1 (98)</td>
<td>90 AN/1 (90)</td>
<td>161 M/1 (161)</td>
<td>155 H/1 (155)</td>
<td>164 C/1 (164)</td>
<td>168 M/1 (168)</td>
<td>160 E/1 (160)</td>
</tr>
<tr>
<td>125 KA/2 (125)</td>
<td>157 DL/1 (157)</td>
<td>135 G/2 (135)</td>
<td>170 G/1 (170)</td>
<td>84 NP/2 (84)</td>
<td>42 GA/1 (42)</td>
<td>42 FL/1 (42)</td>
<td>4 REL/1 (4)</td>
</tr>
<tr>
<td>8 NL/1 (8)</td>
<td>46 ML/1 (46)</td>
<td>127 AD/1 (127)</td>
<td>192 SM/1 (192)</td>
<td>193 ER/1 (193)</td>
<td>61 EN/1 (61)</td>
<td>136 CV/1 (136)</td>
<td>129 CH/1 (129)</td>
</tr>
<tr>
<td>133 G/4 (133)</td>
<td>159 EVE/1 (159)</td>
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</table>
APPENDIX 6: THE FIVE NEAREST NEIGHBOURS TO EACH OF THE 194 SITES

This appendix provides a listing of the five nearest neighbors, as measured by values of the Jaccard association coefficient, to each of the 194 sites. The nearest neighbors are those as given in the NTP (NUMERICAL TAXONOMIC PACKAGE) diagnostic program 'NEAREST NEIGHBOURS'. This listing of nearest neighbors given below was found to provide a simple, useful basis for reallocating outlying sites among the four major groups (see APPENDIX 5) and, as well, for checking the robustness of the classification (see APPENDIX 7).

<table>
<thead>
<tr>
<th>Neighbours Listed in Decreasing 'Distance'</th>
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</thead>
<tbody>
<tr>
<td>1 KNG/1 (1)</td>
<td>2 KNG/2 (2)</td>
<td>0.3866</td>
<td>7 NLROCK (7)</td>
<td>0.5763</td>
</tr>
<tr>
<td>1 KNG/1 (1)</td>
<td>1 KNG/1 (1)</td>
<td>0.3866</td>
<td>54 YR/4 (54)</td>
<td>0.4511</td>
</tr>
<tr>
<td>3 P.1SL (3)</td>
<td>76 V.SET (76)</td>
<td>0.5714</td>
<td>47 CML/1 (47)</td>
<td>0.5806</td>
</tr>
<tr>
<td>4 RLL (4)</td>
<td>46 MAL/1 (46)</td>
<td>0.5952</td>
<td>124 KUM/1 (124)</td>
<td>0.6122</td>
</tr>
<tr>
<td>5 BS/1 (5)</td>
<td>30 DA/7 (30)</td>
<td>0.6116</td>
<td>19 JK/1 (19)</td>
<td>0.5306</td>
</tr>
<tr>
<td>6 BS/2 (6)</td>
<td>15 RG/3 (15)</td>
<td>0.4103</td>
<td>13 RG/1 (13)</td>
<td>0.4752</td>
</tr>
<tr>
<td>7 HJOCK (7)</td>
<td>14 RG/2 (14)</td>
<td>0.4961</td>
<td>51 YR/1 (51)</td>
<td>0.4928</td>
</tr>
<tr>
<td>8 NL/1 (8)</td>
<td>46 MAL/3 (46)</td>
<td>0.5000</td>
<td>87 DPP/1 (87)</td>
<td>0.5821</td>
</tr>
<tr>
<td>9 NLROCK (9)</td>
<td>112 WW/1 (112)</td>
<td>0.5439</td>
<td>20 JK/2 (20)</td>
<td>0.5926</td>
</tr>
<tr>
<td>10 UJIM (10)</td>
<td>101 BR/1 (101)</td>
<td>0.5059</td>
<td>100 KUM/1 (100)</td>
<td>0.5647</td>
</tr>
<tr>
<td>11 NL/1 (11)</td>
<td>12 NL/3 (12)</td>
<td>0.4194</td>
<td>49 SA/11 (49)</td>
<td>0.4648</td>
</tr>
<tr>
<td>12 NL/3 (12)</td>
<td>11 NL/2 (11)</td>
<td>0.4194</td>
<td>49 SA/11 (49)</td>
<td>0.4648</td>
</tr>
<tr>
<td>13 RG/1 (13)</td>
<td>15 RG/3 (15)</td>
<td>0.3859</td>
<td>89 CASCA (89)</td>
<td>0.4596</td>
</tr>
<tr>
<td>14 RG/2 (14)</td>
<td>41 BS/4 (41)</td>
<td>0.4500</td>
<td>180 LD/1 (180)</td>
<td>0.4500</td>
</tr>
<tr>
<td>15 RG/3 (15)</td>
<td>13 RG/1 (13)</td>
<td>0.3859</td>
<td>6 BS/2 (6)</td>
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<tr>
<td>16</td>
<td>105</td>
<td>0.5026</td>
<td>189</td>
<td>0.4458</td>
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<td>106</td>
<td>0.3929</td>
<td>196</td>
<td>0.4678</td>
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<tr>
<td>18</td>
<td>107</td>
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<td>122 BJ/2 (122) 0.5333</td>
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<td>140 TARI (140) 0.6176</td>
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<td>133 G/4 (133) 0.6190</td>
<td>21 JJ/3 (21) 0.6750</td>
<td>42 KO/1 (42) 0.7143</td>
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**Notes:**
- A6-10
- The values are likely coordinates or identifiers related to a specific context, possibly for mapping or location purposes.
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<td>0.8963</td>
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**AVERAGE DISSIMILARITIES:**

- 0.9165
- 0.9075
- 0.9017
- 0.8991
- 0.8987
- 0.8984
- 0.8981
- 0.8978
- 0.8975
- 0.8972
- 0.8969
- 0.8966
- 0.8963

**AVERAGE DISSIMILARITIES:**

- 0.9165
- 0.9075
- 0.9017
- 0.8991
- 0.8987
- 0.8984
- 0.8981
- 0.8978
- 0.8975
- 0.8972
- 0.8969
- 0.8966
- 0.8963
### APPENDIX 7: FINAL 4-GROUP CLASSIFICATION AFTER SITE REALLOCATIONS

This appendix provides a listing of the final 4-group classification of sites after reallocations made with reference to the diagnostic program 'NEAREST NEIGHBOURS'—see APPENDIX 6. The site composition of each group is given below, along with notes indicating the nature of reallocations undertaken. As well, for group 2, the site composition of subgroups defined in the fourth paper of the thesis (i.e. groups 2(a), 2(b), 2(c) are given here also.

#### GROUP: 1
- 49 MEMBERS

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<tr>
<td>1 KNG/1</td>
<td>(1) 2 KNG/2 (2) 7 KLDQUK</td>
</tr>
<tr>
<td>27 DA/4</td>
<td>(27) 28 DA/5 (28) 32 DA/9 (32) 35 DA/12 (35) 37 DA/14 (37) 38 LNL (38) 41 BS/4 (41) 51 TB/1 (51)</td>
</tr>
<tr>
<td>54 TB/4</td>
<td>(54) 56 NG/1 (56) 57 BG/2 (57) 59 BC/2 (59) 62 KG/1 (62) 63 RG/2 (63) 66 MOL/3 (66) 69 CML/1 (69)</td>
</tr>
<tr>
<td>71 BARS</td>
<td>(71) 72 OR (72) 90 EAR/1 (90) 92 NG/3 (92) 93 NG/5 (93) 94 JAS/1 (94) 95 JA/2 (95) 97 YAW/2 (97)</td>
</tr>
<tr>
<td>100 TF/2</td>
<td>(100) 110 G/3 (110) 120 G/4 (120) 126 D/11 (126) 162 D/12 (162) 164 D/13 (164) 167 HD (167)</td>
</tr>
<tr>
<td>173 M/1</td>
<td>(173) 174 LV/1 (174) 175 PV/1 (175) 176 M/1 (176) 178 M/1 (178) 180 ID/1 (180) 192 GORI (192)</td>
</tr>
<tr>
<td>194. NANG</td>
<td>(194)</td>
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</table>

#### REALLOCATIONS

1. ADDITIONS FROM MINOR GROUPS: SITES 57, 59, (132)
2. ADDITIONS FROM MAJOR GROUPS: SITE 113 (FROM GROUP 2)
3. LOSSES TO OTHER GROUPS: SITES 91 (TO GROUP 2) AND 171 (TO GROUP 4)

#### GROUP: 2
- 79 MEMBERS

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</tr>
<tr>
<td>22 CC/1</td>
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<td>(47) 48 CML/2 (48) 49 SA/1 (49) 50 SA/2 (50) 61 EB/1 (61) 70 YARRA (70) 74 M/1 (74) 76 V/1 (76)</td>
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<tr>
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#### REALLOCATIONS

1. ADDITIONS FROM MINOR GROUPS: SITES 74, 149, 151, (172)
2. ADDITIONS FROM MAJOR GROUPS: SITES 91 (FROM GROUP 2), 138 (FROM GROUP 1), AND 143 (FROM GROUP 3)
3. LOSSES TO OTHER GROUPS: SITES 133 (TO GROUP 1) AND 135 (TO GROUP 4)

#### SUBGROUP: 2(a)
- 18 MEMBERS

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<tr>
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#### SUBGROUP: 2(b)
- 24 MEMBERS

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<td>96 P/1 (96) 86 NW/1 (86) 87 NW/2 (87) 115 CP/2 (115) 120 CAR/2 (120) 260</td>
<td>50 139 YW2 (139) 143 YW/1 (143) 144 CD/1 (144) 145 CD/2 (145) 146 WAND (146) 151 ST/1 (151)</td>
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#### SUBGROUP: 2(c)
- 24 MEMBERS

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APPENDIX A: SITE COMPOSITION AND SPECIES ATTRIBUTES AT 90 EFFECTIVELY SAMPLED, DISCRETE SAMPLED PATCHES

This appendix provides a listing of the 90 effectively sampled MVF patches used for calculating species-area relationships etc. in the fourth paper of the thesis. The composition of these sites may also be derived from data contained in APPENDIX 1. Listings of MVF species attributes used to derive species-area relationships are also given here. It is to be noted that the 8 character site and attribute labels are as used in numerical analyses are given. Ten labels are given on each row. A key for attribute labels is given in APPENDIX 2.

(1) SITE COMPOSITION

(11) ATTRIBUTE LIST OF TOTAL NUMBER OF MVF SPECIES OCCURRING AT THESE 90 SITES (n=103)

ACYPBAN, ABUSAB, ANUBA, ALIAC, ALIAC, ALIAC, ALIAC, ALIAC, ALIAC, ALIAC

(12) ATTRIBUTE LIST OF MVF SHRUB AND TREE SPECIES OCCURRING AT THESE 90 SITES (n=178)

A. ALIAC, ALIAC, ALIAC, ALIAC, ALIAC, ALIAC, ALIAC, ALIAC, ALIAC, ALIAC
APPENDIX 9: SITES AND SPECIES OCCUPYING HOLOCENE LANDFORMS

This appendix lists the sampling sites occurring on or immediately adjacent marine Holocene landforms, and the species sampled on sites occurring entirely on Holocene-derived landforms only. This latter data provides the basis for certain analyses presented in the fourth paper of the thesis. The proximity of sites to Holocene landforms is given also in APPENDIX 1 (site data attribute no. 3).

**SITES ON HOLOCENE LANDFORMS ONLY (n=28)**

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<td>91 CARR</td>
<td>101.87</td>
<td>141.10</td>
</tr>
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**SITES PARITY ON HOLOCENE LANDFORMS (n=24)**

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**SITES IMMEDIATELY ADJACENT HOLOCENE LANDFORMS (n=20)**

**MVF SPECIES SAMPLED AT 28 SITES OCCURRING ENTIRELY ON HOLOCENE LANDFORMS:**

The list given below indicates the frequency with which MVF taxa were encountered at these 28 sites. The 8 character attribute label is given first, then the attribute number (in parentheses), the number at which it was encountered, and last, its proportional occurrence.

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THE STATUS OF MONSOON ININE-FOREST IN THE WESTERN ARNHEM LAND REGION, NORTHERN AUSTRALIA. II. THE FOREST/SAVANNA BOUNDARY.

Jeremy Russell-Smith
Unpublished manuscript, June 1986
Abstract: A variety of factors, but principally substrate moisture conditions and/or fire, have been proposed as delimiting the extent of closed canopy, monsoon vine-forest (MVF) vegetation occurring in small, scattered patches across northern Australia. This paper has two aims. Firstly, as a means for assessing the relative contributions of substrate conditions and fire on the distribution of MVF vegetation in the western Arnhem Land region of the Northern Territory, a study is presented which explores vegetation-environment relations at each of seven MVF/savanna boundaries on freely draining, seasonally dry substrates. These boundary situations are illustrative of common types of MVF/savanna boundary in that region. At each site substrate moisture relations were assessed through the 1983 dry season by measurements of xylem pressure potential of selected reference species, and measurements of soil water content. Soil fertility relations are explored through determinations of soil concentrations of N, P, K, Ca, Mg and Loss on Ignition (as an estimate of organic matter). On the basis of these studies it is concluded that: 1. substrate conditions are improbably limiting to the widespread development of at least MVF vegetations comprising species tolerant of seasonal aridity, and; 2. that the locations of many MVF/savanna boundaries are not interpretable without recourse to interactions with fire.

And secondly, given that MVF (and presumably other relatively fire-sensitive, woody vegetation) is currently under threat due to burning impact over vast areas of northern Australia, in discussion attention is drawn to the ecological ramifications of different fire regimes. In the western Arnhem Land region the active erosion of MVF patch boundaries is associated with a current regime of frequent, extensive, and predominantly hot-burning, late dry season fires. Such a regime differs markedly from that under Aboriginal occupancy of the region, less than 100 years ago.
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1. INTRODUCTION

Across northern Australia, small patches of closed canopy monsoon vine-forest (MVF) vegetation are scattered in an otherwise vast expanse of mostly eucalypt-dominated savanna. A variety of hypotheses have been advanced to account for this distribution pattern (cf. Russell-Smith 1986). Firstly, a number of studies have forwarded the view that favourable substrate conditions, especially water balance, are necessary for the development of MVF vegetation (e.g. Beard 1976; Bowman 1986; Bowman & Dunlop 1986; Hnatiuš & Kenneally 1981; Nix & Kalma 1972; Specht 1958; Specht et al. 1977). Other studies, not being so persuaded, have identified fire as having a greater influence on patterns of MVF distribution (e.g. Beard et al. 1984; Clayton-Greene & Beard 1985; Langcamp et al. 1981; Stocker 1966; Stocker & Mott 1981). A third group of studies have stressed the influence of interactions between water balance conditions and fire (e.g. Bowman & Wightman 1985; Gillison 1983; Kershaw 1985). And finally, Kikkawa et al. (1981) and Russell-Smith & Dunlop (1984) have suggested that, as well as fire and deteriorating late Cainozoic water balance conditions, the interaction of a variety of biotic and environmental factors and processes have been contributive.

In a previously reported study of MVF in the western Arnhem Land region of the Northern Territory, it was noted that: 1. whereas many MVF species would appear to have an obligate requirement for perennial moisture availability (e.g. species restricted to springs); 2. a much greater number of species would appear to have no such requirement (Russell-Smith 1986). In the former case moisture availability is evidently a key limiting condition; the scarcity of such vegetation reflecting, in large part, the rarity of suitable habitat in that region. In the latter case however, given the occurrence of MVF vegetation on ostensibly seasonally xeric, nutrient-poor substrates, it was concluded that harsh substrate conditions per se improbably explain the limited extent of at least types of MVF vegetation.
tollerant of seasonal moisture availability in that region. Given also the demonstrated vagilities of many MVF species (Russell-Smith 1986), it follows equally that MVF would appear to occupy only a fraction of its potential domain. As a means for exploring these latter assertions, this paper first examines vegetation-environment relationships at each of seven MVF/savanna boundaries on freely draining substrates. On the basis of these studies, the influence of substrate conditions on the distribution of MVF vegetation in the western Arnhem Land region is assessed.

