MANGROVE VEGETATION

IN

NORTHERN AUSTRALIA

by

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SUMMARY

Mangrove vegetation was surveyed along 4,525 km of tidal waterways throughout the Kimberley region of Western Australia and the coastline of the Northern Territory. Lists of mangrove species (trees/shrubs) for 110 tidal waterways and ecological information and distributions of the various species are presented. An appreciation of how climatic and other factors may influence floristic diversity of mangrove species in different regions and within waterways, and some of the environmental controls operating on dispersal, survival, growth and reproduction of mangroves are provided.

Within the survey area, tidal waterways are arranged according to seasonal variations in water salinities, into five distinct types. Characteristics of each of these five types are consistent from year to year, although irregular large flushes of freshwater in climatic events such as cyclonic distrubances and resultant rain depressions over any particular catchment area, cause minor fluctuations in time and rate of repenetration of saline waters into a tidal waterway.

Examination of floristic diversity of mangrove species from a regional perspective showed that negligible differences in species diversity occurred between the five types of tidal waterways across the northern coastline of the Northern Territory. For sites within the Gulf of Carpentaria however, it was shown that "Type 1" waterways were - in most instances - more floristically diverse than "Types 2, 3, 4 or 5" whereas in the Kimberley and Joseph Bonaparte Gulf regions, there was no discernible variation. Overall, all types of tidal waterways across the northern coastline of the Northern Territory contain considerably more mangrove species than equivalent types of waterways occurring throughout the Kimberley region of Western Australia and the two Gulf regions (Joseph Bonaparte and Carpentaria).

Distribution of plant species occurring in bankside vegetation is recorded together with a measure of their abundance for many of the major tidal waterways in the survey area. Additionally, all tidal waterways and tidal systems were grouped using computational analyses, of presence/absence of individual mangrove species, and regional patterns are discussed from environmental viewpoints.

Certain species, *Aegiceras corniculatum*, *Aegialitis annulata*, *Avicennia marina*, *Bruguiera exaristata*, *Ceriops tagal* var. *australis*, *Excoecaria agallocha*, *Lumnitzera racemosa*, *Osbornia octodonta*, *Rhizophora stylosa* and *Xylocarpus australasicus*, are shown as quite ubiquitous throughout the survey area, with overall percentage occurrences greater than 75% for the sites surveyed. Other species, *Acanthus ilicifolius*, *Bruguiera gymnorhiza*, *Bruguiera parviflora*, *Camptostemon schultzii*, *Ceriops decandra* and *Sonneratia alba* show overall percentage occurrences of between 25-75%, whereas *Avicennia officinalis*, *Bruguiera sexangula*, *Ceriops tagal*, *Lumnitzera littorea*, *Rhizophora apiculata*, *Scyphiphora hydrophyllacea*, *Sonneratia caseolaris* and *Xylocarpus granatum* only show overall percentage occurrences of less than 25% for sites in this survey area.

In the study area flowering periods of most mangrove species occur towards the end of the "dry" season. Such flowering periods are perplexing, as it is during this period of the year that insect activity appears minimal (when compared to the incessant insect activity during the "wet" season). Most fruiting, however, of the various species occurs during the "wet" season when tidal inundation is more pronounced and a greater range of sites is available for colonization.

Variations in girth, basal area, density and stem xylem pressure potentials in three mangrove species along seasonal salinity gradients in a tidal river system are examined. For species *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa* achievement of large girths may be attributed either to fast growth rates or long life spans or a mixture of the two. The only consistent pattern the three species show over the extremely wide range of salinities of sites in the study area is an inverse relationship between mean girth of canopy individuals and the peak dry season soil salinity of the sites in which they occur. In this study there is no evidence to suggest whether this variation may be primarily attributed to variation in life span of canopy trees or to variation in growth rates of trees between sites.

Basal areas and densities of these three species were found to be high at sites where nearly monospecific stands of the species occur, as in seasonally hypersaline sites (*Avicennia marina*), those sites in the true estuary of the Liverpool/Tomkinson Rivers System which experience seawater salinities for over 75% of the year (*Rhizophora stylosa*) and upstream brackish water sites (*Camptostemon schultzii*). Overall it was shown that each species examined peaked in basal area and density at different salinities.

For these species it was found that all attain greatest canopy heights (20-25 m) at sites inundated by admixtures of fresh/brackish waters throughout the year and have canopy heights only up to ten metres at sites inundated by seawater for at least 30% of the year. These species also show a gradual reduction in canopy heights from around ten to three metres at sites only briefly influenced by freshwaters during the wet season but inundated by seawaters and increasingly hypersaline waters (45-60$^{\circ}/_{oo}$) towards the end of the dry season.

Following on from the above-mentioned investigations, daily and seasonal variations of plateau values of stem xylem pressure potentials of selected mangrove species were determined across gradients of salinity. No evidence was obtained supporting an effect of tidal cycle on xylem pressure potential. Fluctuations in xylem pressure potential had a period close to 24 hours while the tidal cycles observed were considerably shorter.

In xylem pressure potentials, *Avicennia marina* closely followed by *Rhizophora stylosa* showed the largest daily fluctuations in the "late dry" season. However the form of the curve in *Avicennia marina* has a longer nocturnal plateau with more rapid rises and falls in pressure potential. In the "late wet" season *Rhizophora stylosa* shows the largest daily fluctuation in xylem pressure potential, closely followed by *Avicennia marina*, whereas *Camptostemon schultzii*, although having least fluctuations throughout both seasons, had a longer nocturnal plateau in the late dry season. Lowest (most negative) xylem pressure potentials occurred during the "dry" season for all three species examined. There was also a statistically significant correlation between daytime xylem pressure potential and salinity in the three species. Although data are too few for detailed analysis, the xylem pressure potential values for all the other species appear to fit a similar pattern. The findings reported here show that some mangrove species have xylem pressure potentials which would be in equilibrium with 2 to 2.5 times seawater, but that these xylem pressure potentials apparently result mainly from transpiration (since they occur in daytime), although they can be partly related to salinities of the root environment being slightly more concentrated than seawater.

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DEDICATION

To Juliana, Peter
and my parents

CHAPTER 1

1.1 GENERAL INTRODUCTION

Mangrove vegetation is essentially pantropical, although a few species still occur in the warm, temperate zones of both hemispheres. The term 'mangrove' is commonly used for trees and shrubs that grow between the high water mark of spring tides and a level close to, but above, mean sea level (Schimper, 1903, Richards, 1952 and Macnae, 1968). Mangrove vegetation is a characteristic feature of low tropical coastlines bordered by shallow waters and protected from strong wave action. Species colonize suitable habitats on a variety of substrates (viz. silt, sand, coral and mud). Optimum development of mangrove vegetation occurs along sheltered portions of coastlines including estuarine embayments, straits, coastal lagoons, lee sides of islands and the tidal portions of coastal waterways.

The vascular flora is recruited from a number of flowering plants that are not all closely related. A few pteridophytes also occur. Members of the flora must be at least tolerant of varying degrees of freshwater and saline inundation and also be able to withstand the lack of aeration characteristic of the muds often surrounding their root systems. The mangrove flora is thus limited to members of plant families capable of adapting to these conditions. Especially striking is the almost universal occurrence of pneumatophores of some sort, the high incidence of vivipary and dispersal of floating seeds and seedlings.

Zonation of dominant tree and shrub species is commonly observed and is usually now attributed to gradients in salinity and duration of exposure at low tide. The significance of zonation patterns has been a controversial topic in mangrove ecology. Davis (1940) and Chapman (1944, 1970) have argued that zonation patterns are equivalent to seral stages in succession to the climatic climax - a tropical forest. In this Clementsian interpretation, the coastal zone is the pioneer stage and more landward zones are progressively later stages in succession, thereby implying seaward progradation of the system (Davis, 1940; Chapman, 1944, 1970). This classical view is inconsistent with geological data and the zonation patterns of some forests have existed *in situ* for millenia (Thom *et al.*, 1975). Further, studies of the distribution of mangroves in relation to coastal geomorphology have shown that vegetational change occurs in response to changes in the physical characteristics of environment (Thom, 1967; Thom *et al.*, 1975; Cintron *et al.*, 1978; Ball, 1980).

From the present distribution of species, it appears that the Indo-Malaysian region was the historical centre of dispersal of modern mangrove floras (Hou, 1958; Steenis, 1962; Chapman, 1970, 1975, 1976). Such theories are supported by paleobotanical evidence (Muller, 1964). Muller's contribution to the Tertiary history of mangrove vegetation in Borneo shows a gradual change from the Eocene, in which only *Nypa* and *Brownlowia* fossil pollen types were identified to the Oligocene when *Rhizophora* pollen first appears and to the Miocene when pollen evidence of *Avicennia* and *Sonneratia* were found. However Specht (1981) considers that the centre of origin is more likely to have been south western and northern Australia to New Guinea.

Nypa also dates back to the beginning of the Eocene, in areas as widely separated as England, (Chandler 1964), Assam (Lakhanpal, 1952) and Brazil (Dolianiti, 1955) and from the mid to late Eocene in the south-western portion of Western Australia (Churchill, 1973). *Rhizophora* pollen is also known from the Eocene London clay flora (Chandler, 1964) and from the Oligocene onwards in Venezuela, Nigeria and New Guinea (Kuyl *et al.*, 1955; Muller, 1959) and from the early Miocene of Eniwetok Atoll, Marshall Islands and the Miocene of Guam (Leopold, 1969). *Avicennia*, *Ceriops*, *Lumnitzera* and *Sonneratia* are recorded from the Miocene of Eniwetok (Leopold, 1969), although Churchill (1973) records *Avicennia*, *Ceriops* and *Sonneratia* from the late Eocene in the south-west portion of Western Australia. *Bruguiera* pollens occur as far back as the Miocene on Fiji and the youngest Miocene of Eniwetok, and *Scyphiphora* was found in the lower Miocene and also in the youngest Miocene of Eniwetok (Leopold, 1969).

This fossil evidence suggests that a 'core' mangrove flora was beginning to assume a basic genetic composition - *Brownlowia*, *Nypa*, *Rhizophora* - at least by the Eocene period and that by the mid-Miocene a number of other genera - *Avicennia*, *Bruguiera*, *Ceriops*, *Lumnitzera*, *Scyphiphora* and *Sonneratia* had been recruited into the flora . This agrees with the earlier contention of Muller (1964) that only during the Miocene did mangrove forests reach a degree of floristic diversity comparable to present day floras.