And secondly, in discussion, the significance of the fire regime is briefly considered. Unlike Africa, where the results of a number of savanna fire-plot studies are available (e.g. Afolayan 1978; Charter & Keay 1960; Hopkins 1965; Ramsay & Rose Innes 1963; Trapnell 1959), the ecological ramifications of different burning regimes in northern Australian savannas are, as yet, incompletely understood. For example, with notable exceptions (e.g. Braithwaite & Estbergs 1985; Hoare et al. 1980), many recent northern Australian studies consider only the role of fire frequency in effecting vegetation change. As demonstrated conclusively in experimental fire-plot studies however, it is the seasonality of burning rather than simply its frequency which affects the balance between closed-canopied forests and thickets, and their more open-canopied, savanna counterparts.

A better appreciation of the significance of fire regimes is necessary moreover, since, across northern Australia, the integrity of many MVF patches (and other fire sensitive vegetations) is severely threatened by contemporary burning impact. This applies equally to MVF patches occurring on the Cape York Peninsula in northern Queensland (Lavarack & Godwin 1984), as it does in the 'Top End' of the Northern Territory (Russell-Smith & Dunlop 1984) and mainland, northern Western Australia (J.S. Beard pers. comm., 1986). In the western Arnhem Land region at least, the current erosion of MVF patch boundaries (Russell-Smith 1984) is coincident with the findings of other regional studies that, if sustained, the current fire regime is likely to lead to
structural degradation of open forest and woodland savanna communities (Bell 1980; Braithwaite & Estbergs 1985; Hoare et al. 1980).
2. STUDY AREA AND METHODS

2.1 Study Area

Definition of the region described here as western Arnhem Land, along with a relatively detailed account of the regional environment, is given in Russell-Smith (1986). For the purposes of the present study only a resume is provided here.

Western Arnhem Land describes a coastal to subcoastal region of the 'Top End' of the Northern Territory confined generally between latitudes 12°-14°S and longitudes 132°-133°E (Fig. 1). This region is under the influence of a strongly seasonal, summer rainfall regime, with 90% of annual rainfall occurring in the 5 months from November to March. Mean annual rainfall is approximately 1400mm, but is highly variable from year to year. Temperatures are high year-round, the mean approaching 28°C. Frosts are unknown. As to be expected under such a climatic regime, evaporation is excessive.

Three main landform types occur in the region (Fig. 1). Dominating landform relief on the eastern margin of the study area is the Proterozoic sandstone Arnhem Land plateau with its actively eroding escarpment. The plateau rim is generally 200-300m a.s.l., attaining a maximum elevation of 508m at Mt. Gilruth. The escarpment gives way to a laterised lowland plain, the Koolpinyah Surface, which rolls westwards towards Darwin. This surface, comprising sediments derived originally as erosion products of scarp retreat and pediplanation, rarely exceeds 30m in depth. Scattered occurrences of remnant strike ridges and exposed igneous intrusions provide subdued changes in relief, especially in the south of the study area. In the north, coastal estuarine plains and subcoastal freshwater riverine floodplains are associated with the lower reaches of all major river systems in the region. These plains are of Recent origin, having been derived through the deposition of mostly clay sediments in former river valleys drowned by the last post-glacial rise in sea-level.
Fig. 1: Location of study area and study sites.
The vegetation comprises, for the most part, eucalypt-dominated open forests and woodlands with grassy understoreys. Such vegetation occurs mostly in well-drained situations on both the Arnhem Land plateau and the Koolpinyah Surface. In any one locality the structural expression of the vegetation reflects seasonal substrate water balance conditions. With impeded drainage, Eucalyptus typically is replaced by its myrtaceous cousin, Melaleuca. Where soils are alternately waterlogged and desiccated in the course of the seasonal cycle (e.g. as on subcoastal floodplains), Melaleuca-dominated forests and woodlands give way to sedgelands and other herbaceous communities. Mangrove communities are developed under tidal influences.

MVF vegetation occurs typically as small, discrete patches, or occasionally as extensive tracts associated with escarpment gorges and riparian habitats. Three generalised habitat types of MVF may be differentiated thus:

1. At sites of perennial water availability, both in the escarpment and plateau, and in the lowlands, evergreen MVF is associated with isolated springs and seepages, or occurs as riparian forests associated with permanent watercourses.

2. On the Arnhem Land Plateau, and along actively eroding portions of the escarpment margin especially, evergreen/semi-evergreen MVF vegetation is associated with a variety of seasonally dry, sandstone substrates (e.g. bouldery talus slopes, bare-rock pavements, skeletal sand-sheets). This vegetation is dominated typically by the myrtaceous Arnhem Land endemic, Allosyncarpia ternata.

3. In the lowlands, MVF comprising often substantial proportions of deciduous species is associated likewise with a variety of seasonally dry substrates. Typical
habitats include coastal sediments, riverine floodplain alluvia, lateritic substrates, and rock outcrops. This floristically continuous vegetation is concentrated in coastal regions, but extends as disjunct patches well to the south of the study area.

Collectively, these three habitat types occupy less than 2.2% of the land surface area of western Arnhem Land.

Given the relatively long growing period available to shallow rooted herbaceous species (approximately 20 weeks annually), followed by a long rainless period, understorey fires in open communities can be sustained on an annual basis. Crown fires are virtually unknown. The present fire regime is dominated by relatively high intensity, late dry season fires.

2.2 Methods

As a means for considering whether the restricted extent of MVF vegetation in western Arnhem Land can be attributed primarily a consequence of limiting substrate conditions, this paper examines vegetation-environment relationships at each of seven dry-land MVF/savanna boundaries. These seven sites were selected for study on the bases that: 1. upon initial inspection, the sharp vegetation boundaries at each of these sites did not appear to be associated with sharp changes in substrate conditions; and; 2. while not exhaustive, the sites selected for study illustrate a variety of common boundary situations between MVF and savanna vegetation on freely draining, seasonally dry substrates. The localities of the seven study sites are given in Fig. 1.

The studies described here were undertaken in the 1983 dry season, from April to December. At each site sampling of vegetation and substrates was conducted along transects, or at discrete plots along transects, running from inside a patch of closed canopy MVF, across the boundary, and into the surrounding savanna.
Vegetation sampling: Line transects were used to sample vegetation at two rock outcrop sites (Evelyn, Granite Hill). Recording of all trees (> 5cm DBH), their heights, and DBH, was undertaken in consecutive 10x10m^2 quadrats. Sampling of understorey components (e.g. species present, numbers of individuals, height distribution) was undertaken systematically at two 2x2m^2 quadrats in each tree-sampling quadrat. Understorey quadrats were sampled at the start of the study in the early dry season and again in the late dry season (October-November).

Sampling of the other five study sites was undertaken using circular plots, each 20m radius, at set points along a generalised transect. At three sites (Nourlangie, North Point, Oenpelli Rainforest) four circular plots were established thus: A. at the centre of the MVF patch; B. just inside the patch margin; C. just outside the patch margin, and; D. at various distances in the surrounding savanna. At a fourth site (Field Island) three plots were established; in this instance the MVF patch being so small that only one plot could be established therein. At the final site (Ngarrad) only two plots were used. In this instance plot A was established inside a sandstone gorge supporting MVF vegetation and plot B was located at the mouth of the gorge on a sandsheet supporting savanna vegetation. All trees present on each plot were recorded as for the 10x10m^2 quadrats employed at the two rock outcrop sites described previously. Understorey components were recorded at twenty 2x2m^2 quadrats located systematically within each circular plot. As for the rock outcrop sites, these quadrats were sampled at the beginning and at the end of the 1983 dry season.

Substrate sampling: At the start of the study sites were surveyed using a hand-held clinometer in association with a measuring tape. At the two rock outcrop sites, where sampling of vegetation was conducted along continuous line transects, the nature of the substrate (e.g. rock type, % bare rock) was recorded at each 2x2m^2 understorey sampling quadrat. Soil samples for
subsequent analyses (see below) were taken at two sampling stations: A. from the summits of the respective outcrops, and; B. from a station located at the bases of the outcrops in surrounding savanna vegetation. At the other five sites soil profiles and other substrate features were recorded following augering of at least six holes within 10m of each plot centre. Wherever practicable, augering was to 1.5m depth. As with the rock outcrop sites, soil samples for subsequent analyses were collected systematically at the close of field studies, late in the 1983 dry season. At least three soil sample replicates from 0-5cm depth, and also from 10-15, 30-35, and 50-55cm depths (where possible), were collected from each plot or sampling station. These samples were air-dried and then stored in sealed plastic bags.

At each site the substrate moisture status of individual plots (or sampling stations in the case of rock outcrop sites) was assessed indirectly at various times through the 1983 dry season by measuring the predawn xylem pressure potential (predawn \( \psi \)) of selected reference species. A useful reference species was one which occurred on at least two plots (or sampling stations) of each site, preferably on all plots. Measurements of predawn \( \psi \) were made on three individuals of each reference species per plot. These individuals were tagged at the commencement of the study and were sampled on each subsequent visitation. Measurements were made on freshly cut shoots, only on shrubs or small trees, using a Schollander-type pressure chamber in the manner as outlined in Ritchie & Hinckley (1975). As well, at each sampling time augered soil samples were collected from each plot for determination of gravimetric water content. Gravimetric soil water contents were not determined at the two rock outcrop sites however, given that soils in these situations, where present, comprised skeletal veneers.

In the laboratory soil samples were analysed for the following: pH (1:5 water extract); loss on Ignition (L.O.I.) at 550-600°C; particle size analysis (hydrometer method); exchangeable cations - Ca, Mg, K (extracted in 1N ammonium
acetate, with analysis on an Atomic Absorption Spectrophotometer; and total N and P (Kjeldahl digestion, with colorimetric analysis on an Autoanalyser). Methods and procedures used in above chemical analyses follow those as outlined in Lambert (1978).

2.4 Presentation of Results

The results of these seven boundary studies are, for convenience, presented in three sections as follows:

1. Site Descriptions: The sites themselves are first described in Section 3.1. Such description includes a relatively detailed account of the structural and floristic characteristics of the vegetation, and associated substrate characteristics, at each study site. Most of this data is summarised diagramatically (e.g. vegetation profiles, soil profiles), or in tabular form (e.g. plot floristic data). A key for the symbols used in compilation of vegetation profiles is presented as Fig. 2. Floristic nomenclature follows Chippendale (1971) or, for MVP taxa, Russell-Smith (1986). Where given, specimen collection numbers (e.g. Gardenia sp. JRS 815) refer to specimens lodged in the Darwin Herbarium, Northern Territory (DNA). Detailed life-form spectra are not presented here but may be calculated from comprehensive data given in Taylor & Dunlop (1985: Appendix 1). Soil nomenclature and terminology follows Stace et al. (1968).

While most descriptive parameters employed here are self-explanatory, two indices used for describing vegetation characteristics require explanation. The Canopy Index is calculated as follows. At each 2x2m² understorey sampling quadrat canopy cover was scored in the late dry season as: 0 = no canopy cover; 0.5 = < 50% canopy cover; 1 = > 50% canopy cover. At each circular
Fig. 2: Key to floristic symbols used in vegetation profiles.
plot the scores for individual quadrats were summed, and then divided by the number of quadrats sampled (n=20). For the two rock outcrop sites, however, canopy cover at each understorey-sampling quadrat is presented schematically in Figs. 10 and 11.

The Grass Cover Index is calculated as follows. At each understorey sampling quadrat grass cover was scored as: 0 = < 5% grass cover; 1 = > 5% grass cover. As for the Canopy Index, the Grass Cover Index is the mean score of the total number of quadrats sampled.

2. Substrate Moisture: For each study site, the seasonal course of predawn $\psi$ of selected reference species, and the gravimetric soil water content at 10-35 cm depth, is presented in Section 3.2.

3. Soil Fertility: For each study site, the results of nutrient analyses conducted on soil samples collected from each plot (or rock outcrop sampling station) are presented in Section 3.3.
3. RESULTS

3.1 Site Descriptions

Of the seven study sites, two are associated with sandstone escarpment terrain (Oenpelli Rainforest, Ngarradj Warde Djokeng), three are associated with lateritic landforms in lowland regions (Field Island, Nourlangie, North Point), and two are associated with igneous rock outcrops (Granite Hill, Evelyn). These sites are described below:

(1) Oenpelli Rainforest

The Oenpelli Rainforest is a relatively large patch (ca. 8ha) of evergreen MVF associated with a narrow sandstone escarpment gorge, approximately 6km south of the township of Oenpelli (Fig. 1; 12°23'S, 133°02'E). A small spring-fed, but seasonal, creek passes through the gorge. At the mouth of the gorge the creek, lined with MVF vegetation, traverses a small sandsheet deposit for approximately a kilometre before discharging into the floodplain of the East Alligator River (Fig. 1).

A profile of the vegetation where the creek leaves the escarpment is presented as Fig. 3(a). Localities A, B, C and D in this figure are the four plots sampled at this site. As may be observed in Fig. 3(a) (see also Figs. 4(a), 5(a)), evergreen MVF at the left gives way abruptly to more-or-less open canopied savanna vegetation on the right. The MVF patch is dominated by the myrtaceous sclerophyll, Allosyncarpia ternata (Fig. 3(a)). MVF canopy height is ca. 30m. At plot B, at the inner margin of the patch, all but two species present are typical MVF constituents (Table 1). At plots C and D, the vegetation comprises woodland savanna, with scattered trees generally less than 10m tall over dense and tall grasses to 1.5m (Fig. 3(a)). A small number of individuals of typical MVF species occur also at plots C and D (Table 1; Figs. 4(a), 5(a)). As with all other vegetation boundaries examined in this study, the question addressed here is essentially: is this MVF/savanna boundary
Fig. 3: Oenpelli Rainforest study transect profile. Where given, numbers in parentheses refer to numbers of MVP species.

(a) Vegetation profile

Oenpelli Rainforest

- A, D: Gradational profiles with surficial loamy sands and increasing clay with depth
- B: Deep loamy sands presumably with clay illuviation

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(b) Soil profile

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<th>sand</th>
<th>silt</th>
<th>clay</th>
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<tr>
<td>(n=1)</td>
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<tr>
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<td>4.8</td>
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<tr>
<td>1.2-1.4</td>
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<td>4.8</td>
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Data for L.O.I. gravel sand silt clay

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<td>1.0</td>
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<tr>
<td>(n=1)</td>
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<td>15.0</td>
<td>1.0</td>
<td>0.8</td>
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</table>

Profile data:

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<tr>
<td>(n=1)</td>
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<td>15.0</td>
<td>1.0</td>
<td>0.8</td>
<td>0.6</td>
</tr>
</tbody>
</table>

Diagram showing transect (m) in sandy soils, presumably with clay at depth.

Profile pH at 0.25 and 1.00.