In Australia, mangroves occur in small pockets around the coast. They are most predominant around the northern coastline and have only isolated occurrences in Victoria, South Australia and south of Carnarvon in Western Australia; they are absent from Tasmania (Macnae, 1966; Jones, 1971a; Gill, 1975; Lear and Turner, 1977; Saenger *et al.*, 1977; Semeniuk *et al.*, 1978; Bunt *et al.*, 1982; Wells, 1983). In a continent with a coastline of 19,650 km, emcompassing a latitudinal range from 11° to 44°S, a wide variety of mangrove communities occur under various physiographic and edaphic conditions. The areal extent of mangrove vegetation has been estimated by Galloway (1982) as 11,617 km^2, of which 10,827 km^2 occurs north of the tropic of Capricorn (23°S). Galloway's estimate for the Queensland coastline (4,629 km^2) is closely followed by the Northern Territory (4,130 km^2) and Western Australia (2,517 km^2). The southern states of New South Wales, Victoria and South Australia combined only account for 341 km^2, or 3% of total mangrove swamp in Australia.

The previous occurrences of pollens of *Avicennia*, *Ceriops* (and possibly other *Rhizophoraceae*), *Nypa* and *Sonneratia* in core samples taken from the geologically stable margins of Western Australia indicates that tropical coastal waters, some 5-9°C higher than water temperatures now experienced, and a richer mangrove flora extended along west Australian shores during the mid-late Eocene (Churchill, 1973). It is evident from present distributions of mangrove species in this area (Semeniuk *et al.*, 1978) that there has been a loss of all these elements excepting *Avicennia* from the southern portions of Australia since the late Eocene due most likely to a worldwide contraction of the tropical zone and warmer seas from the higher latitudes (Churchill, 1973).

Greatest floristic diversity of mangrove species in Australia (34 species) occurs around the northern portion of Cape York Peninsula, Queensland (Jones, 1971a; Gill, 1975; Saenger *et al.*, 1977; Bunt, 1978; Bunt *et al* 1982; Dowling and McDonald, 1982; Wells, 1983). The number of species decreases with increasing latitude down the east (Jones, 1971a) and west (Semeniuk *et al.*, 1978) coasts of the continent. Most species show attenuated distributions extending further down the eastern coastline (Wells, 1983), however at the southernmost limit of mangroves in the world - Corner Inlet, Victoria (38°45'S, 146°30'E) only one species, *Avicennia marina*, remains.

Distribution and abundance of mangrove species may be supposed to result from complex interactions of biological, chemical and physical environments now and in the past. Present diversity in any area then should be considered as a function of historical events, but also requires the continuous presence of extensive shallow water areas with suitable intertidal substrates for species establishment. Absence of such areas over time often results in elimination of mangrove species from a particular region (Fosberg, 1975). Theories of continental drift, climatic changes and subsequent fluctuations in surface oceanic temperatures at various latitudes around the continents over time are considered by Chapman (1975) and Fosberg (1975) among others as necessary to explain the original spread and subsequent establishment of most mangrove genera around the world.

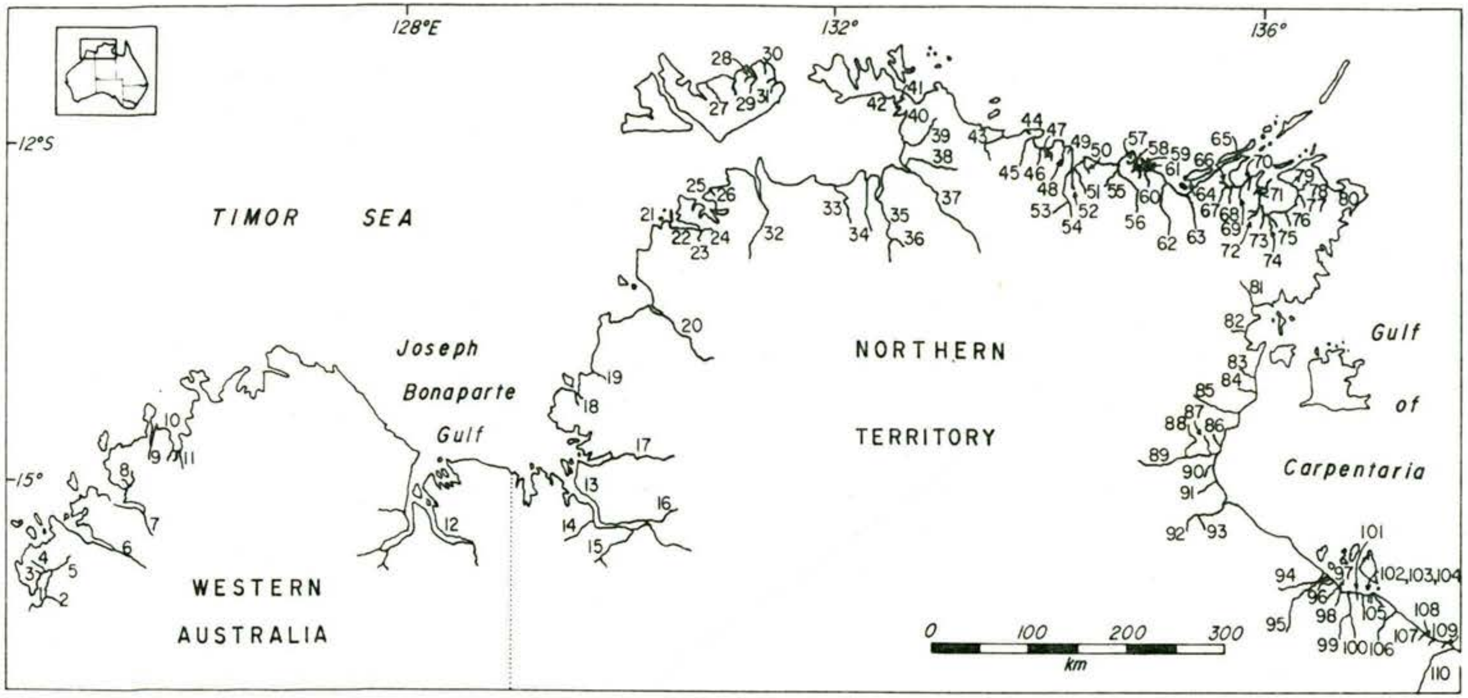
1.2 INTRODUCTION TO SURVEY AREA

Throughout the period 1975 - 1979, surveys of mangrove vegetation fringing 4,525 km along 110 tidal waterways across the northern portion of the Australian continent were undertaken. Tidal waterways and tidal systems (a collection of tidal waterways possessing a common entrance to the sea) within the survey area are shown in Figures 1.2.1 and 1.2.2. Within the Kimberley and Joseph Bonaparte Gulf regions of Western Australia, 527 km of waterways were surveyed while within the Northern Territory - from the Western Australian to the Queensland border - 3,998km of tidal waterways were surveyed.

Limited information is available on mangrove vegetation throughout the survey area. Within the Kimberley and Joseph Bonaparte Gulf regions, brief reports have been provided by Gardner (1923); Sauer (1965); Beard (1967) and Perry (1970). Miles *et al.*(1975); Thom *et al.*(1975); Messel *et al.* (1979); Semeniuk *et al.* (1978); Wells (1981) and Kenneally (1982) have provided more detailed accounts of the mangrove vegetation. In the Northern Territory, only brief reports by Specht (1958); Macnae, (1966); Story (1969), Story *et al.* (1976), Saenger *et al.* (1977), Hegerl *et al.* (1979) and Messel *et al.*(1979-82) for specific regions and a species checklist (Chippendale, 1972) existed until recent studies on mangrove vegetation around the northern coastline were reported by Wells (1982-83).

1.2.1 SCOPE OF THESIS

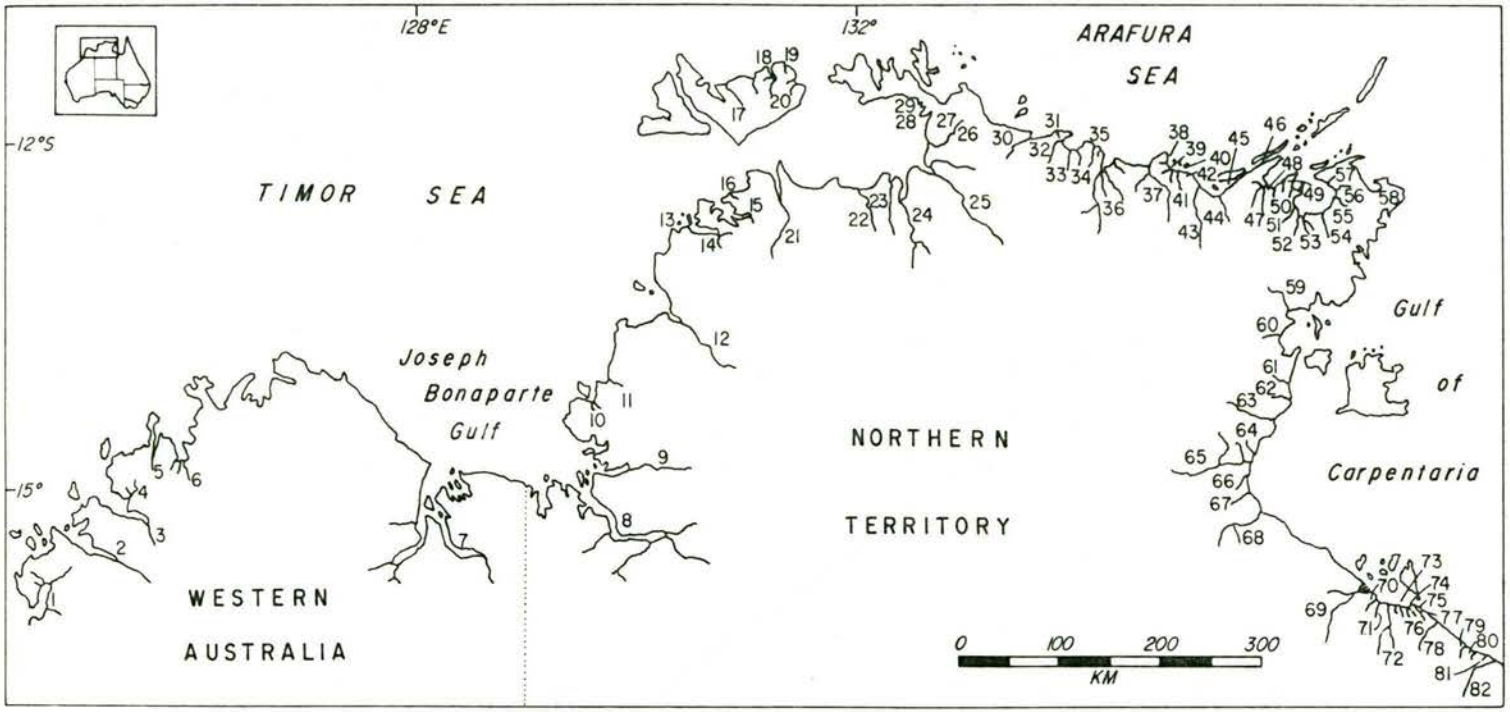
The thesis is presented in a biogeographic approach in Chapters 1-4, an ecologic approach in Chapters 5 and 6 and a physiological approach in Chapter 7. (Amendment 18.9.84) Chapter One provides a general account of waterways entering the coastline around the survey area, mangrove species encountered, and an overview of environmental factors affecting the survey area. Chapter Two concentrates on growth form, occurrence, regeneration and distribution of individual species. Pertinent ecological observations including species associations, field water and soil salinity limits (for each species), and a discussion of possible historical/ environmental factors influencing present distributions are presented.



1 GEORGE WATER
2 SALE R.
3 BARLEE IMPEDIMENT
4 GAIRDNER R.
5 GLENELG R.
6 PRINCE REGENT R.
7 ROE R.
8 HUNTER R.
9 MITCHELL R.
10 PORT WARRENDER
11 LAWLEY R.
12 ORD R.
13 VICTORIA R.
14 BULLO R.
15 BAINES R.
16 ANGALARRI R.
17 FITZMAURICE R.
18 PORT KEATS
19 MOYLE R.
20 DALY R.
21 PORT PATERSON
22 BYNOE HARBOUR
23 ANNIE R.
24 CHARLOTTE R.
25 DARWIN HARBOUR
26 BUFFALO CK.
27 ANDRANANGOO CK.
28 BATH CK.
29 JOHNSTON R.
30 DONGAU CK.
31 TINGANOO CK.
32 ADELAIDE R.
33 WILDMAN R.
34 WEST ALLIGATOR R.
35 SOUTH ALLIGATOR R.
36 NOURLANGIE CK.
37 EAST ALLIGATOR R.
38 COOPERS CK.
39 MURGENELLA CK.
40 MINI MINI CK.
41 IWALG CK.
42 ILAMARYI R.
43 KING R.
44 ARRLA CK.
45 GOOMADEER R.
46 WURUGOIJ CK.
47 MAJARIE CK.
48 NUNGBALGARRIE CK.
49 TOMS CK.
50 GUDJERARMA CK.
51 TOMKINSON R.
52 MUNGADOBOLO CK.
53 MARAGULIDBAN CK.
54 LIVERPOOL R.
55 CADELL R.
56 BLYTH R.
57 NGANDADAUDA CK.
58 DJABURA CK.
59 DJIGAGILA CK.
60 DARBITLA CK.
61 BENNETT CK.
62 GLYDE R.
63 WOOLEN R.
64 HUTCHINSON STRAIT
65 CADELL STRAIT
66 KALARWOI R. (CK. B)
67 KALARWOI R.
68 BUCKINGHAM R.
69 WARAWURUWOI R.
70 KURALA R.
71 SLIPPERY CK.
72 DARWARUNGA R.
73 HABGOOD R.
74 BARALMINAR R.
75 GOBALPA R.
76 GOROMURU R.
77 CATO R.
78 PETER JOHN R.
79 BURUNGBIRINUNG R.
80 MELVILLE BAY
81 KOOLATONG R.
82 WALKER R.
83 HART R.
84 MUNTAK CK.
85 ROSE R.
86 YIWAPA CK.
87 PAINNYILATYA CK.
88 PHELP R.
89 ROPER R.
90 NAYARNPI CK.
91 TOWNS R.
92 LIMMEN BIGHT R.
93 NATHAN R.
94 BATTEN CK.
95 McARTHUR R.
96 'JOHNSON' R.
97 'COULOMB' CK.
98 'FARADAY' CK.
99 WEARYAN R.
100 FOELSCHE R.
101 'BOHR' CK.
102 'PLANCK' CK.
103 'ARCHIMEDES' CK.
104 'GALILEO' CK.
105 FAT FELLOWS CK.
106 ROBINSON R.
107 'EINSTEIN' CK.
108 'NEWTON' CK.
109 'PAULI' CK.
110 CALVERT R.

FIG. 1.2.1

Tidal waterways of the survey area.



1 GEORGE WATER
2 PRINCE REGENT
3 ROE
4 HUNTER
5 MITCHELL
6 PORT WARRENDER
7 ORD
8 VICTORIA
9 FITZMAURICE
10 PORT KEATS
11 MOYLE
12 DALY
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14 BYNOE HARBOUR
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38 NGANDADAUDA
39 DJABURA
40 DJIGAGILA
41 DARBITLA
42 BENNET
43 GLYDE
44 WOOLEN RIVER
45 HUTCHINSON STRAIT
46 CADELL STRAIT
47 BUCKINGHAM/KALARWOI
48 WARAWURUWOI
49 KURALA
50 SLIPPERY
51 DARWARUNGA
52 HABGOOD
53 BARALMINAR/GOBALPA
54 GOROMURU
55 CATO
56 PETER JOHN
57 BURUNGBIRINUNG
58 MELVILLE BAY
59 KOOLATONG
60 WALKER
61 HART
62 MUNTAK
63 ROSE
64 YIWAPA
65 ROPER
66 NAYARNPI
67 TOWNS
68 LIMMEN BIGHT
69 McARTHUR
70 'COULOMB'
71 'FARADAY'
72 WEARYAN
73 'BOHR'
74 'PLANCK'
75 'ARCHIMEDES'
76 'GALILEO'
77 FAT FELLOWS
78 ROBINSON
79 'EINSTEIN'
80 'NEWTON'
81 'PAULI'
82 CALVERT

FIG. 1.2.2

Tidal systems of the survey area.

Following this, seasonal variations in water salinity in tidal waterways are examined in Chapter Three and an attempt to classify waterways into five distinct types is made. This chapter also examines floristic diversity of mangroves in different regions of the survey area and provides information on distribution of bankside vegetation and its relation to seasonal variations in high tide water salinities on selected waterways. Using computational analyses, Chapter Four groups waterways on presence/absence of individual mangrove species, in an attempt to understand present species distributions. In this respect, an appreciation of how climatic and other factors may influence floristic diversity of mangroves at certain sites within the survey area requires knowledge of environmental controls operating on the dispersal, survival, growth and reproduction in individual species. The following three chapters provide more information about environmental controls for certain species and are concerned with flowering and fruiting (Chapter Five), size of surviving plants and population structure in relation to site characteristics (Chapter Six) and daily and seasonal variations of the physiological state of individual mangrove species (Chapter Seven). The extent to which this leads to a better understanding of variation in species composition regionally and between sites is discussed particularly in the concluding chapter (Chapter Eight).

1.2.2 MANGROVE SPECIES IN THE SURVEY AREA

Twenty-seven species of mangroves were recorded (during this survey) in the Northern Territory, although two additional species - *Nypa fruticans* Wurmb. (Dunlop, pers. Comm.) and *Rhizophora lamarckii* Montr. (Hegerl *et.al.*, (1979)) occur at single sites on Melville Island and the Alligator Rivers respectively. Fourteen species were recorded in the Kimberley region of Western Australia (Wells, 1981), although an additional species, *Scyphiphora hydrophyllacea* Gaertn., has been reported by Semeniuk *et al.* (1978) at Cape Londonderry, Western

ACANTHACEAE	*Acanthus ilicifolius* L.
AVICENNIACEAE	*Avicennia marina* (Forsk.) Vierh.
	Avicennia officinalis L.
BOMBACACEAE	*Camptostemon schultzii* Mas.
COMBRETACEAE	*Lumnitzera littorea* (Jack.) Voigt.
	Lumnitzera racemosa Willd.
EBENACEAE	*Diospyros ferrea* (Willd.) Bakh. var. *humilis* (R.Br.) Bakh.
EUPHORBIACEAE	*Excoecaria agallocha* L.
MELIACEAE	*Xylocarpus australasicus* Ridl.
	Xylocarpus granatum Koen.
MYRSINACEAE	*Aegiceras corniculatum* (L.) Blanco
MYRTACEAE	*Osbornia octodonta* F.v.M.
NYPACEAE	* *Nypa fruticans* Wurmb.
PAPILIONACEAE	*Derris trifoliata* Lour.
PLUMBAGINACEAE	*Aegialitis annulata* R. Br.
PTERIDACEAE	***Acrostichum speciosum* Willd.**
RHIZOPHORACEAE	*Bruguiera exaristata* Ding Hou
	Bruguiera gymnorhiza (L.) Lamk.
	Bruguiera parviflora (Roxb.) W. & A. ex Griff.
	Bruguiera sexangula (Lour.) Poir.
	Ceriops decandra (Griff.) Ding Hou
	Ceriops tagal (Perr.) C.B. Rob var. *australis* C.T. White
	Ceriops tagal (Perr.) C.B. Rob
	Rhizophora apiculata Blume
	* *Rhizophora lamarckii*. Montr.
	Rhizophora stylosa Griff.
RUBIACEAE	*Scyphiphora hydrophyllacea* Gaertn.
SONNERATIACEAE	*Sonneratia alba* J.E. Sm.
	Sonneratia caseolaris (L.) Engl.

TABLE 1.2.1 MANGROVE SPECIES RECORDED IN THE SURVEY AREA.

* Denotes species not recorded during this survey.

Australia. Mangrove species recorded in the survey area are shown in Table 1.2.1.

One species, *Avicennia officinalis* L., is a previously unrecorded species for Australia. *Bruguiera sexangula* (Lour.) Poir.; *Ceriops decandra* (Griff.) Ding Hou.; *Ceriops tagal* (Perr.) C.B. Rob.; *Rhizophora apiculata* Blume and *Sonneratia caseolaris* (L.) Engl. are previously unrecorded species in the Northern Territory and *Xylocarpus granatum* Koen. is a previously unrecorded species in Western Australia. Three species, occurring primarily at sites inundated by admixtures of fresh/brackish waters, the mangrove fern *Acrostichum speciosum*, the vine *Derris trifoliata* and the ebony mangrove *Diospyros ferrea* var. *humilis* are not discussed at length in this thesis.

Identifications were based on identifications of mangroves in eastern and northern Australia (Jones, 1971a, Chippendale, 1972); in Sarawak, Malaysia (Chai, 1972, 1973) (specimens inspected at Forestry Department Herbarium, Kuching, Sarawak); in Sabah, Malaysia (Fox, 1970); in Papua New Guinea (Percival and Womersley, 1975); in Thailand (specimens inspected at Phuket Marine Biological Centre, Phuket Province) and the Philippines (specimens inspected at the Mangrove Research Centre, Pagbilao, Luzon Island).

Voucher specimens for most mangrove species recorded in this survey area (Fig. 1.2.1) have been deposited at the John Ray Herbarium (University of Sydney) and the Northern Territory Herbarium (Darwin).