Profile data with pH values.
Fig. 4: Stem densities and diameter class distributions at sampling plots at five study sites. Where unshaded, boxes refer to MVF taxa; where hatched, boxes refer to savanna taxa. 'Total' gives the total number of stems per hectare. 'MVF' gives the percentage of the total which are MVF stems.
Fig. 5: Height class distribution of woody individuals less than 5 cm DBH at five study sites. Where unshaded, boxes refer to MVF taxa; where hatched, boxes refer to savanna taxa. For each height class, numbers of single shoted and multishooted juveniles are given in columns (a) and (b), respectively. 'Total' gives the total number of juveniles per 0.01 ha. 'MVF' gives the percentage of the total which are MVF juveniles. 'M.S.' gives the percentage of the total which are multishooted juveniles.
<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>(a) Trees (Ø≥8 cm DBH)</strong></td>
<td><strong>(a) Trees (Ø≥8 cm DBH)</strong></td>
<td><strong>(a) Trees (Ø≥8 cm DBH)</strong></td>
<td><strong>(a) Trees (Ø≥8 cm DBH)</strong></td>
</tr>
<tr>
<td>Allosyncarpia ternata, Calophyllum sil</td>
<td>Helicia australasia, Oenocarya arnhemiaca, Marantaceae corymbosa</td>
<td>Helicia australasia, Oenocarya arnhemiaca, Marantaceae corymbosa</td>
<td>Ailanthus actinophylla, BAWASIA DENTATA, BUCHANANIA OBOVATA, BUCHANANIA OBOVATA, CALYTRIX ARBORESCENS, EUCALYPTUS KONBOLDIENSIS, E. FORRESTA, GARDENIA MEGASPÉRMA, PARINARI MONDA, SCHNYPHOCARPUS CUNNINGHAMII, TERMINALIA CARPENTARIAE, T. FERDINANDIANA, VITEX acuminata, V. glabrata. (n=9)</td>
</tr>
<tr>
<td>Carallia brachiata, Carpitaria acuminata</td>
<td></td>
<td>Calophyllum sil</td>
<td>Ailanthus actinophylla, BAWASIA DENTATA, BUCHANANIA OBOVATA, BUCHANANIA OBOVATA, CALYTRIX ARBORESCENS, EUCALYPTUS KONBOLDIENSIS, E. FORRESTA, GARDENIA MEGASPÉRMA, PARINARI MONDA, SCHNYPHOCARPUS CUNNINGHAMII, TERMINALIA CARPENTARIAE, T. FERDINANDIANA, VITEX acuminata, V. glabrata. (n=9)</td>
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<td>Helicia australasia, Oenocarya arnhemiaca, Marantaceae corymbosa</td>
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<td>Santalum album. (n=5)</td>
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<tr>
<td><strong>(b) Shrubs, seedlings (Ø≥3 cm DBH)</strong></td>
<td><strong>(b) Shrubs, seedlings (Ø≥3 cm DBH)</strong></td>
<td><strong>(b) Shrubs, seedlings (Ø≥3 cm DBH)</strong></td>
<td><strong>(b) Shrubs, seedlings (Ø≥3 cm DBH)</strong></td>
</tr>
<tr>
<td>Acacia aulacocarpa, Ailanthus conchinensis, Alyxia rusciophila, Antidesma parvifolium, Bridelia tomentosa, Buchanania arborescens, Canarium australium, Canthium sp. (MRS 920), Canthium sp. aff. lucidum, Cupaniopsis anacardioides, Diospyros calycantha, Drypetes lasiogyna, Denhamia obscura, Ervatamia orientale, Ficus scobina, Hopisfieldia australiana, Inor blanderana, Litsea glutinosa, Morinda cimifolia, Phyllanthus coccoides, Polyalthia holtreana, Pouteria sericea, Prema acuminata, Psychotria nesophila, Raphia benthamiana, Saccopetalum brahei, Tarenna dillachiana, Wrightia pubescens. (n=20)</td>
<td></td>
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<tr>
<td>Acacia aulacocarpa, Ailanthus conchinensis, Alyxia rusciophila, Antidesma parvifolium, Bridelia tomentosa, Buchanania arborescens, Canarium australium, Canthium sp. (MRS 920), Canthium sp. aff. lucidum, Cupaniopsis anacardioides, Diospyros calycantha, Drypetes lasiogyna, Denhamia obscura, Ervatamia orientale, Ficus scobina, Hopisfieldia australiana, Inor blanderana, Litsea glutinosa, Morinda cimifolia, Phyllanthus coccoides, Polyalthia holtreana, Pouteria sericea, Prema acuminata, Psychotria nesophila, Raphia benthamiana, Saccopetalum brahei, Tarenna dillachiana, Wrightia pubescens. (n=20)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia aulacocarpa, BUCHANANIA OBOVATA, BUCHANANIA OBOVATA, CALYTRIX ARBORESCENS, EUCALYPTUS KONBOLDIENSIS, E. FORRESTA, GARDENIA MEGASPÉRMA, PARINARI MONDA, SCHNYPHOCARPUS CUNNINGHAMII, TERMINALIA CARPENTARIAE, T. FERDINANDIANA, VITEX acuminata, V. glabrata. (n=9)</td>
<td></td>
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</tr>
</tbody>
</table>

Table 1: **SPECIES COMPOSITION AT DENFELI STUDY PLOTS**
Savanna species given in capital letters.

- **(a) Trees (Ø≥8 cm DBH)**
- **(b) Shrubs, seedlings (Ø≥3 cm DBH)**
- **(c) Climbers**
<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Herbaceous</strong></td>
<td><strong>Brasses</strong></td>
<td><strong>Sedges</strong></td>
<td><strong>Ferns</strong></td>
</tr>
<tr>
<td>Amorphophallus galbra, Anemone</td>
<td>Amorphophallus galbra, Dianella caerulea, Dipodium stenochilium. (n=3)</td>
<td>COMELINA ENSIFOLIA, DESMODIUM CLAVITRICE, HELIOTROPUS sp., PILOTUS sp., SPERMACCE sp. (n=5)</td>
<td>BRACHITARIA PUBIGERA, CHLORIS BARBATA, DIGITARIA BICORUS, ERAGROSTIS sp., PANICUM HETERPOSON TRITICUS, PANICUM HINANAESE, P. trichoides, SETARIA APICULATA, SORGHUM INTRANS, TAPIASTOCHLOA MAJOR. (n=9)</td>
</tr>
<tr>
<td>geophytes, anguils etc.</td>
<td></td>
<td></td>
<td>BULBOYLIS BARBATA, CYPERUS SESQUIFLORUS. (n=2)</td>
</tr>
<tr>
<td></td>
<td>Panicum trichoides. (n=1)</td>
<td>BRACHITARIA PUBIGERA, ERAGROSTIS sp., DIGITARIA BICORUS, ERAGROSTIS sp., PANICUM HETERPOSON TRITICUS, PANICUM HINANAESE, P. trichoides, SETARIA APICULATA, SORGHUM INTRANS, TAPIASTOCHLOA MAJOR. (n=9)</td>
<td>BULBOYLIS BARBATA, CYPERUS SESQUIFLORUS. (n=2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Ferns</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cheilanthes sp., Lindsaea ensifolia ssp. ensifolia. (n=2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Epiphytes</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dendrobium dicuphum. (n=1)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Total Species | 59 | 44 | 35 | 32 |
| Total VHF Species | 59 | 42 | 5  | 3  |
edaphically delimited?

Away from the creek at plot A the terrain slopes gently upwards (plots B, C), then falls away slightly (plot D) to a similar level as that of the creek (Fig. 3(a)). At all plots the substrates comprise deep (> 1.5m), acid, sandy loam or loamy sand soils, with apparent increasing clay content at depth (plots A, D in Fig. 3(b)). The proportion of gravel in these soils increases along the transect, from plot A to D. There is, however, no apparent edaphic discontinuity associated with the abrupt MVF/savanna boundary (plots B, C).

(2) Ngarradj Warde Djobkeng

This study site is associated with a narrow, vertically walled sandstone gorge approximately 5 km west from where the East Alligator River emerges from the escarpment onto the lowland plains (Fig. 1; 12°28'S, 132°55'E). The name of this site refers to a similar nearby cleft in the escarpment where, in Aboriginal legend, the sulphur-crested cockatoo (Ngarradj) caused the rock to split. At the study site semi-evergreen MVF vegetation occupies the centre of the gorge, growing on rocky talus (Fig. 6(a)). At the mouth of the gorge this vegetation gives way abruptly to open canopied vegetation growing on a shallow sandsheet deposit.

More-or-less closed canopy MVF vegetation in the centre of the gorge (plot A) is dominated by the myrtaceous sclerophyllous species, Xanthostemon umbrosus (Fig. 6(a)). Most species present are typical MVF constituents (Table 2). Canopy height is mostly less than 12m. At plot B the vegetation is dominated by typical open forest or woodland species over a developing assemblage of typical savanna and MVF species (Table 2; Figs. 4(b), 5(b)). Some of these trees are over 20m in height.

At plot A, soils, where present, comprise pockets of skeletal sand less than 30 cm deep (Fig. 6(b)). At plot B, there is an almost continuous mantle of organically-stained sand over rock
Ngarradj warde djokkeng: a gorges in sandstone terrain

(a) Vegetation profile

<table>
<thead>
<tr>
<th>Distance along transect (m)</th>
<th>Height (m)</th>
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</thead>
<tbody>
<tr>
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</tr>
<tr>
<td>50</td>
<td>40</td>
</tr>
<tr>
<td>100</td>
<td>30</td>
</tr>
<tr>
<td>150</td>
<td>20</td>
</tr>
<tr>
<td>200</td>
<td>10</td>
</tr>
</tbody>
</table>

- Sandstone escarpment
- Skeletal sand over broken rock
- Gently sloping mantle at base of escarpment
- Colluvial sand of variable depth over boulders

(b) Soil profile

<table>
<thead>
<tr>
<th>Distance along transect (m)</th>
<th>No. of tree species (&gt;5cm DBH)</th>
<th>Total no. of species</th>
<th>Basal area (m² ha⁻¹)</th>
<th>Mean basal area (m² stem⁻¹)</th>
<th>Canopy index</th>
<th>Grass cover index</th>
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</thead>
<tbody>
<tr>
<td>0</td>
<td>17 (16)</td>
<td>49 (45)</td>
<td>15.73</td>
<td>0.018 ± 0.011</td>
<td>0.88</td>
<td>0.00</td>
</tr>
<tr>
<td>50</td>
<td>7 (1)</td>
<td>74 (31)</td>
<td>11.67</td>
<td>0.037 ± 0.015</td>
<td>0.43</td>
<td>0.65</td>
</tr>
</tbody>
</table>

- Light grey sand, fine clay
- Colluvial sand of variable depth over boulders
(b) Soil profile

- No. of tree species (>5cm DBH)
- Total no. of species
- Basal area (m²ha⁻¹)
- Mean basal area (m² stem⁻¹)
- Canopy index
- Grass cover index

(b) Soil profile

**Fig. 6**: Ngarradj Warde Ojobkeng study transect profile. Where given, numbers in parentheses refer to numbers of MVF species.
### Table 2: Species Composition at Neighbour Ward Ujuhehe Study Plots

<table>
<thead>
<tr>
<th>Type</th>
<th>Species</th>
<th>Savanna species given in capital letters.</th>
<th>Neighbour Ward Ujuhehe species given in capital letters.</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Trees (15cm DBH)</td>
<td>Acacia aulacocarpa, Adenia conchocrinensis, Antidesma parvifolium, Bremia rhynchocarpa, Didelphis arborea, Ctenocytos anacardioides, Ficus scobina, Dracaena (JRS 816), Feronia holtzeana, P. nitidissima, Sterculia quadrifida, Vitex acuminata, Xanthosoma umbrosa. (n=7)</td>
<td>Acacia aulacocarpa, Erythrophleum chlorostachys, Eucalyptus kolkwitsiensis, Lophostemon lactiflora, Omelia vernicosa, Pandanus spiralis, Stygiun suborbigulare. (n=7)</td>
<td></td>
</tr>
<tr>
<td>(b) Shrubs, seedlings (5cm DBH)</td>
<td>Alyxia unifoliolata, Calophyllum siliquum, Cryptocarya cunninghamii, Diospyros parvifoliolata, Strychnos anacardioideae, Trachycarpus fortunei, Vitex acuminata, Xanthosoma umbrosa. (n=9)</td>
<td>Acacia tortilis, Antidesma ghaesembilla, A. parvifolium, Bocconia lanciflata, Helicteres tomentosa, Buchanania obovata, Calophyllum siliquum, Cassia hamatoides, Clamaviinae tetragonon, Cleome viscosa, Corchorus sp., Cryptocarya exfoliata, Cupaniopsis anacardioides, Diocorys budeiana, Ervatamia orientale, Exocarpos latifolius, Ficus scobina, Gheeria xanthopetalita, Hibbertia cistoides, H. delilata, Hibiscus ananamensis, Hypoestes furibunda, Litsea glutinosa, Macartunia sp., Phyllanthus sp., Schefflera arguta, Solanum asystremophyllum, Stemodia cerasula, Sterculia quadrifida, Triumfetta microcarpa, Vitex acuminata, Wrightia saliciflora. (n=33)</td>
<td></td>
</tr>
<tr>
<td>(c) Climbers</td>
<td>Abrus precatorius, Adenia heterophylla, Ampelocissus acetica, Capparis sepiaria, Cayratia arborea, Dioscorea transversa, Flagellaria indica, Farnesia velutina, Rukenoffkia sp. (NB 1991), Securinega elliptica, Tinospora sellowiana, Trichosanthes cucumerina, Tylorhopha crelinostro, T. flexuosa, Ufima wardiana. (n=15)</td>
<td>Adenia heterophylla, Cassytha filiformis, Caryatia triloba, Dioscorea bulbifera D. transversa, Flagellaria indica, Prionia sp., Herrema trimontata, Nuckia sp., Parsonsia velutina, Passiflora foetida, Smilax australis, Timonera saliciflora, Tylophora flexuosa. (n=41)</td>
<td></td>
</tr>
<tr>
<td>(d) Herbaceous geophytes, annuals etc.</td>
<td>Anisome siliculosum, Coleus scutellarioides, Lindernia sp., Stylidium sp. (n=8)</td>
<td>Cartonema panarelo, Targonja sp., Coleus scutellarioides, Coppelina disfollia, Desmodium clavatricov, Evolvulus alsinoides, Godetia aristophylla, Heliotropium sp., Lindernia sp., Olaxsacne, Pimelea fimbriata, Spirodactylus sp. (n=12)</td>
<td></td>
</tr>
<tr>
<td>(e) Grasses</td>
<td>Panicum trichoides. (n=1)</td>
<td>Cyrtosperma procumbens, Erichsenia triphosa, Pandion kindtii, P. trichoides, Setaria fimbriata, Triodia sp. (n=6)</td>
<td></td>
</tr>
<tr>
<td>(f) Sedges</td>
<td>Cyperus portae-tartare. (n=1)</td>
<td>Bulboylis sagittata, Cyperus portae-tartare. (n=2)</td>
<td></td>
</tr>
<tr>
<td>(g) Fers</td>
<td>Drimaria quercifolia (epiphyte), Stenoclea palustris (climber). (n=2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total Species</strong></td>
<td>49</td>
<td>74</td>
<td></td>
</tr>
<tr>
<td><strong>Total MF Species</strong></td>
<td>45</td>
<td>31</td>
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</tr>
</tbody>
</table>
debris. This sandy mantle is mostly less than a metre in depth (Fig. 6(b)).

(3) Field Island

Field Island is situated at the mouth of the South Alligator River in the van Dieman Gulf (Fig. 1). The island comprises an emergent, more-or-less planar fragment of the Koolpinyah Surface which is encircled by estuarine muds and other coastal sediments. Maximum elevation is probably less than 6 metres above the mean high water spring tide level. The study site is on the eastern margin of the island and describes a transect running at right angles to a short beach (Fig. 7(a); 12°07'S, 132°55'E).

At the rear of the beach a small dune has been thrown over the eroded, seaward margin of the lateritic surface (Fig. 7(a)). Behind this dune there is a narrow fringe of MVF vegetation, totalling less than a hectare in extent. This vegetation (plot A) comprises a dense tangle of vines, mostly evergreen shrubs and small trees, and deciduous emergents up to 20m tall. At plot B small clumps of MVF species are developing beneath a diffuse canopy of eucalypts (Figs: 4(c), 5(c), 7(a)). At plot C the vegetation is essentially of a savanna type, with eucalypts to 16m height over sand palms (Livistona humilis) and dense, tall grasses to 1.5m. A large number of MVF taxa occur in lower strata of this savanna vegetation (Table 3).