1.3 SURVEY AREA

The area surveyed (Fig. 1.2.1) incorporates tidal waterways showing major structural control of drainage, as in the north-west Kimberley region of Western Australia, where entire river courses follow geological jointing planes (viz. Glenelg, Prince Regent, Roe, Hunter and Mitchell Rivers) and in the upstream portions of waterways such as the Ord, Victoria and Fitzmaurice Rivers, which finally drain into Cambridge and Joseph Bonaparte Gulfs. A detailed discussion on deltaic estuarine geomorphology for the Ord River is given by Thom *et al.* (1975).

Other rivers (Moyle, Daly) enter Hyland and Anson Bays in this region after meandering across extensive alluvial floodplains. Port Paterson, Bynoe and Darwin Harbours are wide, shallow embayments with numerous tidal creeks and rivers entering into them. Along the north coast of Melville Island the Johnson River and Andranangoo, Bath, Dongau and Tinganoo Creeks are relatively short coastal creeks not draining any appreciable catchment areas, although Andranangoo Creek meanders across a relatively broad floodplain.

Waterways entering Van Diemen Gulf (i.e., Adelaide, Wildman, West, South and East Alligator Rivers, Nourlangie, Coopers and Murgenella Creeks) all drain quite extensive catchment areas and meander across a floodplain that often partially interconnects them during the wet season (Williams, 1979). Other waterways, Mini Mini and Iwalg Creeks, Ilamaryi River, are only short coastal inlets not draining any substantial upstream catchment areas.

The King River on the northern Arnhem Land coast shows features of a drowned river valley and has numerous side-creeks. Arrla, Wurugoij and Majarie Creeks are short coastal creeks draining small catchment areas. The Goomadeer River - entering Junction Bay - meanders across an extensive floodplain after draining a considerable upstream catchment area in escarpment country. Nungbalgarrie Creek, which enters Rolling Bay, although draining a considerable area, does not show any appreciable floodplain development.

The Liverpool/Tomkinson and Blyth/Cadell River Systems both show structural control of drainage in their upstream reaches (Rushworth, 1975) but in their lower reaches meander across broad alluvial floodplains. Ngandadauda, Djabura, Djigagila and Darbitla Creeks all meander across coastal saline mudflats, although Darbitla Creek drains a somewhat larger catchment area. The Glyde River drains the extensive Arafura Swamp and the freshwater Goyder River, and meanders across an extremely broad floodplain before entering Castlereagh Bay. The Woolen River, lying adjacent to the Glyde, shows features of a drowned river valley, with little floodplain development.

The Buckingham and Kalarwoi Rivers entering into the southern portion of Buckingham Bay show some floodplain development, however the Warawuruwoi and Kurala Rivers are short coastal inlets with small catchment areas and negligible floodplain development. In Arnhem Bay the Darwarunga and Burungbirinung Rivers are short coastal inlets draining small catchment areas, whereas the Habgood, Goromuru, Cato and Peter John Rivers drain larger catchment areas and meander in their tidal reaches across floodplains.

The Koolatong River, entering Blue Mud Bay in the Gulf of Carpentaria, has no floodplain although this river drains a considerable catchment whereas the Walker River (also entering this bay) has considerable floodplain development along its tidal reaches.

The short coastal waterways on the eastern shores of Arnhem Land - Hart and Rose Rivers; Muntak, Yiwapa and Nayarnpi Creeks drain small catchment areas and show limited floodplain development whereas the extensive Roper River System meanders across broad floodplains.

Tidal waterways entering into the southern portion of the Gulf of Carpentaria in the survey area show little floodplain development with larger rivers such as the Limmen Bight, Towns, McArthur, Robinson, Wearyan and Calvert having high, steep banks along most of their upstream tidal reaches. Floodplain development only occurs around the lower estuaries. Smaller coastal waterways along this coastline, such as Fat Fellows Creek, show some floodplain development but these creeks do not drain any appreciable catchment areas.

1.3.1 CLIMATE

The broad character of climate throughout the survey area is strongly conditioned by seasonal shifting of the prevailing winds and consequent marked changes in air-mass properties. Two distinct seasons can be identified - the 'wet' season, with dominant winds from the north-west to west, occurring from November - March, and the 'dry' season with prevailing south-easterly winds from May - September. April and October are transitional months (Specht, 1958; Gentilli, 1971).

With the southward progression of the intertropical convergence zone, the true 'wet' or 'monsoon' season is normally established by late December or early January. Prior to this establishment there occurs a period of rising temperatures (Fig. 1.3.1) and humidity (Fig. 1.3.2), normally from October to December. During this time, variable light winds and widespread intense daytime convection become characteristic throughout the survey area. Although local thunderstorms occur during this transitional period, rainfall is both sporadic and unreliable (Anon., Climatic Averages of South Australia & Northern Territory, 1975).

The monsoon is only a stream of Indian Ocean air (trade wind air) deflected by the north-western Australian heat low and therefore is considered by Gentilli (1971) to be not normally connected with the Asian winter monsoon. The relative humidity of this maritime air is not very high although it is true that during January and February some intermittent equatorial airstreams emanating from Asia do push southwards far enough to reach the north Australian coast

Normally in October, the first monsoonal rains appear near Darwin (Southern, 1966). During November, monsoonal situations (convectional thunderstorms of a highly localized and patchy distribution) normally extend south-eastwards over the survey area at the rate of about 30 km/day (Gentilli, 1971). Thus the 'wet' season starts in areas like the southern portion of the Gulf of Carpentaria towards the end of December - slightly later than its occurrence along the Kimberley and northern Arnhem Land coastlines.

Throughout January and February the frequency of monsoonal situations reaches a peak throughout the survey area with irregular intrusions of moist maritime air blowing in from the Indian Ocean and the Arafura and Timor Seas (Southern, 1966). These intrusions are associated with low pressure trough development brought about by the instability of these maritime airs spreading over continental areas. Widespread overcast conditions and general rain characterize this period, making January and February the wettest months of the year at all stations in the survey area (Fig. 1.3.3).

It should be emphasized that during the intervals between these moist air intrusions, a return to south-easterly winds bringing hot, dry weather may occur (Fitzpatrick, 1961). Such reversals do not persist but may, on occasions, extend over several weeks. As well as these widespread monsoonal rains, which are of varying intensity throughout the survey area, some extremely heavy falls of rain result from tropical cyclones. These cyclones - or areas of extremely low pressure - are relatively infrequent (average 3.3/year around the Northern Territory

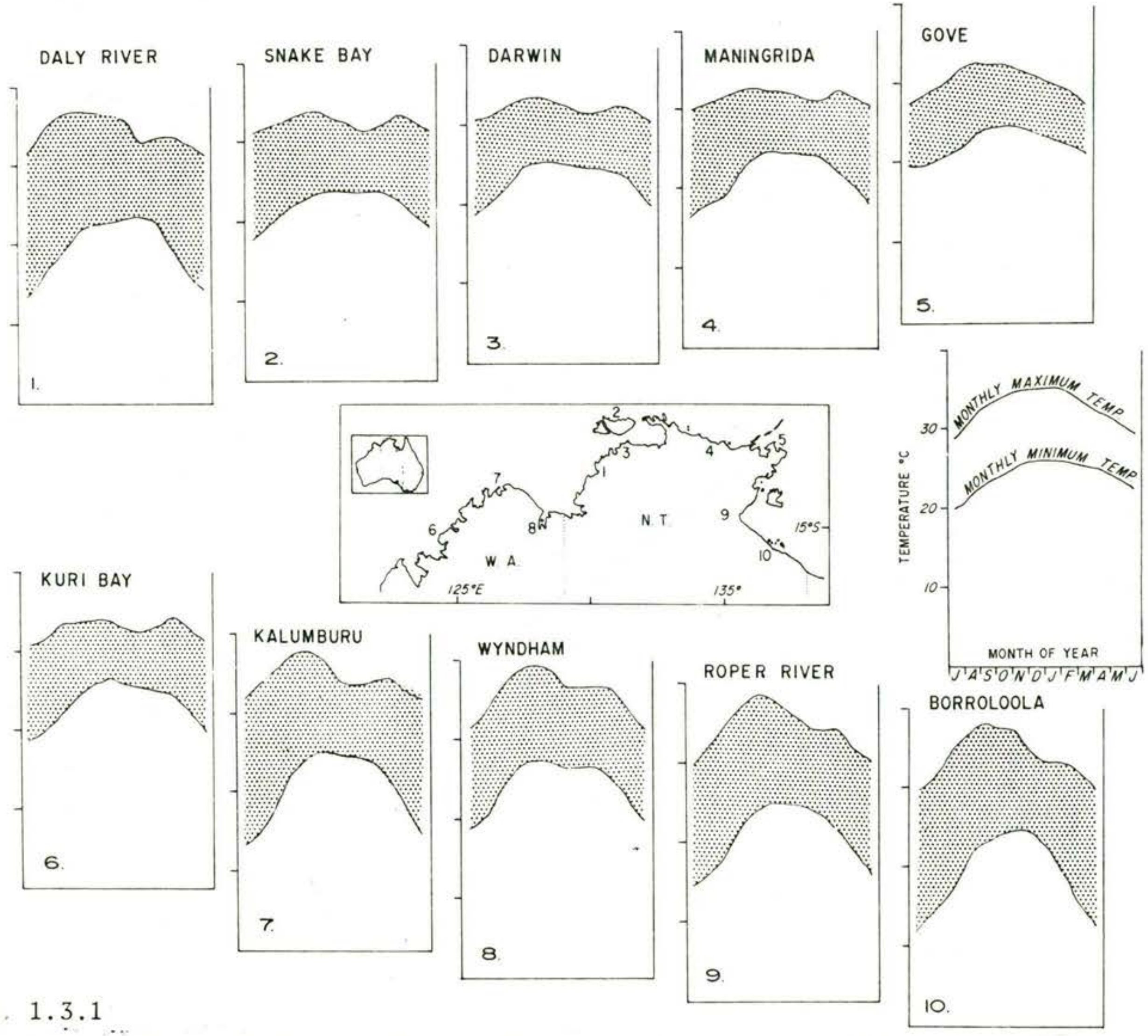


FIG. 1.3.1

Monthly mean maximum and minimum temperatures at ten selected localities within the survey area. (All years of record to 1975.) (Data source - Bureau of Meteorology.)

coastline; 2.1/year around the Kimberley coastline (Gentilli, 1971)) and after degenerating into rain depressions - normally after striking continental land masses - produce intense, steady rain over large regions (falls of up to 200 mm/day from rain depressions are not uncommon). Within the survey area, rain depressions resulting from cyclonic activity are the major cause of largescale flooding of any river system.

With the general northward return of the intertropical convergence zone during March (Gentilli, 1971), maritime influences become weaker. During this period, maritime air intrusions become less frequent in the Kimberley region of the survey area whereas in regions around the southern portion of the Gulf of Carpentaria, intrusions of moist maritime monsoonal airstreams continue and may advance southwards. Both incidence and quantity of rain falling at any site within the survey area normally decrease rapidly by late March and this decline continues throughout April. With decreased cloud cover, somewhat higher daytime temperatures are typical although occasional thunderstorms at this time impart to the daily weather, characteristics not unlike those of the months preceding the establishment of the 'wet' season.

Sustained south-easterly winds and the influence of a strong continental air mass are normally established throughout the survey area during May, bringing the very stable, dry and sunny weather conditions characteristic of the normally rainless, cooler months of the year (June - September). This period is termed the 'dry' season.

1.3.2 HUMIDITY

Atmospheric humidity is expressed as a percentage of the moisture that the atmosphere can hold at the prevailing temperature (index of relative humidity). Within the survey area, 9am and 3pm monthly averages of mean relative humidity at 10 selected localities are shown in Fig. 1.3.2 and it is seen that humidity varies considerably between sites (Anon, Climatic Averages of South Australia and Northern Territory, 1975).

Snake Bay on Melville Island in the Northern Territory experiences highest annual mean relative humidity with 76/59% (9 am/3 pm humidities), closely followed by Maningrida (74/60%); Gove (72/64%); Daly River (72/45%) and Darwin (71/52%). For the survey area, Kuri Bay, in the Kimberley region of Western Australia experiences a medium range of humidity (i.e. 60/52%), whereas stations that occur in considerably more arid regions of the survey area such as Borroloola (58/38%); Roper River (58/34%); Kalumburu (53/45%) and Wyndham (46/37%) experience low 9 am and 3 pm mean annual relative humidities.

The highest average monthly humidity, 91%, is recorded for the Daly River during February, although Snake Bay, Darwin and Maningrida consistently have 9 am mean monthly relative humidities greater than 80% during the most intense period of the wet season - December - March.

All other stations within the survey area never attain mean 9am humidities above 80% and 'stations' such as Roper River and Wyndham rarely, if ever, achieve 9 am humidities above 70% in any month of the year. The lowest 3 pm relative humidites are also recorded for the dryest sites, i.e. Roper River, Borroloola and Wyndham.

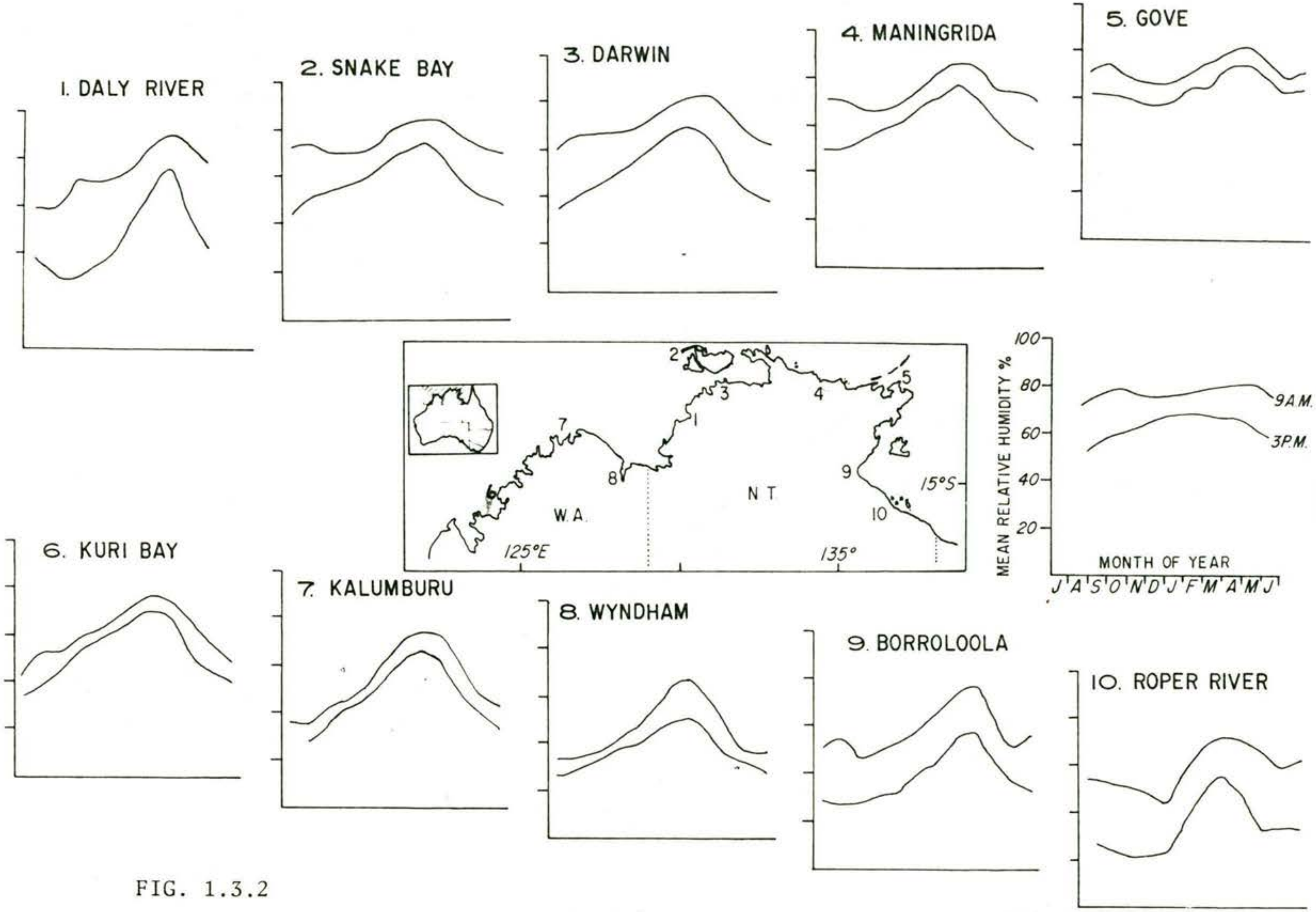


FIG. 1.3.2

9am and 3pm monthly averages for mean relative humidity at ten selected localities within the survey area. (All years of record to 1975.) (Data source - Bureau of Meteorology.)

1.3.3 AIR TEMPERATURES

A prominent climatic feature of the survey area is the high air temperatures sustained throughout the year. The range between mean monthly maximum and minimum temperatures is seldom more than 10°C at the ten localities described within the survey area (Fig. 1.3.1).

At localities along the northern coastline of the Northern Territory, mean monthly maximum temperatures, even during the cooler months of June, July and August, seldom fall below 30°C and mean monthly minimum temperatures seldom fall below 20°C.

Within the survey area, largest air temperature variations occur at Daly River, Kalumburu, Roper River and Borroloola - particularly at the latter two localities. Although monthly maximum temperatures usually remain above 30°C at these sites and may even reach 38°C at Borroloola and Roper River and 39°C at Wyndham during dry season months; such high temperatures are not maintained throughout the remainder of the year. During dry season months, temperatures above 35°C are relatively common around the semi-arid Kimberley coastline of Western Australia, the Joseph Bonaparte Gulf region and the semi-arid coastline bordering the southern portion of the Gulf of Carpentaria.

At localities such as Borroloola and Roper River, mean monthly minimum temperatures between 14 - 18°C typically occur during the mid-dry season (June - August) with the minimum monthly temperature (of 11.9°C, July) recorded for Borroloola being the lowest mean temperature recorded for any locality in the survey area.

The coolest night-time temperature experienced on any of the tidal waterways in the survey area was 12°C recorded during June,]979 in Hutchinson Strait (on the northern Arnhem Land coastline) (Messel *et al*, 1980, Mono 9), although night-time temperatures below 15°C are extremely uncommon on the actual tidal waterways, even during the dry season.

1.3.4 RAINFALL

Within the survey area considerable variation in annual precipitation is evident. Histograms showing mean monthly rainfall for ten localities within the survey area are shown in Fig. 1.3.3. Monthly variation in intensity of rainfall at the different localities is quite evident as is the fact that for the remainder of the year, each locality experiences virtual drought. A generalized map showing variations in annual rainfall in a series of isohyets for the entire survey area is shown in Fig. 1.3.4.

It is seen in both Figs. 1.3.3 and 1.3.4 that the Snake Bay-Darwin-Daly River area of the Northern Territory receives considerably more rainfall than any other portion of the survey area. Mean annual rainfall for these three localities is 1,594, 1,594 and 1,484 mm, respectively (Anon, Climatic Averages S.A. and N.T. 1975).

The area encompassing the George Water System in Western Australia, the Port Keats/Fitzmaurice River Systems, waterways bordering Van Diemen Gulf, the northern coastline of Melville Island and Cobourg Peninsula and the north-eastern portion of Arnhem Land (Buckingham, Arnhem, Melville and Blue Mud Bays; Groote Eylandt) annually receive between 1,250 - 1,500 mm of rainfall.

The major portion of the Kimberley area northwards and including the Prince Regent River together with mid portions of the northern and eastern coastlines of Arnhem Land fall within the 1,000 - 1,250 mm isohyets, whereas the Ord-Victoria River Systems draining into Joseph Bonaparte Gulf and tidal waterways entering into the southern portion of the Gulf of Carpentaria all lie within the 750 - 1,000 mm rainfall isohyet.