With the exception of an evident trend of diminishing sandiness of the soil surface away from the beach (i.e. from plot A to C), augering to 1m depth at each plot reveals the soils to be markedly similar (Fig. 7(b)). The soils comprise yellowish-red, acid, sandy loams with abundant small laterite pisolith inclusions. As evidenced by the extensive exposure of eroded ferruginous laterite blocks and sheets in adjacent beach sedimentary facies, the surficial soils at plots A to C are developed over an indurated lateritic horizon occurring probably within 1-2 metres of the soil surface. While not ascertained, this iron-enriched indurated horizon is in turn probably developed
Fig. 7: Field Island study transect profile. Where given, numbers in parentheses refer to numbers of MVF species.

(a) Vegetation profile

Field Island

ESTUARINE MUD FLAT BEACH

Distance along transect (m)

<table>
<thead>
<tr>
<th>Distance (m)</th>
<th>Estuarine clay</th>
<th>Siliceous beach sand</th>
<th>Loam, with pisoliths increasing at depth, over ferruginous laterite</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
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<td></td>
</tr>
<tr>
<td>200</td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

(b) Soil profile

<table>
<thead>
<tr>
<th>Profile</th>
<th>pH</th>
<th>L.O.I.</th>
<th>gravel</th>
<th>sand</th>
<th>silt</th>
<th>clay</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>5.9</td>
<td>7.6</td>
<td>30.8</td>
<td>32.4</td>
<td>14.0</td>
<td>2.8</td>
</tr>
<tr>
<td>0.2</td>
<td>5.9</td>
<td>7.6</td>
<td>30.8</td>
<td>32.4</td>
<td>14.0</td>
<td>2.8</td>
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<tr>
<td>0.4</td>
<td>5.9</td>
<td>7.6</td>
<td>30.8</td>
<td>32.4</td>
<td>14.0</td>
<td>2.8</td>
</tr>
<tr>
<td>0.6</td>
<td>5.9</td>
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<td>30.8</td>
<td>32.4</td>
<td>14.0</td>
<td>2.8</td>
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<tr>
<td>0.8</td>
<td>5.9</td>
<td>7.6</td>
<td>30.8</td>
<td>32.4</td>
<td>14.0</td>
<td>2.8</td>
</tr>
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</table>
Where given, numbers in italics.

Profile. loam, with pisoliths increasing at depth, over ferruginous laterite.

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<th>Distance along transect (m)</th>
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### A

- **pH:** 7.0 (5)
- **L.O.I.:** 25 (12)
- **Gravel:** 0.0
- **Sand:** 0.2
- **Silt:** 0.4
- **Clay:** 0.8

### B

- **pH:** 8.30
- **L.O.I.:** 0.013 ± 0.004
- **Gravel:** 0.23
- **Sand:** 0.55

### C

- **pH:** 6.79
- **L.O.I.:** 0.018 ± 0.009
- **Gravel:** 0.25
- **Sand:** 0.80

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<th>Gravel</th>
<th>Sand</th>
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<th>Clay</th>
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<td>C</td>
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<td>0.018 ± 0.009</td>
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### Profile pH L.O.I. Gravel Sand Silt Clay

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### Profile pH L.O.I. Gravel Sand Silt Clay

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<th>Gravel</th>
<th>Sand</th>
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<td>7.0 (5)</td>
<td>25 (12)</td>
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<td>B</td>
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<td>C</td>
<td>6.79</td>
<td>0.018 ± 0.009</td>
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Table 3: Species Composition at Field Island Study Plots

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<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Trees (5cm DDB)</td>
<td>Breynia cernea, Canarium australianum, Drypetes lasiogyna, Glycosmis pentaphylla, Micromelum minutum, Pouteria sericata, Rubiaceae spp (JRS 718), Saccopetalum braheii, Vitex acuminata. (n=9)</td>
<td>Acacia auriculiformis, Canarium australianum, EUCALYPTUS Bleezeri, E. MINIATA, LIVISTONA HUMILIS, PANDANUS SPIRALIS, PLANCHONIA CAREYA, Pouteria sericata, Saccopetalum braheii, Sterculia quadrifida. (n=10)</td>
<td>BRACHYCHITON DIVERSIFOLIUS, ERYTHROPHLEUM CHLOROSTACHYS, EUCALYPTUS BLEESEI, F. TETRORDONTA, LIVISTONA HUMILIS, PANDANUS SPIRALIS, TERMINALIA FERMINANDIANA. (n=7)</td>
</tr>
<tr>
<td>(b) Shrubs, seedlings (5cm DDB)</td>
<td>Carpentaria acuminata, Cupaniopsis anamardioides, Dodonaea platyptera, Exocarpos latifolius, Myrsine corymbosa, Trema aspera. (n=6)</td>
<td>Alliophyllum obtusum, Breynia cernea, Bridelia tomentosa, Denhamia obscura, Drypetes lasiogyna, ERYTHROPHLEUM CHLOROSTACHYS, Exocarpos latifolius, LIVISTONA HUMILIS, Micromelum minutum, Pomea acuminata, P. serratifolia, Trema aspera, Vitex acuminata. (n=13)</td>
<td>BRIDELIA TOMENTOSA, BUCHANANIA OBOWATA, Canarium australianum, Denhamia obscura, Drypetes lasiogyna, PLANCHONELLA POLYMANTHA, PSIDIOBAHROEMUS VARIABLE, Saccopetalum brashear, Sterculia quadrifida, Trema aspera. (n=10)</td>
</tr>
<tr>
<td>(c) Climbers</td>
<td>Abrus precatorius, Capparis sepiaria, Dioscorea transversa, Flugellaria indica, Jasminum simplicifolium, Malaisia scandens, Opilia asetacea, Parsonia velutina, Secamone elliptica. (n=9)</td>
<td>Abrus precatorius, Ampellocissus acetosa, Capparis sepiaria, Dioscorea bulbifera, D. transversa, Malaisia scandens, MERRELLA TRIDENTATA, Parsonia velutina, Secamone elliptica, Salix australis, Tinospora smilacina. (n=11)</td>
<td>Ampellocissus acetosa, Asparagus racemosus, Dioscorea bulbifera, D. transversa, Ipomoea abrupta, Marsdenia sp. (n=6)</td>
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<tr>
<td>(d) Herbaceous annuals</td>
<td>HIBISCUS MEXUAHENSIS. (n=1)</td>
<td>HIBISCUS MEXUAHENSIS. (n=1)</td>
<td>CRITALARIA MEDICAGNEA. (n=1)</td>
</tr>
<tr>
<td>(e) Grasses</td>
<td>HETEROPOGON TRITICEUS, (n=1)</td>
<td>HETEROPOGON TRITICEUS, SORGHUM sp. (n=2)</td>
<td>SORGHUM sp. (n=1)</td>
</tr>
<tr>
<td>Total Species</td>
<td>25</td>
<td>37</td>
<td>25</td>
</tr>
<tr>
<td>Total MWF Species</td>
<td>24</td>
<td>25</td>
<td>12</td>
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over a deeply weathered, highly mineralised profile, such as occurs widely in the region (Hays 1967; Williams 1969).

(4) Nourlangie

The Nourlangie study site is situated on a small, gently sloping (ca. 1\% promontory of the Koolpinyah Surface which protrudes into an extensive riverine floodplain system (Fig. 1; 12°45'S, 132°39'E). The study transect describes the change in vegetation along this slope, from tall paperbark (Melaleuca spp.) forest associated with floodplain sediments, through fringing, dense MVF (plots A, B), into eucalypt-dominated woodland savanna (plots C, D) (Fig. 8(a)).

At plot A, closed canopy, evergreen MVF is developing under emergent, light-demanding species (Alstonia actinophylla, Erythrophloeum chlorostachys) up to 23m in height (Fig. 8(a)). The occurrence here of such emergents signifies that, at some time in the recent past, open canopy conditions conducive to the development of shade-intolerant species must have prevailed. From the 1930's to 1950's this area was logged intensively. Such logging was associated principally with the extraction and milling of the valuable termite-resistant timber, cypress pine (Callitris intratropica, Gymnospermae). At Nourlangie now, cypress pine occurs only as scattered clumps, or remnant individuals, in a mosaic of developing closed canopy MVF patches, and open canopied eucalypt-and Acacia-dominated vegetation. Plot B is situated at the upslope margin of the zone where dense MVF clumps are developing. The plot supports a diverse mixture of MVF and typically savanna woody species (Table 4), growing beneath tall, scattered Callitris individuals, or in gaps where remnant stumps indicate that Callitris previously grew (Fig. 8(a)). Plots C and D are situated at increasing distances upslope, well beyond the present distributional limits of Callitris or stumps thereof. The vegetation at both these plots comprises eucalypt-dominated woodland savanna with inclusions of small numbers of MVF species and individuals in their respective understoreys (Table 4; Figs. 4(d), 5(d)).
Fig. 8: Nourlangie study transect profile. Where given, numbers in parentheses refer to numbers of MVF species.

(a) Vegetation profile

(b) Soil profile

<table>
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<tr>
<th>Profile</th>
<th>pH</th>
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<th>gravel</th>
<th>sand</th>
<th>silt</th>
<th>clay</th>
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**C** red earth 10YR (sandy loam) with abundant ironstone pisoliths

**D** skeletal soils 10YR (clay loam) over ferruginous laterite

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<th>silt</th>
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**Profile**

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<tr>
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<td>9.65</td>
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**Correclional laterite**
### Table 4: Species Composition at Hourangie Study Plots

Savanna species given in capital letters.

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<th>B</th>
<th>C</th>
<th>D</th>
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</thead>
<tbody>
<tr>
<td>A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>(a) Trees (15cm DBH)</td>
<td>Alstonia actinophylla, Cryptocarya cunninghamii, Cephalostoma anacardioides, Diospyros calycanthus, Drypetes jasminoides, Erythrophleum chlorostachys, Sanophyllum falcatum, ... sea gum, Polyalthea mutabilis, Pouteria sericata, Strychnos lucida, Vitex glabrata. (n=12)</td>
<td>Acacia aulacocarpa, Alstonia actinophylla, CALLITRIS MINIATA, E. FORRESTA, FADINUMA SPINOSA, PETALOSTOMA PUBESSENS, SYZYGIUM SUBORBITACULARE, TERMINALIA FERDINANDIANA. (n=7)</td>
</tr>
<tr>
<td>(b) Shrubs, seedlings (15cm DBH)</td>
<td>Allophyllum coccineum, Rhabar bar casba, Bremia cernua, Bridel la tomentosa, Canarium australianum, Clerodendrum floribundum, Elaeocarpus arborescens, Glycosmis pentaphylla, Hyptis floribundum, Marantaceae corymbosa, Morinda citrifolia, Securinega wyethoides, Sterculia quadridita, Vitex acuminata. (n=16)</td>
<td>Acacia aulacocarpa, A. DIFFICILIS, A. DINGIATA, A. LATIFOLIA, Alphitonia excelsa, Asterecta glaberrima, ARNHEMIA CRYPTANTHA, BREYNIA cernua, Bridelia tomentosa, Canarium australiense, Clerodendrum floribundum, Elaeocarpus arborescens, ERYTHRROPHLOE OS ARTHEMICA, Planchonella foliata, Schizophragma parviflorum, Hibbertia dentata, Persoonia falciata, Phyllanthus sp., Planchonella foliata, Planchonella careya, Scaevola auriculata, Stedocarpus cuinimarum. (n=17)</td>
</tr>
<tr>
<td>(c) Climbers</td>
<td>Adenia heterophylla, Cayratia acris, Ichnocarpus frutescens, Luffa cylindrica, Malaisia scandens, Salix australis, Tinospora siulacina, (n=7)</td>
<td>Abru s precatorius, Cayratia acris, C. triflora, Dioscorea transversa, Flagellaria indica, Ichnocarpus frutescens, Jussiaea simplicifolia, Malaisia scandens, Salix australis, Fylpohora flexuosa, Unona wardiana. (n=11)</td>
</tr>
<tr>
<td>(d) Herbaceous</td>
<td>Schyranthes aspera, Amorphophallus galbra, Coleus scutellarioides, Hyptis suaveolens. (n=4)</td>
<td>Amorphophallus galbra, Butes biginiana, Coleus scutellarioides, HIBIOS MERAHNKINSIS, Hyptis suaveolens. (n=5)</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>-------</td>
<td>--------------------------------------</td>
<td>--------------------------------------</td>
</tr>
<tr>
<td>Brasses</td>
<td>Opismenii burmannii, Panicum trichoides</td>
<td>Opismenii burmannii, Panicum mindanae, Eriachne ciliata, Panicum mindanaeense</td>
</tr>
<tr>
<td>(n=2)</td>
<td>(n=3)</td>
<td>(n=2)</td>
</tr>
<tr>
<td>Sedges</td>
<td>ARTHROSTYLIS APHILLA, (n=1)</td>
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</tr>
</tbody>
</table>

| Total Species | 41 | 56 | 36 | 34 |
| Total MIF Species | 40 | 41 | 2  | 2  |
The soils associated with these four plots increase in depth down the slope (i.e. from plot D to A). At the top of the slope (plot D), soils comprise shallow, gravelly, acid, yellowish sandy loams to clay loams over massive laterite blocks (Fig. 8(b)). This laterite outcrops as a pavement over part of the plot. Between plots D and C, there is a marked pedological discontinuity. Soils at plot C comprise deep (>1.5m), acid, reddish sandy loams with increasing clay and lateritic pisoliths at depth. Similar surface soils occur at plots B and A, with only minor inclusions of pisoliths. The soils at plot A, B and C are thus most probably derived through colluvial transport of the products of former upland surface wastage and laterite disintegration (Hooper 1969; Williams 1969). At plot A, the stratigraphic log of a nearby water bore indicates such colluvium to be at least 18m deep. The upper limit of MVF distribution (plot B) is not associated, however, with any evident substrate discontinuity.

(5) North Point

As at Nourlangie, the North Point study site is situated on gently sloping terrain (ca. 0-2%) at the margin of an extensive riverine floodplain (Fig. 1; 12°22'S, 132°22'E). From seasonally inundated herbaceous vegetation associated with floodplain sediments, the study transect proceeds upslope through fringing MVF vegetation (plots A, B), into eucalypt-dominated woodland savanna (plots C, D) (Fig. 9(a)). Plot A is dominated by two huge deciduous figs (Ficus virens), ca. 25m in height, over lower strata of evergreen and deciduous MVF trees and shrubs (Fig. 9(a)). Plot B is situated at the upland margin of the MVF fringe, and encompasses a small isolated MVF clump surrounded by eucalypt-dominated woodland savanna. Plots C and D occur at increasing distances upslope. At both plots the vegetation comprises eucalypt-dominated savanna with relatively large numbers of MVF species and individuals in their respective understoreys (Table 5; Figs. 4(e), 5(e), 9(a)).

As at Nourlangie, soil depth tends to increase downslope
Fig. 9: North Point study transect profile. Where given, numbers in parentheses refer to numbers of MVF species.

(a) Vegetation profile

North Point

Annual herbaceous swamp
sandstone outcrop

A, B loamy soils with abundant laterite pisoliths
C, D relatively shallow loamy soils with abundant lateritic pisoliths over ferruginous laterite

No. of tree species (>5cm DHB) 16 (1)
Total no. of species 60 (50)
Basal area (m² ha⁻¹) 61.66
Mean basal area (m² stem⁻¹) 0.106 ± 0.132
Canopy index 0.65
Grass cover index 0.00

(b) Soil profile

<table>
<thead>
<tr>
<th>Profile</th>
<th>pH</th>
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<th>sand</th>
<th>silt</th>
<th>clay</th>
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<td>2.5YR 3/6</td>
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Profile pH L.O.I. gravel sand silt clay
(n-3) (n-6) (n-1) (n-1) (n-1)

Profile pH L.O.I. gravel-sand silt clay
(n-3) (n-6) (n-1) (n-1)

B

C

Distance along transect (m)
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<th>Profile</th>
<th>pH</th>
<th>L.O.I.</th>
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<th>sand</th>
<th>silt</th>
<th>clay</th>
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<td>46.0</td>
<td>16.1</td>
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<tr>
<td>D</td>
<td>5.3</td>
<td>3.3</td>
<td>38.2</td>
<td>38.1</td>
<td>13.3</td>
<td>9.8</td>
</tr>
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</table>

**Concretionary laterite**

Distance along transect (m)
Table 5: SPECIES COMPOSITION AT NORTH POINT STUDY PLOTS

Savanna species given in capital letters.