Within the survey area, the greater amount of rainfall falls during four peak months of the 'wet' season (January - March). In this period, at least 85% of total annual rainfall falls for

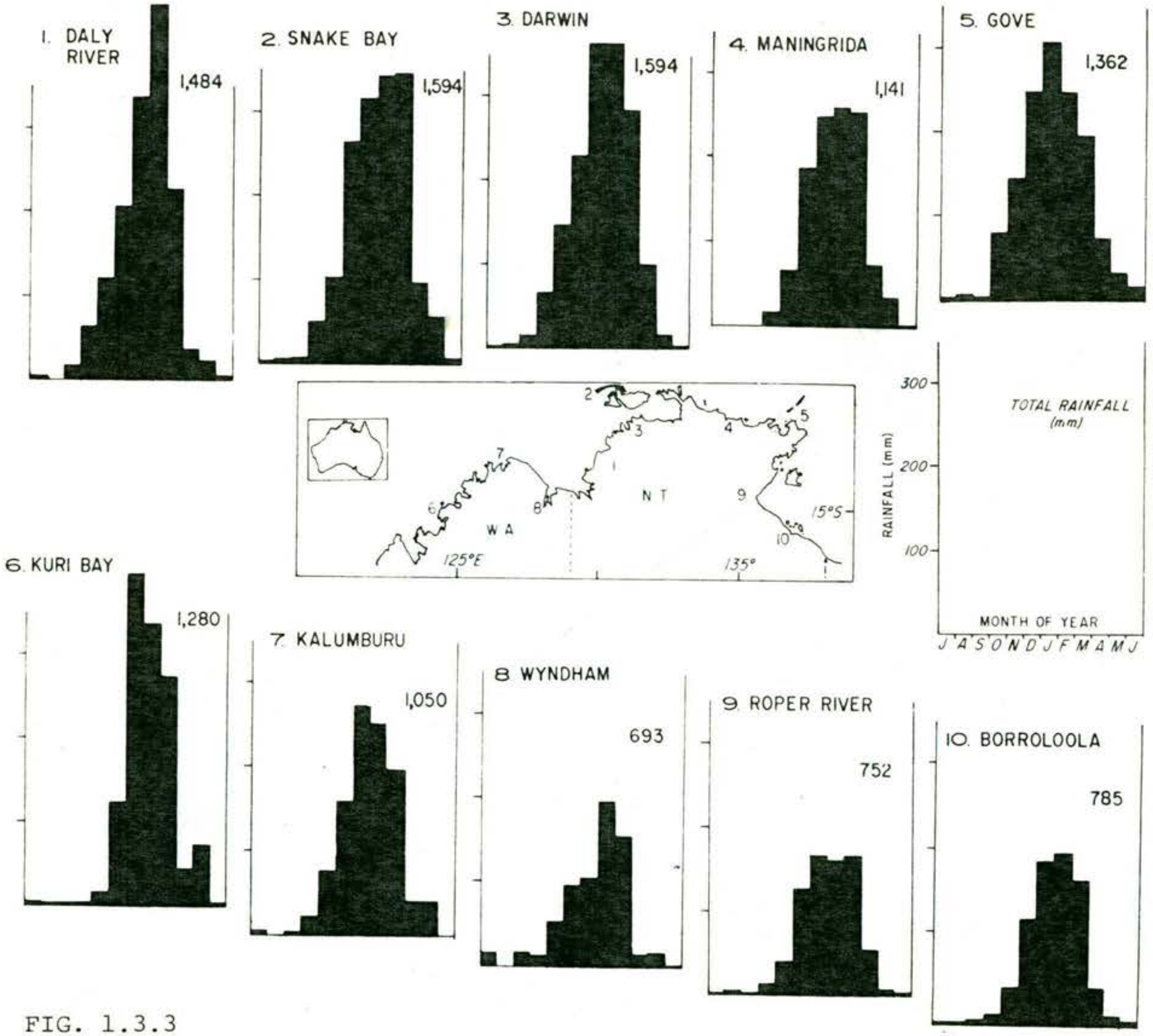


FIG. 1.3.3

Monthly distribution of rainfall and mean annual rainfall at ten selected localities within the survey area. (All years of record to 1975.) (Data source - Bureau of Meteorology.)

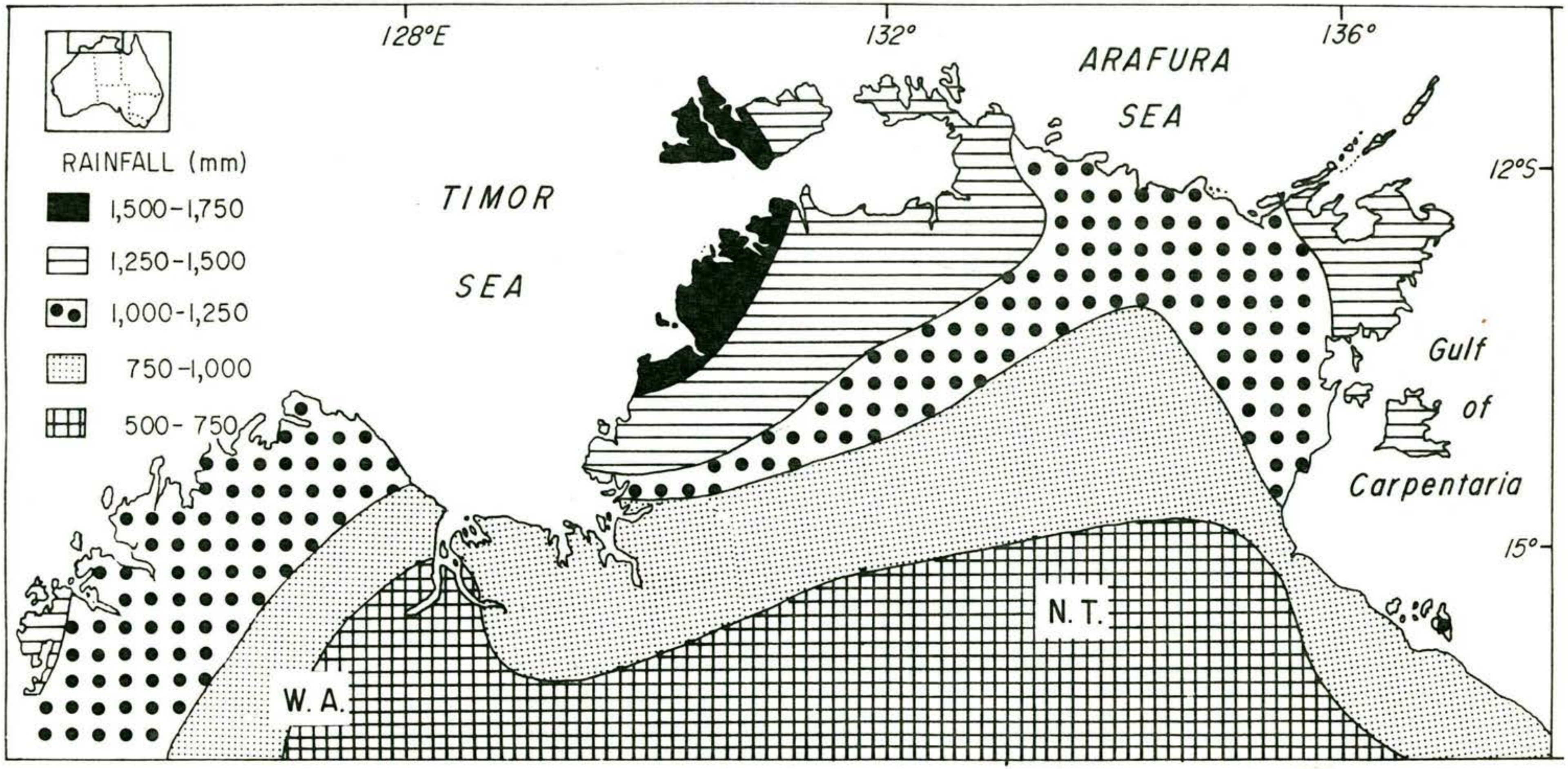


FIG. 1.3.4

Variation in mean annual rainfall (in isohyets) for the survey area. (All years of record to 1975, source Bureau of Meteorology.)

all localities (Fig. 1.3.3).

In some localities within the survey area - notably along the mid north coast of Arnhem Land (i.e. Maningrida), negligible rainfall occurs during the dry season. At other localities - Kuri Bay, Snake Bay, Darwin, Gove, Roper River and Borroloola, it is shown (Fig. 1.3.3) that rainfall is recorded during all months of the year, although amounts of precipitation falling during dry season months are small.

1.3.5 EVAPORATION

Evaporation is affected by net radiation, accompanying temperatures, humidity and local wind conditions at any particular locality. Variations in these factors act to modify evaporation loss. The temperature-rainfall diagrams shown in Fig. 1.3.5 illustrate variations in precipitation and aridity at ten localities in the survey area. The area between the rainfall and mean temperature curves (when evaporation exceeds rainfall) is taken as an indication of aridity although this aridity is only relative to the 'wet' season of the particular climate under consideration. The temperature-rainfall diagrams follow the methodology of Walter (1973) and utilize available climatic statistics for the selected stations in the Northern Territory (Fig. 1.3.5).

Within the survey area temperature-rainfall diagrams are especially useful for distinguishing 'homoclimes', i.e. localities with essentially similar climates. Stations such as Daly River, Snake Bay, Darwin, Maningrida and Gove are reasonably similar climatically although local variations are evident. Only one evaporation pan (Class A Type) occurs within this area (i.e. at Darwin) where mean annual pan evaporation is 2,073 mm. Slightly more evaporation occurs during dry season months (e.g. July, 184 mm) as opposed to wet season months (e.g. January, 146 mm).

The localities Kuri Bay, Kalumburu, Wyndham, Roper River and Borroloola in Fig. 1.3.5 are considerably more seasonally arid than those