<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Trees (95cm DBH)</td>
<td>Abies conchinchinensis, Bobax ceiba, Celtis philippensis, Cupaniospis anacardioides, Diospyros calycantha, Drypetes lasiogyna, Ficus virmens, Banophyllum fallatum, Litsea glutinosa, Malotus philippensis, Planchonia caerulea, Polyalthia holteana, Sacopeletalia braeni, Sterculia quadridita, Stychnos lucida, Terminalia sericea, Vitea glabra. (n=11)</td>
<td>Acsis altitudinaria, Acsis actinophylla, BRACHYCHITON DIVERSIFOLIUS, Demania obscura, ERYTHRONEURUM OBDUMETRICHIA, E. MINIATA, E. TETRONDIA, Ficus opposita, PLANCHONIA CAEYRA, TERMINALIA CARPELIARIAE, Vitea glabra. (n=12)</td>
<td>Demania obscura, EUCALYPTUS BLEEDING, E. MINIATA, E. TETRONDIA, PANDANUS SPARCULIS, PERSONIA FALCATA, STENOCARPUS CUNSINGHAMII, TERMINALIA CARPELIARIAE, T. FERDINANDIANA. (n=9)</td>
</tr>
<tr>
<td>(b) Shrubs, seedlings</td>
<td>CASSIA OBEDISIFOLIA, C. OCCIDENTALIS, Celastrus truncatus, Clerodendrum floribundum, Cupaniospis anacardioides, Diospyros var. reticulata, EUCALYPTUS CLAVIGENA, Ficus scobina, Glycosmis pentaphylla, Murraya paniculata, Myristica insipida, Psychotria nesophila, SIDA ACUTA, Triumfetta rhombodea, Wrightia pubescens. (n=16)</td>
<td>Acsis actinophylla, Erysma cernua, Bredelia tomentosa, CARAXANIA OOSIATA, Canarium australiun, Cupaniospis anacardioides, FLOREALIA LINEATA, Glochidion sericea, Glycosmis pentaphylla, GREWIA RENUSIFOLIA, Malotus philippensis, Murraya paniculata, Polyalthia holteana, Pruna acuminata, Psychotria nesophila, Sacopeletalia braeni, Securinea orientalis, SIDA ACUTA, Tironius tigro, Triumfetta rhombodea, Vitea glabra, WALTHERIA INDICA, Zanthoxylum parvifolium. (n=27)</td>
<td>Acsis aulacocarpa, A. MIMU, Alphitonia excelsa, Antidesa glabrescens, Breynia cernua, Bredelia tomentosa, Bobax ceiba, BUCHANANIA OOSIATA, Canarium australiun, CASSIA OBEDISIFOLIA, Clerodendrum floribundum, C. VITEA, Cochlospermum fraseri, COELOSPERMUM RETICULATUS, Crotalaria arnhemica, EUCALYPTUS CLAVIGENA, Ficus opposita, FLEUMIA LINEATA, GADUA MESSOPHILA, GARDNIA SUFFRUTICOSA, HIPPEASTRUM SP., PETALOSTIGMA PARSECENS, PLANCHELLA PICTANDRA, Pruna acuminata, SIDA ACUTA, STENOCARPUS CUNSHAMII, Stychnos lucida, SKYPSIUS SUBREXIFOLIUS, TERMINALIA FERDINANDIANA, Triumfetta rhombodea, WALTHERIA INDICA, TANTHESTOK PARADUS, Zanthoxylum parvifolium. (n=26)</td>
</tr>
<tr>
<td>(c) Climbers</td>
<td>Abrus precatorius, Adenia heterophylla, Asparagus rasegous, Canaxis segar, Caryatia maritima, Dioscorea bulbifera, Flagellaria indica, Ichneumon frutescens, Luffa cylindracea, Malacia scandens, Opilia montanea, Pavignone ovata, Passiflora foetida, Pisonia aculeata, Snaila australis, Tinopora smilacina. (n=16)</td>
<td>Abrus precatorius, AMPELLOCISSUS ACUTUS, Asparagus rasegous, Canaxis segar, Caryatia maritima, Dioscorea bulbifera, F. scobina, F. virmens, PLANCHONIA CAEYRA, Sterculia quadridita, Stychnos lucida, SKYPSIUS SUBREXIFOLIUS, Terminalia sericea, Vitea glabra. (n=14)</td>
<td>Abrus precatorius, AMPELLOCISSUS ACUTUS, Canaxis segar, Caryatia triloba, Dioscorea transversa, Ichneumon frutescens, Jasminum simplicifolium, Malacia scandens, Pisonia aculeata, Snaila australis, Stephania japonica. (n=14)</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>(d) Herbaceous geophytes, annuals etc.</th>
<th>(e) Grasses</th>
<th>(f) Sedges</th>
<th>(g) Arboreal parasites</th>
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</thead>
<tbody>
<tr>
<td><em>Amorphophallus paeonifolius</em>, <em>Bidens bipinnata</em>, <em>Coleus scutellarioides</em>, <em>Cochlearia aestivalis</em>, <em>D. leonatus</em>, <em>Hyptis suaveolens</em>, <em>Physalis minima</em>, <em>Teca leontopetaloidea</em>, <em>Vernonia cinerea</em>. (n=10)</td>
<td><em>Opismenis bummanni</em>, <em>Panicum trichoides</em>, (n=2)</td>
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<td>-</td>
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<tr>
<td>(n=4)</td>
<td>(n=2)</td>
<td>(n=26)</td>
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<table>
<thead>
<tr>
<th>(c)</th>
<th>(d)</th>
<th>(e)</th>
<th>(f)</th>
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</thead>
<tbody>
<tr>
<td><em>Baccharis</em> sp., <em>Charapaphis koracca</em>, <em>Eriachne triisseta</em>, <em>Setaria apiculata</em>, <em>Themeda arguens</em>. (n=5)</td>
<td><em>Spermacoce</em> spp., <em>Sepriococcus</em> spp., <em>Tephrosia</em> sp., <em>Eriachene triisseta</em>, <em>Schizachyrium fragiile</em>, <em>Themeda arguens</em>. (n=5)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(n=10)</td>
<td>(n=11)</td>
<td>(n=59)</td>
<td>(n=5)</td>
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<table>
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<th>Total Species</th>
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<th>51</th>
<th>66</th>
<th>59</th>
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<tr>
<td>Total MF Species</td>
<td>51</td>
<td>36</td>
<td>26</td>
<td>16</td>
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</tbody>
</table>
(Fig. 9(b)). By contrast however, the North Point transect describes only the bottom part of a gentle, but long, slope on a relatively unweathered, remnant sandstone strike-ridge. At plot D shallow, gravelly, acid, yellowish sandy loams occur over massive laterite blocks at ca. 0.3m depth. At plot C similar soils occur over laterite blocks at ca. 0.8m depth. Between plots B and C a pedological discontinuity occurs. As at Nourlangie this discontinuity is associated with major deposition of colluvium downslope of the laterite-capped, weathered profile. At plots A and B, at the bottom of the slope, slightly acid colluvial sandy loams with major inclusions of lateritic pisoliths occur at depths >1.5m. Given outcropping of basement sandstone between plot A and the floodplain sediments (Fig. 9(a)), however, it is improbable that the colluvial soils at plots A and B are anywhere near as deep as those occurring at Nourlangie.

(6) Granite Hill

The study site described here as Granite Hill is one of a large number of granite tors which outcrop in undulating terrain in the south of the study area (Fig. 1; 13°04'1 S, 132°02'E). The tor protrudes ca. 45m above a weathered surface and comprises rounded, exfoliated corestores, many of which are of huge dimension. A small MVF thicket comprising many deciduous elements is established on the upper slopes, mostly on the southern aspect (Fig. 10(a)). The tor is surrounded by eucalypt-dominated woodland savanna at its base.

The study transect describes a line running south to north over the main summit of the outcrop (Fig. 10(a)). The two stations where sampling of soils and measurements of predawn were undertaken are at positions A and B as shown. The savanna vegetation at the base of the outcrop is dominated by small scattered trees of woodland form to 10m height, over dense, tall grasses (ca. 1.0m). The canopy of the MVF thicket is patchy, reflecting the rooting of individuals in small pockets of soil trapped between boulders. Individual MVF trees range in height from 3 to 12.5m. The distribution of trees (>5cm DBH) and
Granite Hill

SOUTH

(a) Evergreen species
- Acacia auriculiformis
- Antidesma parvifolium
- Celtis philippensis
- Denhamia robusta
- Drypetes hirsuta
- Ficus scabina
- Pouteria sericea

(b) Deciduous species
- Canarium australanum
- Crotalaria arachnoides
- Grewia breviflora
- Saccopetalum braconii
- *Strychnos turkei
- *Virex acuminate

Woodland trees (≥5cm DBH)
(a) Evergreen species
- Buchanania obovata
- *Erythrophleum chlorostachys
- Enterolobium edgeworthianum
- Eucalyptus tereticornis
- *Sarcodes megasperma
**Figure 10**: Granite Hill study transect profile.
vegetation characteristics along the study transect are summarised in Figs. 10(a), (b), (c).

Where present, soils on the outcrop itself comprise skeletal, acid (pH = 5.8, n = 3), sandy loams with high organic matter contents (L.O.I. = 12.7%, n = 6). At sampling station B, colluvial, yellowish, acid (pH = 6.0, n = 6), sandy loam soils of variable, but shallow depth (ca. 0-0.8m) mantle underlying granite. Organic matter content of the surface 0.05m of these soils is relatively low (L.O.I. = 3.2%, n = 6).

(7) Evelyn

The Evelyn study site is situated near the site of the abandoned Evelyn silver mine, approximately 15km north of the Granite Hill site described previously (Fig. 1: 13°41'S, 132°07'E). The study transect runs south to north over a small outcrop of dolerite (Fig. 11(a)). Sampling of soils and measurements of predawn water were undertaken at positions A and B as shown.

The vegetation associated with this transect is described in Figs. 11(a), (b), (c). On the main outcrop, and also on a minor dolerite outcrop at the southern end of the transect, is developed dense MVF thicket vegetation. Canopy height is generally from 5-7m, with occasional individuals up to 11-13m in height. Rooting of trees and shrubs occurs both in surficial cracks and fissures in the rock, as well as at small pockets of soil accumulation. More-or-less open canopy woodland savanna, dominated by eucalypts and ironwoods (Erythrophloeum chlorostachys) over dense, tall (ca. 1m) grasses, occupies shallow, rocky soils lying between the two rock outcrops, and also on the bottom northern slope (Fig. 11(a)).

At A, on the summit of the main outcrop, soils, where present, comprise skeletal, neutral reaction (pH = 6.9, n = 3), red loams with high organic matter contents (L.O.I. = 13.5%, n = 6). At B, under savanna vegetation on the northern slope, soils
Vine-forest trees (> 5cm DBH)
(a) Evergreen species
- Acaea auriculiformis
- Celtis philippensis
- Drypetes australiensis
- Ficus aureomarginata
- Pouteria sericea
(b) Deciduous species
- Angonia reticulata
- Conocarpus australiogynus
- Ficus venosa
- Grewia breviflora
- Premna acuminata
- Saccopetalum brachiatum
- Syzygium lucidum
- Vitis acuminata

Woodland trees (> 5cm DBH)
(a) Evergreen species
- Buchanania ebata
- Erythrophorum chlorostachys
- Eucalyptus petersiana
- Grevillea viridescens
(b) Deciduous species
- Cochlospermum fraseri
- Eucalyptus foehniana

*Exotic  **Facalitarian deciduous species  ***Species subject to a short period of leaflessness
Fig. 11: Evelyn study transect profile.
comprise rock strewn, slightly acid (pH = 6.1; n = 3); red loams, also with high organic matter contents (L.O.I. = 9.9%; n = 6).

3.1.1 Summary

Descriptions of vegetation and substrate conditions at each of seven MVF/savanna boundary study sites are given in Section 3.1. These sites are illustrative of commonly occurring boundary situations between MVF and savanna vegetations on freely draining, seasonally dry substrates in the western Arnhem Land region.

At three sites (Oenpelli Rainforest, Nourlangie, North Point), MVF vegetation occupies the lower position of a topographic sequence (Fig. 12(a)). It is reasonable to assume that such vegetation is developed over water tables which, in the dry season, are relatively closer to the surface than those occurring upslope. Only at the North Point site however, is there any indication that the more-or-less sharp MVF/savanna boundary may be associated with a relatively sharp substrate discontinuity. At one site (Field Island) the sharp transition between MVF and savanna vegetations occurs on level ground, also in the absence of evident substrate discontinuity (Fig. 12(b)). At the three remaining sites (Ngarradj Warde Djobkeng, Granite Hill, Evelyn), MVF vegetation occupies the higher ground (Fig. 12(c)). At each of these sites MVF occurs on skeletal or bare rock substrates, whereas woodland savanna vegetation occupies positions with demonstrably greater soil development. It would appear reasonable to assume that seasonal water relations of the substrates occupied by MVF in these situations maybe relatively less favourable than those at the bases of the respective rock formations. Substrate water relations at each of these seven sites are assessed in the following section.

3.2 Substrate Water Relations

In the absence of sophisticated drilling apparatus to monitor the seasonal flux of water tables at each plot (or sampling
Fig. 12: Schematic summary of vegetation - substrate relationships at the seven study sites (see text for details). Species symbols as for Fig. 2.
station in the case of rock outcrop sites), substrate moisture availability is assessed here indirectly by the measurement of predawn xylem pressure potential (predawn $\psi$) of selected references species (see Methods). As outlined in Ritchie & Hinckley (1975), it is assumed here that predawn $\psi$ provides not only a measure of plant water status under non-transpiring conditions but, as well, is a useful indicator of substrate moisture availability at the integrated root-substrate interface.

As well, at all plots except at the rock outcrop sites, gravimetric soil water contents were determined from samples collected at each sampling of predawn $\psi$ (see Methods). In summarising these results it has been found useful here to lump moisture content determinations made for both the 10-15 cm and 30-35 cm soil levels. The resultant mean value ($n=6$) provides a measure of soil water content in the lower rooting zone of developing germinates and seedlings. The results of studies undertaken at each of the seven study sites are presented separately below.

**Tenpelli Rainforest**

Measurements of predawn $\psi$ and sampling for determinations of soil water content were undertaken on each of four occasions in the 1983 dry season. The first sampling was in May, approximately one month after the last rains of the preceding wet season. Sampling was thereafter at bimonthly intervals with the last sampling in mid-November, just after the first rains of the new wet season. Such rainfall distribution is reflected in the moisture contents of surface soils (10-35 cm) at the four study plots, A-D (Fig. 13(d)).

Measurements of predawn $\psi$ were made on three MVF species (Allosyncarpia ternata, Acacia auracocarpa, Vitex acuminata). Whereas Allosyncarpia is restricted to the closed canopy MVF patch (plots A, B), the other two species occur also in savanna vegetation at plots C and D (see Fig. 3(a)). The results of measurements made on three shrub or small tree individuals of
Fig. 13: Measurements of predawn $V$ and soil moisture content through the 1983 dry season at Oenpelli study site. Notes: (1) Each value given is the mean ± its standard error, where: $n=3$ for measurements of predawn $V$ and; $n=6$ for soil moisture content. (2) Capital letters on graphs refer to plots. (3) Where given, $n =$ new shoot growth and $* =$ plants more or less deciduous. (4) Letters in parentheses after species names refer to: (e) = evergreen species; (d) = deciduous species; (1f) = species given to short period of deciduousness associated with dry season leaf flush; (w) = species with leaves which lose turgor and wilt considerably in the dry season.
each species at each of these plots are given in Figs. 13(a),(b),(c). For Vitex acuminata (Fig. 13(c)) it may be observed that individuals sampled at all plots registered high (ca. -2 to -3 bars) predawn $\psi$ at the end of the 1982/83 wet season (May). By July, individuals at plots B-D were dropping leaves and mean values of predawn $\psi$ were declining (more negative) markedly at plots B and C. By the late dry season (Sept.) values of predawn $\psi$ had declined markedly at all plots, with individuals at plots B and C registering most negative values. In November, after the onset of the first rains of the new wet season, individuals bore new shoot growth and mean predawn $\psi$ had increased (more positive) on all plots. For Acacia aulacocarpa (Fig. 13(b)), an evergreen species, predawn $\psi$ declines similarly through the dry season, with only individuals at plot B registering increased predawn $\psi$ following rain. As expressed also by Vitex acuminata, dry season substrate moisture conditions at plot D are indicated as being relatively favourable whereas those at plot C are indicated as being least favourable. For Allosyncarpia ternata (Fig. 13(a)), another evergreen species, the seasonal decline of predawn $\psi$ is similar on both plots A and B.

Collectively, these results provide evidence for a gradient of declining seasonal substrate moisture conditions from plot A to C. However, as indicated both by soil moisture determinations (Fig. 13(d)) and measurements of predawn $\psi$, the substrate moisture status of plot D is relatively favourable with respect to plots B and C. This latter result is thus in accordance with the observation that plot D occupies a similar topographic position as that occupied by plot A (see Fig. 3(a)).

(2) Ngarradj Warde Djobkeng

This site, comprising two plots, was sampled on five occasions from April through November. The first four samplings were associated with a drying soil whereas the final sampling evidently occurred after rain (Fig. 14(d)).

Results of measurements of predawn $\psi$ conducted on three
Fig. 14: Measurements of predawn $\Psi$ and soil moisture content through the 1983 dry season at Ngarradj Warde Djobkeng. Notes as for Fig. 13.

Fig. 15: Measurements of predawn $\Psi$ and soil moisture content through the 1983 dry season at the Field Island study site. Notes as for Fig. 13.
species (Acacia aulacocarpa, Gardenia sp. JRS 815, Croton bynesii) are given in Figs. 14(a),(b),(c). Through the course of the dry season measurements of predawn \( \psi \) on individuals of Acacia aulacocarpa (Fig. 14(a)) were consistently more negative at plot A under MVF, than at plot B in savanna vegetation. For the other two species, however, values of predawn \( \psi \) were relatively similar at both plots (Figs. 14(b),(c)). These latter results are mirrored also in the water contents of surface soils (Fig. 14(d)).

Collectively, these results suggest that seasonal availability of substrate moisture is similar at both plots. However, for individuals of one species (Acacia aulacocarpa) at least, substrate moisture conditions under savanna vegetation (plot B) are evidently more favourable than those under MVF (plot A).

(3) Field Island

This site, comprising three plots, was sampled on only two occasions due to logistic problems. The first sampling was undertaken at the end of June, approximately three months after the last of the preceding rains. The second sampling was undertaken in October, approximately one month before the onset of the succeeding wet season. Sampling on both occasions was undertaken under drying soil conditions (Fig. 15(d)).

Measurements of predawn \( \psi \) were undertaken on three species. Only one species was associated with all three plots (Erythrophloeum chlorostachys; Fig. 15(a)). The other two species, Micromelum minutum (Fig. 15(b)) and Trrema aspera (Fig. 15(c)), both MVF shrub species, occurred at plots A and B, and plots B and C, respectively. The results of predawn \( \psi \) measurements (Figs. 15(a),(b),(c)) provide no evidence for a gradient in substrate moisture conditions associated with the vegetation gradient from MVF (plot A) to savanna (plot C). Thus, while measurements of predawn \( \psi \) in the late dry season (October) are consistently slightly lower on plot C (Figs. 15(a),(c)).
species occurring at plot B register slightly more positive mean predawn $\Psi$ than those at plot A (Figs. 15(a), (b)). The moisture contents of surface soils are likewise similar (Fig. 15(d)).

(4) Nourlangie

This site, comprising four plots, was sampled on four occasions. The first three samplings were undertaken under drying soil conditions, and the fourth sampling, in late November, after substantial rains (Fig. 16(d)).

The results of measurements of predawn $\Psi$ are given for three species (Acacia aulacocarpa, Eucalyptus miniata, Vitex glabrata) in Figs. 16(a), (b), (c). Whereas Acacia aulacocarpa occurs at all four plots, Vitex glabrata occurs at plots A-C and Eucalyptus miniata at plots B-D. For Acacia aulacocarpa (Fig. 16(a)), the seasonal decline of predawn $\Psi$ is similar at plots A, B and C. At plot D, however, late dry season values of predawn $\Psi$ are considerably more negative than for the other three plots which occupy lower positions on the topographic gradient (see Fig. 8(a)). While not occurring at plot A, similar trends are evident in values of predawn $\Psi$ for Eucalyptus miniata coppice regrowth (Fig. 16(b)). The results of predawn $\Psi$ for Vitex glabrata however, provide an apparent anomaly (Fig. 16(c)). Thus, while late dry season (late Sept.) values of predawn $\Psi$ at plot C are more negative than those at plot B, values at plot A are substantially lower again by a factor of two. As indicated also in Fig. 16(c), Vitex glabrata individuals at plot A were markedly deciduous by late July whereas individuals at plots B and C were not recorded as being deciduous until the third sampling in late September. Presumably, these observations reflect either that the root systems of Vitex glabrata individuals at plot A were less well developed than those at plots B and C, and/or that there was greater competition for substrate moisture from mostly evergreen species occurring at plot A (Fig. 8(a)). Given that surface soils were consistently more moist at plot A than at other plots (Fig. 16(d)), the former of these two suggestions is the more likely explanation.
Fig. 16: Measurements of predawn ψ and soil moisture content through the 1983 dry season at Nourlangie. Notes as for Fig. 13.

Fig. 17: Measurements of predawn ψ and soil moisture content through the 1983 dry season at North Point. Notes as for Fig. 13. Eucalyptus clavigera is a facultatively deciduous species which, at North Point, was evergreen through the 1983 dry season.
Collectively, these results indicate that dry season substrate moisture conditions at plot D are substantially harsher than at the other three plots. There is little indication, however, that the sharp MVF/savanna discontinuity (at plot B) is associated with an equally sharp change in substrate moisture conditions occurring between plots B and C.

(5) North Point

This site, comprising four plots, was sampled likewise on four occasions. The first three samplings were undertaken under drying soil conditions, and the fourth sampling (late November) after substantial rain (Fig. 17(c)).

Sampling for predawn $\Psi$ was undertaken on three species (Eucalyptus clavigera, Erythrophloeum chlorostachys, Strychnos lucida). Only one species (E. clavigera) was sampled at all four plots. Erythrophloeum was sampled at plots B-D, and Strychnos at plots A-C. Results for E. clavigera (Fig. 17(a)) show an initial steep decline in predawn $\Psi$ (June-late July) at the savanna plots (C, D), with a delayed response (July-October) at plots supporting MVF (plots A, B). While not sampled at plot A, Erythrophloeum responded similarly (Fig. 17(b)). Moreover, for both these species, dry season values of predawn $\Psi$ are most negative at plots C and D.

Strychnos, however, responded quite differently to drying substrate conditions (Fig. 17(c)). Firstly, it may be noted that whereas the seasonal course of predawn $\Psi$ ranged between ca. -2 to -13 bars in both E. clavigera and Erythrophloeum, mean predawn $\Psi$ for Strychnos ranged between -2 and -50 bars. The implication here is that Strychnos would appear to have a less well developed, probably shallower root system than that typically possessed by E. clavigera and Erythrophloeum. While not ascertained, differential shallow rooting by sampled Strychnos individuals would certainly help account for the steep, differential decline of predawn $\Psi$ recorded at plots A-C between...
May and July. Secondly, as may be observed in Fig. 17(c), mean predawn $\Psi$ exhibits a positive increase at all plots in the late dry season (October), and substantially so at plots B and C. Although Strychnos individuals were deciduous at this time, new shoot development was observed on some. Such substantial improvement in plant water status would appear improbable without access to previously untapped reserves of substrate moisture through initiation of root growth, especially at depth.

While interpretation of predawn $\Psi$ measurements for Strychnos remains problematic, complementary results for E. clavigera and Erythrophloeum indicate that substrate moisture conditions at plots supporting MVF (plots A, B) are relatively favourable with respect to plots supporting savanna vegetation (plots C, D). Moreover, given the steep decline of predawn $\Psi$ for both species early in the dry season at plots C and D, it may be inferred that the change from closed canopy to relatively open canopied vegetation between plots B and C is associated with a relatively steep gradient in substrate moisture conditions. Similar, although slight, trends are expressed also in the moisture contents of surface soils (Fig. 17(d)).

(6) Granite Hill

Measurements of predawn $\Psi$ were undertaken at the summit of the outcrop (A), supporting a mixture of MVF and woodland species, and at a position at the base of the outcrop (B) in surrounding savanna vegetation (see Fig. 10(a)). Sampling was undertaken on four occasions; at three times through the developing dry season, and again at the onset of the succeeding wet season in early December. Measurements were made on a number of species, only two of which (Erythrophloeum chlorostachys, Eucalyptus tetrodonta) occurred at both A and B. As expressed by shrubby individuals of both these species (Figs. 18(a), (b)), substrate water conditions at the base of the outcrop (B) are substantially more favourable than on the rock outcrop itself.

In Fig. 18(a) it may be observed that, as for Strychnos at
Fig. 18: Measurements of predawn water potential through the 1983 dry season Granite Hill. Notes as for Fig. 13.
the North Point site, mean predawn $\psi$ of Erythrophloeum at both A and B shows a marked positive increase in the late dry season (October), following an earlier decline (early June-late July). This increase in predawn $\psi$ was associated with extensive new shoot development. Presumably, this improvement in plant water status is likewise attributable to initiation of (increased?) rooting activity, especially at depth.

(7) Evelyn

As at the preceding site, sampling for predawn $\psi$ was conducted on four occasions, at sampling stations at the summit of the outcrop (A), supporting MVF, and at the base of the outcrop (B), in woodland savanna vegetation (see Fig. 11(a)). Sampling was conducted on a number of species, only two of which (Erythrophloeum chlorostachys, Saccopetalum brahei) occurred at both A and B. As at Granite Hill, the results of these measurements (Figs. 19(a),(b)) both support the contention that substrate moisture conditions at the top of the outcrop are harsher than those at its base.

As at Granite Hill, mean predawn $\psi$ for Erythrophloeum (Fig. 19(a)) again shows an evident, if slight, positive increase in the late dry season (Sept.), at least at A. For Saccopetalum brahei (Fig. 19(b)), the magnitude of the decline of predawn $\psi$ in the late dry season, ca. -70 bars at A, suggests that this is a relatively shallow rooted species.

3.2.1 Summary

The availability of substrate moisture was assessed at all sampling plots through the 1983 dry season by the measurement of predawn $\psi$ of selected reference species. As well, at five sites (excluding rock outcrops), surface moisture availability was assessed by determination of gravimetric soil moisture content at 10-35cm depth.

Collectively, the results of these studies confirm the
Fig. 19: Measurements of predawn \( \Psi \) through the 1983 dry season at Field Island. Notes as for Fig. 13.
expectation (3.1.1) that, under freely draining conditions, substrate moisture relations are generally more favourable for plant growth at the bottom of a topographic sequence. At three sites (Oenpelli, Nourlangie, North Point), where MVF gives way to savanna up gentle, freely draining slopes, substrate moisture availability is greater at plots supporting MVF than at plots supporting savanna. At North Point, the sharp MVF/savanna boundary possibly is associated with a distinct substrate moisture-pedological discontinuity. At Oenpelli and Nourlangie sites; however, the MVF/savanna boundary occurs in the absence of revealed discontinuity. At Field Island, on essentially level terrain, and at Ngarradji Warde Djobkeng, at the mouth of an escarpment gorge, substrate moisture relations are shown to be similar at plots supporting MVF and savanna vegetations. At these sites, therefore, the MVF/savanna boundary is not relatable to substrate moisture condition. At Granite Hill and Evelyn, the two rock outcrop sites, substrate moisture conditions are demonstrably harsher under MVF at the summits of the respective outcrops, than under savanna vegetations at their bases. It is thus concluded that favourable substrate moisture conditions are not prerequisite for development of MVF vegetation. Indeed, as exemplified by the latter two sites, such vegetation may occupy even the most excessively drained substrates.

While this conclusion is not surprising given that many MVF species are deciduous or geophytic types with self-evident capacities for regulating seasonal water usage, seasonal aridity is nonetheless likely to affect individuals differentially through the course of their development, especially while root systems are only surficially developed. For example, estimates of soil matric potential are given in Fig. 20 for surficial, loamy sands at Oenpelli plots B and C. These estimates, using moisture content data given in Fig. 13(d), are derived from a power function model describing the drying soil moisture characteristic of apedal loamy sands (Williams et al. 1983). Figure 20 illustrates that, for developing seedlings, moisture in the surfaces of freely-draining soils often is practically unavailable for substantial periods of
Fig. 20: Estimation of soil matric potential for surficial, apedal loamy sands through the 1983 dry season at the Oenpelli study site, plots B and C.

Notes: Gravimetric soil moisture contents (% or g.g⁻¹) are those as given in Fig. 13(d). To calculate soil matric potential these were converted to volumetric moisture contents (cm³ cm⁻³) by multiplying by the bulk density of apedal sands (ca. 1.6 g.cm⁻³) as given in Stace et al. (1968). These values were then substituted in a power function model describing the drying soil moisture characteristic of apedal loamy sands as given in Williams et al. (1983).
the annual dry season.

3.3 Soil Fertility Relations

Soil fertility is assessed here by the measurement of soil concentrations of five nutrient elements (N, P, K, Ca, Mg) essential for plant growth (e.g. Clarkson & Hanson 1980). Results of nutrient analyses undertaken on soil samples collected from each plot (see Methods) are given in full in Appendix 1 and summarised in Fig. 41. Nutrient determinations are given for two soil levels; 0-15cm and, where applicable, 30-55cm. Results for the 0-15cm level combine determinations made for each of three 0-5cm and 10-15cm replicate samples, giving a sample size of 6. For rock outcrop sites, however, results are given only for 0-5cm samples (n=6). Similarly, results for the 30-55cm level combine determinations made for each of three 30-35cm and 50-55cm replicate samples. For plot D at both Nourlangie and North Point study sites, however, where augering below 35cm was not possible, only results for samples from 30-35cm (n=6) are given.

The relative soil fertilities of plots at each site are assessed here by calculation of the relative soil fertility index (RSFI). This index is calculated as follows. For each soil level (i.e. 0-15cm, 30-55cm) at respective sites, plots are ranked by summing their individual rankings with respect to each of the five nutrients. At sites comprising four plots, for each nutrient the plot with the largest mean is scored a value of 4, with other plots ranked in decreasing order as either 3, 2 or 1. For sites comprising either three or two plots, for each nutrient plots are ranked similarly from 3 to 1, or as 2 and 1, respectively. Where the mean nutrient value is equivalent at two or more plots, plots are ascribed an equal, mean rank value. To calculate the index the individual nutrient scores are summed for each plot, and then standardised by dividing by the maximum sum attainable. For sites comprising four plots this maximum value is 20 (i.e. 4 plots x 5 nutrients). For sites comprising either 3 or 2 plots, maximum values are 15 and 10, respectively. For each site, calculated
Fig. 21: Soil nutrient concentrations at the seven study sites. All data derived from Appendix 1. Soil nutrient concentrations are given in all cases for the 0-15cm level. Where given, hatched boxes indicate nutrient concentrations for the 30-55cm level; in no case does the concentration of nutrients at the lower depth exceed that of the surface soils. Note that scales of K and Ca vary between sites.
values of the RSFI for respective plots are given in Table 6.