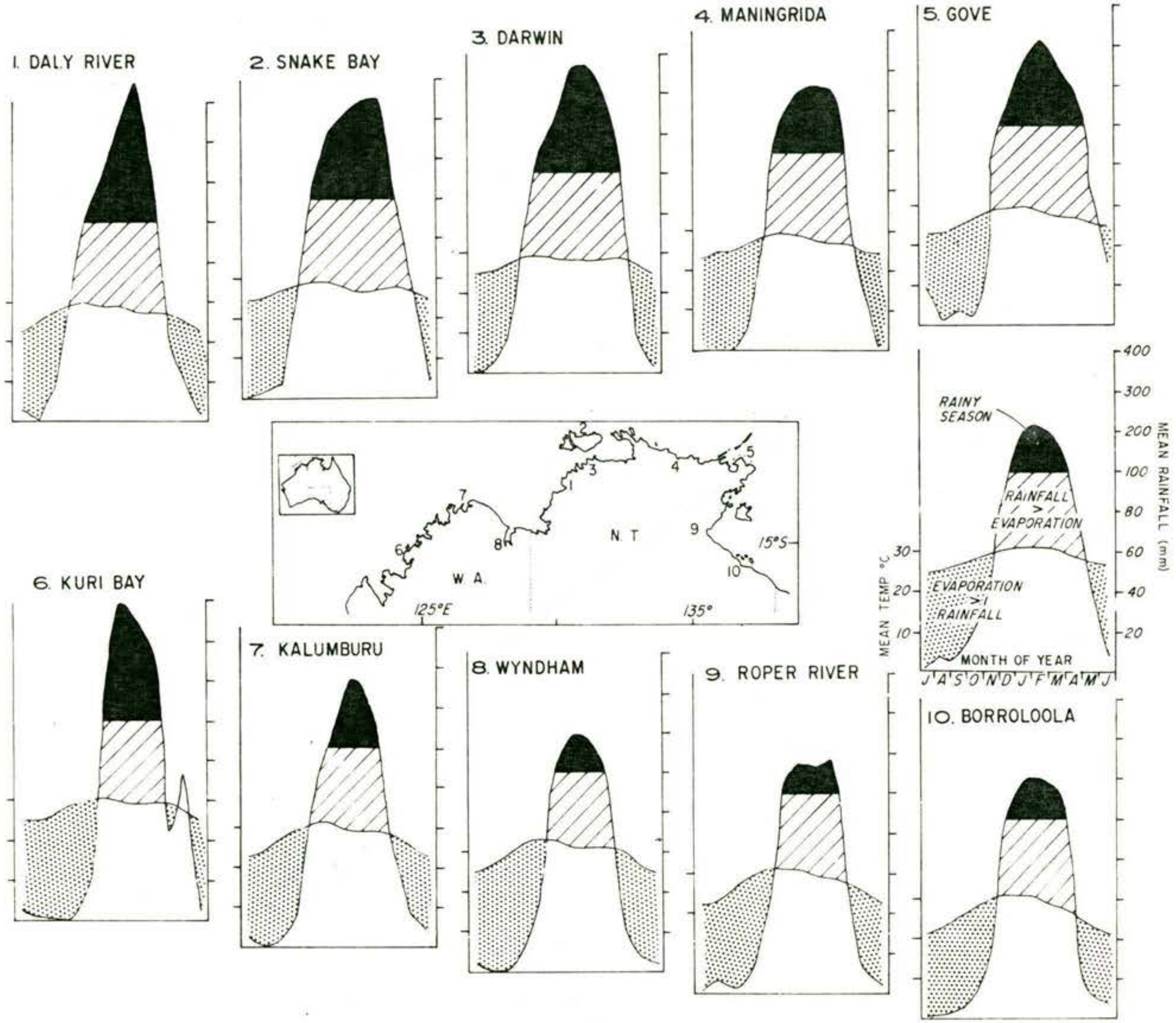


FIG. 1.3.5

Temperature-rainfall diagrams for ten selected sites in the survey area. Solid areas represent the 'wet' season.

localities previously mentioned with major differences being in the lesser amount of annual rainfall and the greater area between the rainfall and mean temperature curves in which evaporation exceeds rainfall. Wyndham is the most arid site within the survey area with a mean annual pan evaporation of 2,846 mm with slightly higher amounts of evaporation occurring during the wet season (e.g. January, 235 mm) as compared to dry season months (e.g. July, 199 mm) (data source: Bureau of Meteorology - Climatic Averages, 1975).

The only other locality within the survey area where pan evaporation data have been collected is at Port George IV (near Kuri Bay), Western Australia, with a mean annual pan evaporation of 1,944 mm with slightly higher evaporative losses occurring during dry season months (159 mm in July) than those in wet season months (e.g., January 125 mm).

Although annual evaporation data are non-existent for the remainder of the survey area, the 2,469 mm-mean annual evaporative loss recorded for Normanton, Queensland, most likely is representative of annual evaporation occurring along waterways entering into the southern portion of the Gulf of Carpentaria in the survey area.

It is quite evident that the Kimberley and Joseph Bonaparte Gulf regions, together with the southern portion of the Gulf of Carpentaria, are considerably more seasonally arid than the northern coastline of the Northern Territory.

1.3.6 SEA SURFACE TEMPERATURES

Sea surface temperature data of oceanic waters surrounding the survey area have been collected somewhat haphazardly over the years by naval and oceanographic research vessels. Ships from Australia, Britain, Indonesia, Japan, Taiwan, USSR and the United States have undertaken surveys but not all data obtained are readily available. More recent data collection through satellites has been greatly disrupted

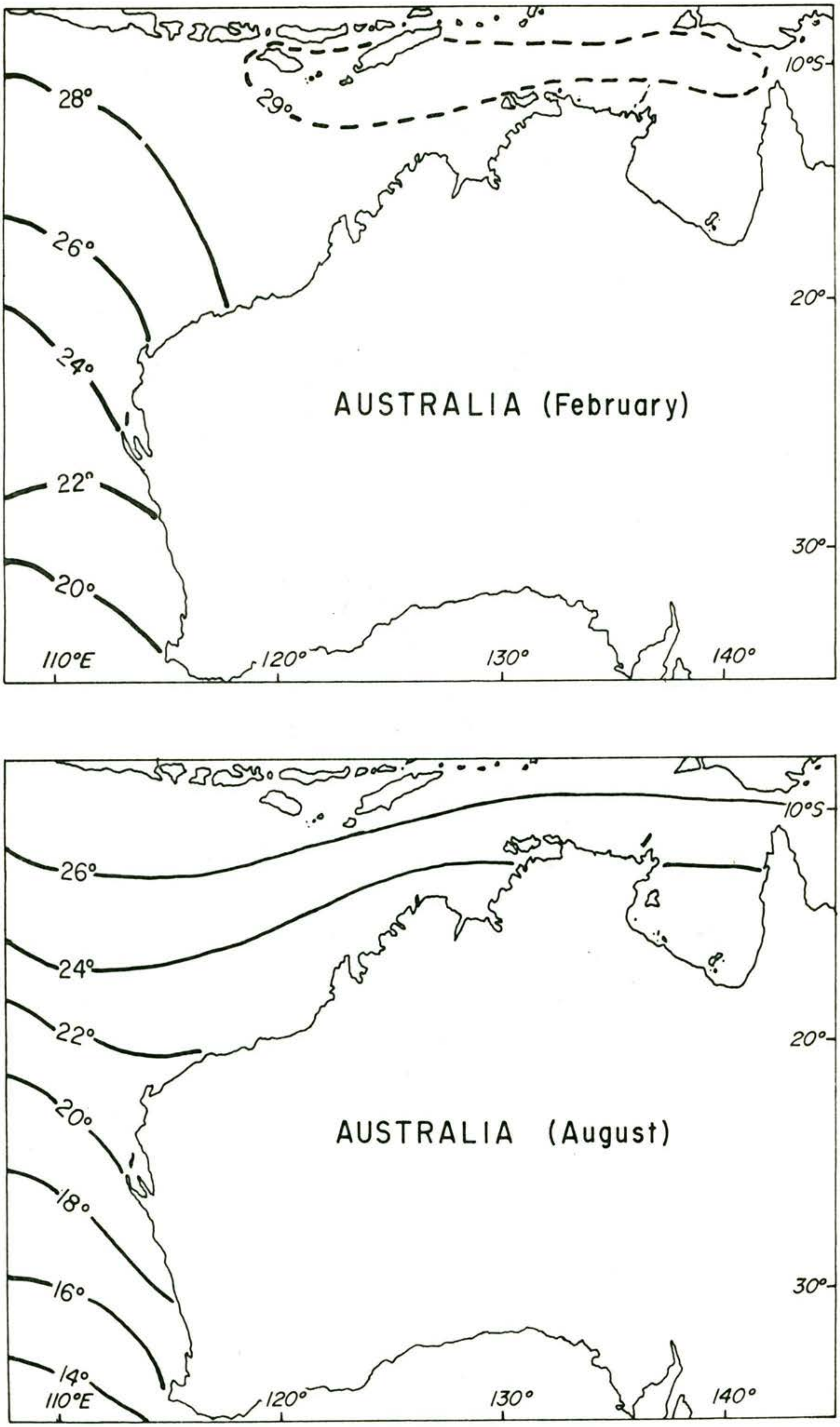


FIG. 1.3.6
Mean sea surface temperatures during summer and winter for the survey area and west Australian coastline (courtesy of Australian Hydrographic Office)

with the failure of SEASAT.

Distribution of sea surface temperatures during summer and winter throughout the survey area and also down the west Australian coastline is shown in Fig. 1.3.6. It is seen that in winter (August) there is more change of sea temperature with latitude than in summer (February) along the west Australian coastline. Proceeding down the coastline from Walcott Inlet (16°10'S, 124°24'E) (immediately south of the George Water System - survey area) where water temperature is 29°C to Fremantle (32°03'S, 115°44'E) where it is 21°C, involves a temperature drop of 8°C in February, whereas during August the drop is only 6°C from 23°C in the north (Walcott Inlet) to 17°C in the south (Perth).

Within the survey area, there is relatively little variation of sea temperature, during the 'wet' season, being around 29°C although inshore waters may remain one or two degrees warmer (30 - 31°C). During the dry season, sea surface temperature varies from around 23°C in the Kimberley region to only 24°C across the remainder of the coastline encompassed in the survey area.

Overall, throughout the survey area sea surface temperature gradually rises towards and during the 'wet' season to around 29 - 30°C and falls to between 23 - 24°C during the dry season.

1.3.7 SEA SURFACE CURRENTS

Unique to the western coast of Australia, among the mid latitude regions, is the seasonal reversal of its surface ocean flow (Rochford, 1975). Seasonal changes in current flow and constancy throughout the survey area and along the west Australian coastline are shown in Fig. 1.3.7. The absence of a definite cool current of sub-antarctic water is an outstanding characteristic of the Australian continent and this is borne out by the sea surface temperatures (Fig. 1.3.6).

Despite variability of current directions off the west Australian coastline, due largely to local wind conditions, the predominant