As summarised in Table 6, it may be observed that soils at plots supporting MVF are generally, often markedly (Fig. 21), more fertile than those supporting savanna vegetation. In the two instances where surface or subsurface soils supporting savanna vegetation are ranked as being more fertile (i.e. Ngarradj Warde Djobkeng plot B [Table 6(a)]; North Point plot C [Table 6(b)]), concentrations of nutrients are relatively similar in value to those at plots supporting MVF (Fig. 21). Similar observations, that soils under closed forest vegetation generally are more fertile than those under adjacent savanna vegetation are widely reported in the literature (e.g. Ahn 1970; Aldrick 1976a; Aekew et al. 1970a,b; Aubreville 1966; Blydenstein 1967,1968; Cole 1960,1982; Eiten 1972,1975,1978,1982; Eiten & Goodland 1979; Goodland & Pollard 1973; Hills 1969; Jones,1963; Kellman 1979; Markham & Babbedge 1979; Montgomery & Askew 1983; Nye & Berthaux 1957; Nye & Greenland 1961; Ratter et al. 1973; Swaine et al. 1976; Tinley 1982). However, as noted also by many of the above authors, the greater fertility of closed forest soils is often derivative through the relatively greater accumulation of nutrients in uppermost, organic horizons as a product of the vegetation itself, as against closed forest soils necessarily being inherently more fertile (see Montgomery & Askew 1983 for a recent discussion). Similarly, that the relative fertilities of MVF and adjacent savanna soils observed in this study are likely to be essentially expressions of the vegetation they support, is indicated by various lines of evidence.

Firstly, while inherent nutrient gradients doubtlessly occur at various of the study sites (e.g. colluvial transport on slopes), at none is there major lithological discontinuity which might account for often substantial differences in the measured fertilities of MVF and savanna soils (e.g. Granite Hill, Fig. 21). Thus, of the seven sites, two describe transects on leached skeletal sands (Ngarradj) or sandsheets (Oenpelli), three describe transects on deeply weathered, leached, lateritic substrates
Table 6: Relative Soil Fertility Index (see text) of sample plots at each site
* denotes occurrence of MVF vegetation.

<table>
<thead>
<tr>
<th>Site</th>
<th>(a) 0-15cm depth</th>
<th>(b) 30-55cm depth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>(1) Oenpelli Rainforest</td>
<td>1.00*</td>
<td>0.68*</td>
</tr>
<tr>
<td>(2) Ngarradj Warde Djobkeng</td>
<td>0.70*</td>
<td>0.80</td>
</tr>
<tr>
<td>(3) Field Island</td>
<td>0.97*</td>
<td>0.63*</td>
</tr>
<tr>
<td>(4) Nourlangie</td>
<td>0.90*</td>
<td>0.85*</td>
</tr>
<tr>
<td>(5) North Point</td>
<td>0.80*</td>
<td>0.78*</td>
</tr>
<tr>
<td>(6) Granite Hill</td>
<td>1.00*</td>
<td>0.50</td>
</tr>
<tr>
<td>(7) Evelyn</td>
<td>0.90*</td>
<td>0.60</td>
</tr>
</tbody>
</table>
(Field Island, Nourlangie, North Point), and two occur on outcroppings of acid igneous (Granite Hill) or basic igneous (Evelyn) rocks. Thus, while the inherent fertilities of soils between different sites may be anticipated to vary considerably (e.g. soils derived from dolerite vs. leached, deeply weathered soils, Fig. 21), at none is it likely that soils supporting MVF are inherently more fertile than those supporting savanna. Moreover, whereas colluvial enrichment may favour MVF at three study sites (Oenpelli, Nourlangie, North Point), at three other sites (Ngarradj, Granite Hill, Evelyn) colluvial transport is presumably to the advantage of extant savanna.

Secondly, as is indicated in Fig. 21 for four sites where nutrient determinations were undertaken at both surface (0-15cm) and subsurface (0-35cm) levels, nutrient concentrations are mostly much greater in surface soils or, occasionally, equivalent. This general concentration of nutrients in surface soils is likely to be associated with the input and accumulation of organic matter, as suggested by significant correlations between Loss on Ignition (as an estimate of organic matter) and nutrients at plots at each of the study sites (Table 7). It is likely, therefore, that differences in the soil fertilities of plots at each site express substantially the differential pedological influences of the vegetations (and associated biota) they support. Such differential influences are likely to be various: for example, greater litter production in MVF, especially at plots comprising large numbers of deciduous individuals; disproportionately greater consumption of organic matter in savanna soils by termites; more rapid mineralisation and associated leaching in savanna soils due to recurrent fires.

Further, given the capacity for MVF vegetation to overcome possible nutrient deficiency at patch margins simply through organic input, the notion of critical nutrient limitation at the MVF/savanna boundary is theoretically improbable. As may be observed in Fig. 21, the soil nutrient status of four sites is particularly low (i.e. Oenpelli, Ngarradj, Field Island,
Table 7: Correlations between Loss on Ignition and Soil Nutrients at the seven study sites. Values given are those of the correlation coefficient (r): *=p<0.1; **=p<0.01; ***=p<0.001.

<table>
<thead>
<tr>
<th>Site</th>
<th>Plot</th>
<th>No. of Samples (n)</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Oenpelli Rainforest</td>
<td>1A</td>
<td>12</td>
<td>0.9359**</td>
<td>0.7957**</td>
<td>0.6345*</td>
<td>0.6030*</td>
<td>0.4851</td>
</tr>
<tr>
<td></td>
<td>1B</td>
<td>12</td>
<td>0.9714***</td>
<td>0.8466***</td>
<td>0.8362***</td>
<td>0.8463***</td>
<td>0.8675***</td>
</tr>
<tr>
<td></td>
<td>1C</td>
<td>12</td>
<td>0.9063**</td>
<td>-0.4314</td>
<td>0.6295**</td>
<td>0.7645**</td>
<td>0.6079**</td>
</tr>
<tr>
<td></td>
<td>1D</td>
<td>12</td>
<td>0.9605***</td>
<td>0.7487**</td>
<td>0.9039**</td>
<td>0.9386***</td>
<td>0.8045**</td>
</tr>
<tr>
<td>(2) Ngarradj Warde Djobkeng</td>
<td>2A,B</td>
<td>12</td>
<td>0.9496***</td>
<td>0.0327</td>
<td>0.8945***</td>
<td>0.3082</td>
<td>0.4774</td>
</tr>
<tr>
<td>(3) Field Island</td>
<td>1A</td>
<td>12</td>
<td>0.9318***</td>
<td>0.9641***</td>
<td>0.8929***</td>
<td>0.9098***</td>
<td>0.9514***</td>
</tr>
<tr>
<td></td>
<td>1B</td>
<td>12</td>
<td>0.9418***</td>
<td>0.8983***</td>
<td>0.9717***</td>
<td>0.7884**</td>
<td>0.9825***</td>
</tr>
<tr>
<td></td>
<td>1C</td>
<td>12</td>
<td>0.9234***</td>
<td>0.8713***</td>
<td>0.8490***</td>
<td>0.9687***</td>
<td>0.8881***</td>
</tr>
<tr>
<td>(4) Nourlangie</td>
<td>1A</td>
<td>12</td>
<td>0.9721***</td>
<td>0.9047***</td>
<td>0.9669***</td>
<td>0.8364***</td>
<td>0.8614***</td>
</tr>
<tr>
<td></td>
<td>1B</td>
<td>12</td>
<td>0.9456***</td>
<td>0.9124***</td>
<td>0.8757***</td>
<td>0.7623**</td>
<td>0.8205**</td>
</tr>
<tr>
<td></td>
<td>1C</td>
<td>12</td>
<td>0.8305**</td>
<td>0.7266</td>
<td>0.6257**</td>
<td>0.9042**</td>
<td>0.8856**</td>
</tr>
<tr>
<td></td>
<td>1D</td>
<td>12</td>
<td>0.9780***</td>
<td>0.5504*</td>
<td>0.9608**</td>
<td>0.9667**</td>
<td>0.9571**</td>
</tr>
<tr>
<td>(5) North Point</td>
<td>1A</td>
<td>12</td>
<td>0.9536***</td>
<td>0.9487***</td>
<td>0.5164*</td>
<td>0.7619**</td>
<td>0.4956</td>
</tr>
<tr>
<td></td>
<td>1B</td>
<td>12</td>
<td>0.9818***</td>
<td>0.9891***</td>
<td>0.9439***</td>
<td>0.9911***</td>
<td>0.9697***</td>
</tr>
<tr>
<td></td>
<td>1C</td>
<td>12</td>
<td>0.9160***</td>
<td>0.8680***</td>
<td>0.3209</td>
<td>0.9832***</td>
<td>0.9781***</td>
</tr>
<tr>
<td></td>
<td>1D</td>
<td>12</td>
<td>0.9402***</td>
<td>0.4100</td>
<td>0.8446***</td>
<td>0.8791***</td>
<td>0.7651**</td>
</tr>
<tr>
<td>(6) Granite Hill</td>
<td>2A,B</td>
<td>12</td>
<td>0.9602***</td>
<td>0.9761***</td>
<td>0.9191***</td>
<td>0.6939*</td>
<td>0.9305**</td>
</tr>
<tr>
<td>(7) Evelyn</td>
<td>2A,B</td>
<td>12</td>
<td>0.9133**</td>
<td>0.9253***</td>
<td>-0.1102</td>
<td>0.6705*</td>
<td>0.5992*</td>
</tr>
</tbody>
</table>

1 Values of r based on correlations between values of L.O.I. and nutrient concentrations for each of 12 surface and subsurface soil samples from each plot.
2 Values of r based on correlations between values of L.O.I. and nutrient concentrations for each of 12 surface samples only, from two adjacent plots.
Nourlangie), especially when surficial organic influences are ignored. Only soils at Evelyn are indicated as being inherently eutrophic; these being derived from basic igneous dolerite.
4. DISCUSSION

Much of the terrain of western Arnhem Land is freely or excessively drained, and comprises mostly oligotrophic soils/substrates derived from sandstone and laterised erosion products (Aldrick 1976a, b; Hooper 1969). In land surveys covering an area somewhat larger than, but including much of this region, figures provided by Story (1969, 1976) indicate that, of a total area of 23,400 km\(^2\) surveyed, at least 14,000 km\(^2\) (ca. 60%) is covered by vegetation occupying such freely-draining, nutrient-depleted substrates (Table 8). Occurring also on such substrates, the total area of vegetation types termed here as MVF is given by Story as being 520 km\(^2\), or 2.2% (Table 8). The question addressed here is simply: are substrate conditions over at least 58% of western Arnhem Land so harsh as to prohibit development of MVF vegetation?

In preceding sections, this paper has examined vegetation-substrate relationships at each of seven MVF/savanna boundaries. These sites were selected for study specifically on the grounds that: 1. upon initial inspection, sharp changes in vegetation did not appear simply relatable to substrate conditions, and; 2. that these situations; while not exhaustive, are illustrative of a variety of common types of boundary between MVF and savanna vegetations on freely draining, seasonally dry substrates, in the western Arnhem Land region.

Descriptions of vegetations and substrates at these sites are given in 3.1. Two sites (Oenpelli, Ngarradj) illustrate sharp MVF/savanna boundaries on freely draining substrates derived from sandstone. Three sites (Field Island, Nourlangie, North Point) illustrate vegetation change on weathered, lateritic substrates. The remaining two sites (Granite Hill, Evelyn) illustrate vegetation change at igneous rock outcrops.

Substrate water relations at each of these sites are examined in 3.2. Collectively, the results of measurements of predawn \(\psi\)
Table 8: Vegetation Types on freely draining landforms in the western Arnhem Land region, following Story (1969, 1976).

<table>
<thead>
<tr>
<th>Vegetation Types on freely draining substrates (Story 1969, 1976)</th>
<th>Area (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Story(1969)</td>
</tr>
<tr>
<td>Tall open forest</td>
<td>1410</td>
</tr>
<tr>
<td>Woodland</td>
<td>2875</td>
</tr>
<tr>
<td>Stunted woodland</td>
<td>495</td>
</tr>
<tr>
<td>Mixed open forest</td>
<td></td>
</tr>
<tr>
<td>Sandstone woodland</td>
<td></td>
</tr>
<tr>
<td>Sandstone scrub</td>
<td></td>
</tr>
<tr>
<td>MVF: (i) Rainforest, semideciduous forest</td>
<td>&lt;10</td>
</tr>
<tr>
<td>(ii) Allosyncarpia forest</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>4790</td>
</tr>
<tr>
<td>Total area surveyed</td>
<td>9600</td>
</tr>
</tbody>
</table>

Area occupied by vegetation types on freely draining substrates

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>49.9%</td>
<td>68.1%</td>
<td>60.6%</td>
</tr>
</tbody>
</table>

Area occupied by MVF

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;0.1%</td>
<td>3.7%</td>
<td>2.2%</td>
</tr>
</tbody>
</table>
and soil moisture content through the 1983 dry season confirm the expectation that, under freely draining conditions, moisture availability is generally greater at the bottom of slopes. Thus, at three sites where MVF gives way to savanna upslope, moisture conditions were found to be relatively favourable under MVF. At two sites substrate conditions were found to be similar under MVF and savanna vegetations. At the two rock outcrop sites, moisture relations were found to be demonstrably harsher under MVF at their summits, than under savanna vegetations at their bases. As exemplified by the last two situations moreover, MVF vegetation can occupy the most excessively drained substrates.

Soil fertility relations are considered in 3.3. Collectively, the results of determinations of soil concentrations of N, P, K, Ca, Mg show that, at six sites, soils developed under MVF are relatively, often markedly, more fertile than those developed under adjacent savanna. At the seventh site, nutrient concentrations were similar in soils under both MVF and savanna. Various evidence indicates that differences in the soil fertilities of plots at each site are likely to be derived substantially as products of the respective vegetations they support, as against their reflecting significant inherent fertility differences.

The results of these studies indicate that neither seasonal substrate moisture availability nor nutrient availability are, by themselves, critically limiting the development of MVF at the study sites. Such a conclusion is amplified by the occurrence of MVF woody individuals at all savanna plots (e.g. Figs. 4, 5, 10, 11), including those comprising seasonally arid, oligotrophic soils. Thus, on the basis of the situations examined here, and observations generally concerning the occurrence of MVF on a variety of extenuating substrates (e.g. elevated, bare sandstone pavements; skeletal soils over concretionary laterites), it is quite conceivable that MVF could occupy the full range of freely draining substrates in the western Arnhem Land region. That, it does not however, illustrates the significance of other controls.
through time:

In northern Australian studies where it has been recognised that MVF may occur widely on substrates occupied by savanna vegetations, fire has been considered the foremost constraining factor on MVF patch margins (e.g. Beard et al. 1984; Clayton-Greene & Beard 1985; Kikkawa et al. 1981; Langcamp et al. 1981; Russell-Smith 1986; Stocker 1966; Stocker & Mott 1981; Webb 1968). As indicated in the introduction, the destructive influence of fire is often all too evident at the present time (Fig. 22).

The results of studies undertaken here suggest likewise, that the locations of MVF patch margins at each of the study sites are not interpretable without recourse to the agency of fire. For example, at three sites (Narradj, Granite Hill, Evowyn) MVF occupies elevated, rocky substrates that would appear to confer no advantage (3.2, 3.3) other than the degree of fire protection they afford. In these situations fire protection is essentially a consequence of the unsuitability of rock substrates for grass establishment, thereby effectively excluding the encroachment of grass-borne savanna fires. At the other four sites MVF patch margins are openly exposed to fire influence, and, with the possible exception of the North Point site, occur in the absence of revealed substrate discontinuity (3.2, 3.3). As indicated previously MVF individuals also occur widely, if sparsely, in adjacent savanna vegetations at each of these sites; such individuals comprising mostly multishooted shrub and vine coppice (e.g. Fig. 5, Tables 1-5). The capacity for many MVF species, once established, to resprout after even frequent burning has been noted elsewhere by Kahn & Lawrie (1984) and Russell-Smith & Dunlop (1984). The seral status of these fringing savannas is thus indicative that fires have occurred with sufficient regularity, at least in the recent past, such that succession towards MVF has been arrested at an incipient stage of development. It indicates also that edaphic conditions, while adequate for the persistence of MVF individuals, are inadequate for effecting their escape.
Fig. 22: The effect of a late dry season fire on a MVF patch boundary at Couramoul, Kakadu National Park. Photo taken November 1981.
within the periodicity of the fire regime. As Kellman (1984:159) observes for Neotropical savannas: "any condition slowing the rate of tree canopy establishment ... will make the vegetation more fire prone".

**MVF and the current fire regime**

The current fire regime of the western Arnhem Land region is characterised by frequent (annual), extensive, and predominantly hot burning, late dry season fires (Day, 1986; see Russell-Smith, 1986: Table 2). Under such a regime the margins of many MVF patches are eroding actively at the present time, especially where topographically unprotected (Table 9). Current fire impact is also threatening MVF patches in other, mostly occupied regions of northern Australia (e.g. mainland, northern Western Australia [J.S. Beard personal communication, 1986]; Cape York Peninsula [Lavarack & Godwin, 1984]).

The destructiveness of such a fire regime to woody vegetation in savanna biomes is demonstrated in a number of experimental fire studies. In a western Arnhem Land study late dry season burning was found to have the following effects on eucalypt-dominated savanna vegetation after five years:

"Annual fires, burning late in the dry season, caused severe damage to the vegetation, and suppressed the growth and development of tall open forest and woodland communities ... Repeated hot fires have prevented plants of many species from attaining their normal life-forms. They have restricted growth by confining many tree and shrub species to a multiple-stemmed coppice growth habit and have promoted the formation of plant clones. Hot fires tend to promote tall annual grasses which in turn provide for hot fires in each succeeding year", (Hoare et al., 1980).

Such findings mirror those reported for similar quantitative African savanna fire-plot studies (e.g. Afolayan, 1978; Charter & Keay, 1960; Hopkins, 1965; Ramsay & Rose Innes, 1963; Trapnell, 1959).
Table 9: Impact of current fire regime on MVF boundaries in the western Arnhem Land region. All data from Russell-Smith (1984: Tables 2a,b).

<table>
<thead>
<tr>
<th>MVF Habitat Types</th>
<th>No. sites</th>
<th>No. sites where MVF patch boundaries are visibly retreating at the present time under fire impact</th>
</tr>
</thead>
<tbody>
<tr>
<td>Escarpment and plateau</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a) Topographically protected habitats</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>(b) Topographically unprotected habitats</td>
<td>58</td>
<td>27 (47%)</td>
</tr>
<tr>
<td>Lowlands</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(c) Topographically protected habitats (rock outcrops)</td>
<td>5</td>
<td>3 (60%)</td>
</tr>
<tr>
<td>(d) Topographically unprotected habitats</td>
<td>33</td>
<td>15 (45%)</td>
</tr>
<tr>
<td></td>
<td>127</td>
<td>45 (35%)</td>
</tr>
</tbody>
</table>
Clearly, if conservation of relatively fire sensitive communities in fire-prone monsoonal northern Australia is an objective, regional fire regimes will require modification.

Further, the collective results of these fire plot studies indicate that, with strategic burning, such an objective is rapidly achievable. The capacity for effecting vegetation change through the manipulation of fire is well illustrated by Rose Innes (1971:159) who, in summarising the results of west African fire-plot studies says:

"It is accepted (a) that fire retards the natural development of vegetation towards a forest or woodland type 'climax' and may hold it more or less permanently in a tree savanna stage; (b) that fierce hot fires occurring late in the dry season are particularly destructive of woody elements, especially seedlings and suckers; (c) that moderate 'cool' fires occurring early in the dry season are less destructive and will allow slow development of woody vegetation towards a woodland type climax; (d) that fire is responsible not only for shaping the physiognomic structure of plant communities but exerts a powerful selective influence on floristic composition, with fire-tolerant species being encouraged and fire-tender one eliminated; and (e) that fire, properly used, is a powerful tool for shaping vegetation towards chosen objectives."

The contemporary fire regime of the western Arnhem Land region is markedly different to that of 100 or so years ago under traditional Aboriginal occupancy. Burning of country effectively commenced then at the beginning of the dry season, as soon as grasses were sufficiently cured to carry fire, by people moving in family bands through their territories (cf. Chaloupka & Giuliani 1984; Jones 1975, 1980; Lewis 1982; Thomson 1949a,b). Such burning effectively eliminated (or at least reduced) the potential for lightning or human lit, extensive late dry season fires such as occur at the present day (Haynes 1970, 1985). Indeed, in the western Arnhem Land region people deployed fires in the late dry
season, 'gurrung', with considerable circumspection given their potentially catastrophic effect on food resources (cf. Chaloupka & Giuliani 1984; Russell-Smith 1984). Such a burning regime was demonstrably more conservative of woody vegetation than that now extant in many areas of northern Australia.
5. ACKNOWLEDGEMENTS

This study was undertaken with the generous support of the Australian National Parks and Wildlife Service, Canberra; the Kakadu National Park, Northern Territory; the Departments of Prehistory (Research School of Pacific Studies) and Geography (The Faculties), ANU, Canberra; the North Australia Research Unit, Darwin; a Commonwealth Post-graduate Research Scholarship; and Meg Russell-Smith. Taxonomic assistance was provided by Clyde Dunlop (Conservation Commission of the Northern Territory, Darwin) and Lyn Craven (Australian National Herbarium, CSIRO, Canberra). The pressure bomb apparatus used in this study, and advice on its usage, was provided by Peter Cochrane (Dept. Environmental Biology, Research School of Biological Sciences, ANU). Assistance in the field was provided by officers of Kakadu National Park, Diane Lucas, Rob Muller and Helen Thomson. Assistance with soil analyses was provided by Patricia Abonyi, Frank Darlington, Terry Johnson (Dept. Forestry, ANU), Jim Bailey (Division of Soils, CSIRO, Canberra), and John Williams (Division of Soils, CSIRO, Townsville). Geoff Hope (Dept. Geography, ANU) provided constructive criticism of the manuscript. Val Lyon (Dept. Geography, ANU) prepared the Figures, and the manuscript was typed by Jan Watson (Computext, Canberra). Thank you.
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Appendix 1: Soil nutrient determinations at the seven study sites
Each value given is the mean of 6 samples ± its standard error.

<table>
<thead>
<tr>
<th>Site</th>
<th>Plot</th>
<th>Sample depth (cm)</th>
<th>N (%)</th>
<th>P (%)</th>
<th>K (p.p.m.)</th>
<th>Ca (p.p.m.)</th>
<th>Mg (p.p.m.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Oenpelli Rainforest</td>
<td>A (0-15)</td>
<td>0.024 ± 0.004</td>
<td>0.004 ± 0.0005</td>
<td>61.8 ± 8.1</td>
<td>101.8 ± 46.2</td>
<td>82.3 ± 20.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(30-55)</td>
<td>0.007 ± 0.0005</td>
<td>0.003 ± 0.0005</td>
<td>23.8 ± 2.1</td>
<td>6.5 ± 1.1</td>
<td>24.0 ± 6.0</td>
</tr>
<tr>
<td></td>
<td>B (0-15)</td>
<td>0.017 ± 0.003</td>
<td>0.003 ± 0.0005</td>
<td>28.0 ± 5.1</td>
<td>41.2 ± 20.2</td>
<td>30.7 ± 11.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(30-55)</td>
<td>0.006 ± 0.001</td>
<td>0.003 ± 0.0005</td>
<td>12.0 ± 1.8</td>
<td>7.0 ± 2.0</td>
<td>7.7 ± 1.4</td>
</tr>
<tr>
<td></td>
<td>C (0-15)</td>
<td>0.008 ± 0.001</td>
<td>0.002 ± 0.0005</td>
<td>19.2 ± 2.2</td>
<td>54.5 ± 21.3</td>
<td>19.5 ± 5.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(30-55)</td>
<td>0.003 ± 0.0005</td>
<td>0.002 ± 0.0005</td>
<td>10.3 ± 0.7</td>
<td>6.7 ± 1.3</td>
<td>5.5 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>D (0-15)</td>
<td>0.012 ± 0.002</td>
<td>0.003 ± 0.0005</td>
<td>10.7 ± 2.4</td>
<td>14.8 ± 4.7</td>
<td>5.5 ± 1.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(30-55)</td>
<td>0.003 ± 0.0005</td>
<td>0.003 ± 0.0005</td>
<td>5.2 ± 0.2</td>
<td>3.7 ± 0.6</td>
<td>2.0 ± 0.5</td>
</tr>
<tr>
<td>(2) Ngarradj Warde Djobkung</td>
<td>A (0-15)</td>
<td>0.014 ± 0.008</td>
<td>0.008 ± 0.003</td>
<td>14.2 ± 4.1</td>
<td>11.5 ± 1.4</td>
<td>3.2 ± 1.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>B (0-15)</td>
<td>0.011 ± 0.002</td>
<td>0.003 ± 0.0005</td>
<td>16.7 ± 2.2</td>
<td>15.7 ± 4.9</td>
<td>8.0 ± 2.4</td>
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</tr>
<tr>
<td>(3) Field Island</td>
<td>A (0-15)</td>
<td>0.045 ± 0.007</td>
<td>0.004 ± 0.0005</td>
<td>47.0 ± 7.1</td>
<td>1003.5 ± 145.1</td>
<td>379.3 ± 47.4</td>
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<tr>
<td></td>
<td></td>
<td>(30-55)</td>
<td>0.004 ± 0.0005</td>
<td>0.002 ± 0.0005</td>
<td>6.5 ± 0.5</td>
<td>78.7 ± 9.3</td>
<td>92.5 ± 14.4</td>
</tr>
<tr>
<td></td>
<td>B (0-15)</td>
<td>0.042 ± 0.011</td>
<td>0.004 ± 0.0005</td>
<td>13.2 ± 3.2</td>
<td>860.7 ± 245.4</td>
<td>315.2 ± 67.4</td>
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<tr>
<td></td>
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<td>(30-55)</td>
<td>0.005 ± 0.001</td>
<td>0.002 ± 0.0005</td>
<td>2.5 ± 0.4</td>
<td>182.5 ± 35.1</td>
<td>68.2 ± 11.0</td>
</tr>
<tr>
<td></td>
<td>C (0-15)</td>
<td>0.020 ± 0.005</td>
<td>0.002 ± 0.0005</td>
<td>15.7 ± 3.4</td>
<td>495.5 ± 187.0</td>
<td>147.5 ± 37.6</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>(30-55)</td>
<td>0.003 ± 0.0005</td>
<td>0.001 ± 0.0005</td>
<td>2.3 ± 0.3</td>
<td>50.2 ± 8.2</td>
<td>76.0 ± 24.0</td>
</tr>
<tr>
<td>(4) Nourlangie</td>
<td>A (0-15)</td>
<td>0.040 ± 0.010</td>
<td>0.005 ± 0.0005</td>
<td>41.7 ± 10.4</td>
<td>331.8 ± 163.3</td>
<td>89.0 ± 38.9</td>
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<tr>
<td></td>
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<td>(30-55)</td>
<td>0.008 ± 0.002</td>
<td>0.004 ± 0.0005</td>
<td>10.2 ± 1.3</td>
<td>15.5 ± 4.4</td>
<td>8.5 ± 1.5</td>
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<tr>
<td></td>
<td>B (0-15)</td>
<td>0.028 ± 0.005</td>
<td>0.004 ± 0.0005</td>
<td>27.5 ± 7.0</td>
<td>489.2 ± 193.2</td>
<td>104.5 ± 49.4</td>
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<td>(30-55)</td>
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<td>0.003 ± 0.0005</td>
<td>7.2 ± 1.7</td>
<td>12.7 ± 3.9</td>
<td>9.5 ± 7.0</td>
</tr>
<tr>
<td>Site</td>
<td>Plot</td>
<td>Sample depth</td>
<td>N (%)</td>
<td>P (%)</td>
<td>K (p.p.m.)</td>
<td>Ca (p.p.m.)</td>
<td>Mg (p.p.m.)</td>
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<tr>
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<td>(cm)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td></td>
<td>(0-15)</td>
<td>0.011±0.002</td>
<td>0.003&lt;0.0005</td>
<td>10.5±2.6</td>
<td>59.2±32.6</td>
<td>67.7±15.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(30-55)</td>
<td>0.003&lt;0.0005</td>
<td>0.003&lt;0.0005</td>
<td>6.2±2.1</td>
<td>14.5±3.0</td>
<td>31.3±1.5</td>
</tr>
<tr>
<td>D</td>
<td></td>
<td>(0-15)</td>
<td>0.013±0.004</td>
<td>0.002&lt;0.0005</td>
<td>16.3±4.4</td>
<td>91.7±40.5</td>
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<td>0.004&lt;0.0005</td>
<td>0.002&lt;0.0005</td>
<td>5.3±0.5</td>
<td>10.2±1.3</td>
<td>33.7±0.8</td>
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<td>(5) North Point</td>
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<tr>
<td>A</td>
<td></td>
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<td>0.032±0.009</td>
<td>0.007&lt;0.002</td>
<td>100.7±20.6</td>
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<td>142.5±35.2</td>
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<td>50.0±10.4</td>
<td>446.2±92.8</td>
<td>63.5±10.4</td>
</tr>
<tr>
<td>B</td>
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<td>(0-15)</td>
<td>0.039±0.008</td>
<td>0.005&lt;0.0005</td>
<td>43.2±13.1</td>
<td>1851.7±242.0</td>
<td>203.2±48.3</td>
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<tr>
<td></td>
<td></td>
<td>(30-55)</td>
<td>0.009±0.001</td>
<td>0.003&lt;0.0005</td>
<td>7.8±0.9</td>
<td>665.8±73.4</td>
<td>51.2±5.5</td>
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<tr>
<td>C</td>
<td></td>
<td>(0-15)</td>
<td>0.033±0.007</td>
<td>0.004&lt;0.0005</td>
<td>43.2±14.6</td>
<td>589.2±182.4</td>
<td>234.0±70.5</td>
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<td>9.2±0.6</td>
<td>81.2±28.7</td>
<td>68.2±12.8</td>
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<tr>
<td>D</td>
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<td>0.003&lt;0.0005</td>
<td>14.3±3.8</td>
<td>78.3±25.6</td>
<td>47.2±11.1</td>
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<td></td>
<td>(30-55)</td>
<td>0.007±0.001</td>
<td>0.002&lt;0.0005</td>
<td>6.7±1.2</td>
<td>21.3±2.8</td>
<td>30.3±12.4</td>
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<td>(6) Granite Hill</td>
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<td>A</td>
<td></td>
<td>(0-15)</td>
<td>0.074±0.012</td>
<td>0.008&lt;0.001</td>
<td>285.5±13.3</td>
<td>2924.0±743.5</td>
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<tr>
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<td>0.001&lt;0.0005</td>
<td>60.8±6.7</td>
<td>441.5±76.9</td>
<td>45.5±15.3</td>
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<td>(7) Evelyn</td>
<td></td>
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<tr>
<td>A</td>
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<td>(0-15)</td>
<td>0.088±0.013</td>
<td>0.019&lt;0.002</td>
<td>213.0±47.8</td>
<td>3311.0±804.1</td>
<td>386.0±38.5</td>
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<tr>
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<td>0.051±0.003</td>
<td>0.012&lt;0.0005</td>
<td>273.8±25.6</td>
<td>2679.0±157.2</td>
<td>377.0±33.7</td>
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