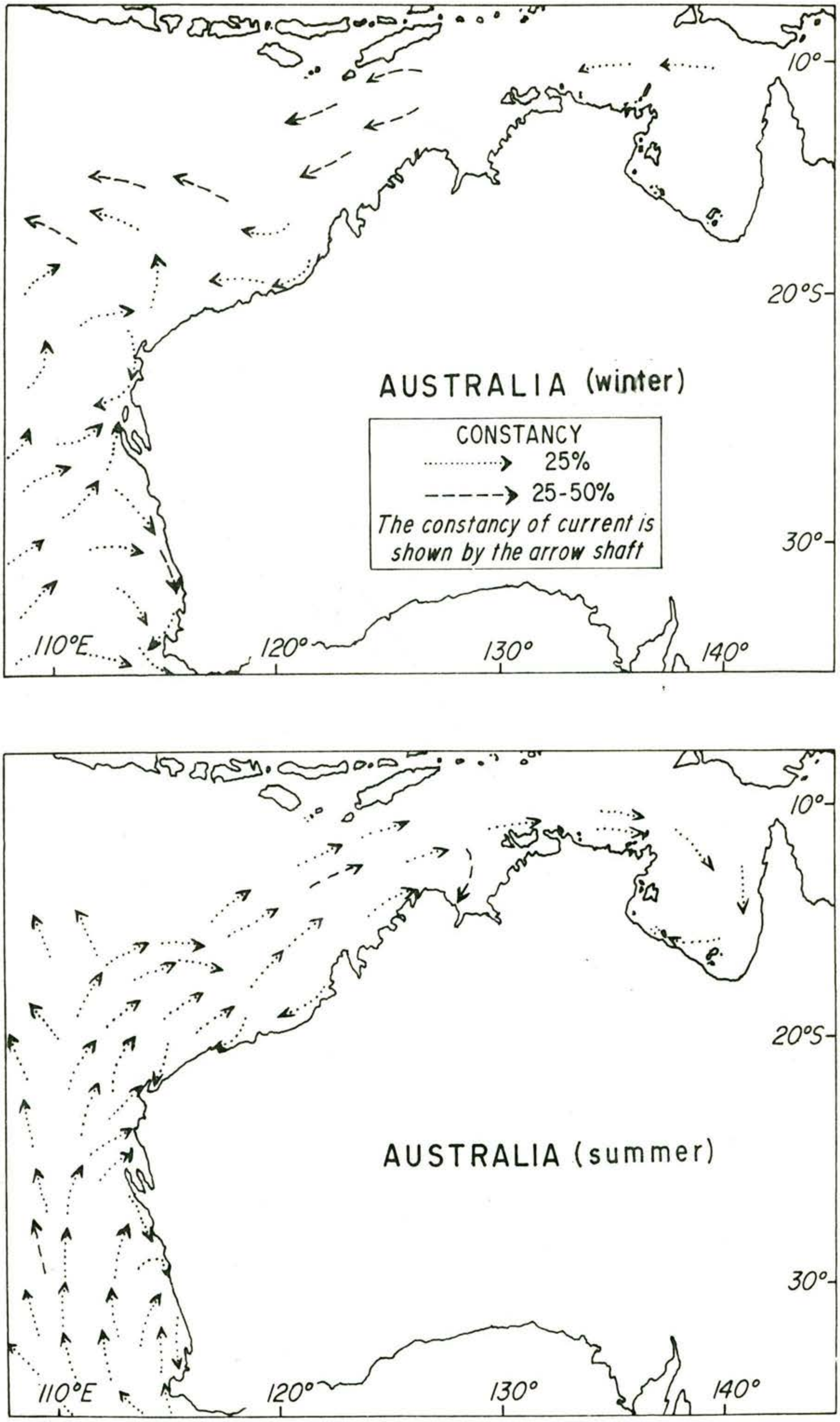


FIG. 1.3.7

Predominant current directional constancy during summer and winter for the survey area and the west Australian coastline (courtesy of Australian Hydrographic Office) currents form part of the general pattern of counterclockwise current circulation over the south Indian Ocean (Australian Hydrographic Office), whilst the seasonal changes in current flow, particularly throughout the survey area and along the north-west coastline of Western Australia, are responses to the north-west monsoonal winds of the 'wet' season (summer) and the largely prevailing south-east trade winds that blow across these oceanic waters during the dry season (winter).

In the 'wet' season (December - April), the predominant current direction is from the west with waters moving east-north-east from the Indian Ocean, through the Timor and Arafura Seas across the western and northern portions of the survey area (Rochford, 1975). Offshoots of this east-moving current reach into Joseph Bonaparte Gulf and also into the Gulf of Carpentaria, mainly due to waters being driven towards the coastline by monsoon winds. During the dry season (May - November) the predominant direction of the current is reversed now moving west-south-west, firstly through the Arafura and Timor Seas and then further westwards into the Indian Ocean to form the south equatorial current.

1.3.8 TIDAL VARIATION

Within the greater portion of the survey area - from the Kimberley region of Western Australia to Gove in the Northern Territory, semi-diurnal (4 tides/day) tidal patterns occur. The rise and fall of these tides typically follow a symmetrical sine wave (on the coast) passing through lunar cycles in which spring tides (attaining greater levels above and below mean water level) alternate with neap tides with much smaller amplitudinal fluctuations. Within the Gulf of Carpentaria only diurnal (two tides/day) tidal patterns normally occur and lunar differences, particularly for spring and neap tides, are not nearly so pronounced and may even be opposite in effect to those experienced in regions of the survey area under semi-diurnal tidal influence. Tidal bores may occur on river systems within the Kimberleys during spring high tides.

Tidal charts based on tide gauge records (Easton, 1970) show both diurnal and semi-diurnal tides entering the survey area from the Indian Ocean. Easton, (1970) and Webb, (1981) both show that these tides progress steadily across the Arafura Sea before forming a clockwise rotating system in the Gulf of Carpentaria (Fig. 1.3.7). In the region of Joseph Bonaparte Gulf Webb (1981) shows that the semi-diurnal tide is affected by a shallow continential shelf resonance, with the shallow Gulf of Carpentaria also being affected, via Torres Strait, by the tides of the Pacific Ocean. However Torres Strait is so choked with reefs that little tidal energy flows through it. Thus the age of the tide at Weipa on the western shore of Cape York Peninsula is, as McMurtree and Webb (1975) have shown, closer to that of the Indian Ocean tides than those of the nearby Coral Sea.

Spring tidal ranges, within the survey area, vary from up to 11 metres in the Kimberleys, 8 metres in the Darwin region, 3 metres in the Gove region and 2.5 metres along the south-western portion of the Gulf of Carpentaria (Australian National Tide Tables - all years). The noticeable decrease in tidal amplitudes inside the Gulf of Carpentaria is said to be due to the shallowness of its waters (Radok, 1976) and the constriction of Torres Strait - where tidal patterns are extremely complicated.

During the 'wet' season (November - April) prevailing winds from the north-west monsoon drive seawaters for several months into inshore regions of the survey area - in particular into Joseph Bonaparte Gulf and the Gulf of Carpentaria, and this effectively raises mean sea levels. In the 'dry' season (May - October) however, when the prevailing south-east winds blow across the continent, these waters are effectively driven out of the Gulfs and other coastal embayments along the north coast, and mean levels are considerably reduced from mean sea levels previously occurring during the 'wet' season (Radok, 1976). These seasonal variations in mean sea levels affect the width of intertidal zones and tidal inundation patterns for mangrove vegetation throughout the survey area, as patterns during the 'wet' season are completely different to tidal inundation patterns occurring during the 'dry' season.

Within waterways, effects such as bottom friction, discharge and channel width influence tidal ranges and rates of tidal penetration upstream. The progress of tides along waterways is often very complex and for the survey area, Messel *et al.* (1979) estimate tidal delays (upstream) of between 2 - 3 minutes/km during the 'dry' season. Tidal delays during the 'wet' season are generally longer for any point upstream, being greatly influenced by quantities of freshwater entering tidal portions of waterways from areas of upstream drainage. During periods of peak flooding, negligible tidal effect may occur.

Although a complete tidal cycle upstream is the same as that experienced in the surrounding seas, the duration of the ebb tide is normally ½ - 1 hour longer than flood tides. In some exceptional cases such as in the Victoria River, the flood tide has been known to rise in 2½ hours whereas the following ebb tide has lasted for 9½ hours (Messel *et al.*, 1979, Mono 2).

Along some of the lengthy waterways such as the Victoria, Daly, Adelaide, South Alligator, East Alligator and Roper Rivers, several different tides may be occurring along the length of the river (i.e. whereas the tide may be approaching a low in its upstream reaches, the following high tide is already approaching a high in the mouth region). In waterways of this survey area only up to two tides may be out of phase with each other and the situation is not nearly as complex as the eight tides that have been stated to be moving along the Amazon River at any one time (Day, 1951).

CHAPTER 2

MANGROVE SPECIES IN THE SURVEY AREA

2.1 INTRODUCTION

Observations on the structure and floristic composition of mangrove swamps fringing 110 tidal waterways in this survey area reveal a picture of considerable complexity with local site to site, regional and latitudinal variations that reflect a complex interaction of many factors. Structural characteristics of mangrove vegetation in the different regions are probably best described in relation to direct and indirect influences of climate, whereas distributions of the 27 mangrove species recorded in this survey (Table 1.2.1), as well as being influenced by climate, are also the result of complex interactions of physical, chemical and biological environments now and in the past.

Within Australia, considerable information on occurrences, distributions and associations of the various mangrove species around this continent is now on hand from studies by various workers, including Specht (1958); Macnae (1966, 1967); Beard (1967); Clarke and Hannon (1967); Wester (1967); Jones (1971a,b); Bird (1972 a, b); Hutchings (1973); Shine *et.al.* (1973); George and Kenneally (1975); Hegerl and Tarte (1974); Specht *et.al.* (1974); Gill (1975); Saenger and Hopkins (1975); Thom *et al.* (1975); Hegerl and Davie (1976); Lear and Turner (1977); Messel *et al.* (1977); Saenger *et al.* (1977); Saenger and Robson (1977); Specht *et al.* (1977); Semeniuk *et al.* (1978); Bunt (1978); Duke and Bunt (1979); Messel *et al.* (1979 - 1982); Bunt and Williams (1980); Dowling (1980); Semeniuk (1980); Stoddart (1980; Williams and Bunt (1980); Bunt *et al.* (1982); Wells (1981); Dowling and McDonald (1982); Kenneally (1982); Wells (1982, 1983); Spencely, (1983) and the present studies being undertaken by the Australian Institute of Marine Science.

Previous knowledge of the distributions of mangrove species in this survey area was sparse and localized, and consisted of species lists for the Gove region (Specht, 1958), the Ord River

(Thom *et al.* 1975) and brief lists for portions of the Kimberley region and Joseph Bonaparte Gulf (Gardner, 1923; Speck, 1960; Perry, 1970; George and Kenneally, 1975 and Semeniuk *et al.* 1978), Darwin Harbour (Macnae, 1966), Adelaide-Alligator Rivers region (Story, 1969, Story *et al.* (1976); Hegerl *et al.* 1979) and a checklist of Northern Territory plants provided by Chippendale (1972). Saenger *et al.* (1977) presumably used some of these studies in their overview of mangrove swamps in this area of Australia, however it is not clear on what basis they reached their stated levels of floristic diversity for different regions. In fact, some species recorded by Chippendale (1972) as occurring in the Northern Territory (ex Herbarium specimens) are still not included in the overview of Saenger *et al.* (1977).

Additional mangrove species recorded in this present survey increase by around 100% the number of mangrove species previously published for the Gove Peninsula (Specht, 1958) and for the Ord River (Thom *et al.* 1975). In the Kimberley region, however, more recent lists of mangroves (11 species) recorded in the Prince Regent River Reserve (George and Kenneally, 1975) and for the entire Kimberley region (14 species) (Semeniuk *et al.* 1978) are in agreement with the fourteen species recorded by Wells, (1981).

Considerable work on distribution of mangroves in relation to coastal geomorphology has shown that vegetational change at a particular site or within a region occurs largely in response to changes in physical characteristics of the environment (Lugo and Snedaker, 1974; Thom, 1967; Thom *et al.* 1975; Cintron *et al.* 1978; Ball, 1980, among others) and that the influence of physical factors on competitive abilities of the various species probably accounts for characteristic zonation patterns often seen in mangrove vegetation. However, Mizrachi *et al.* (1980) suggest that salt resistance mechanisms of the various species could also be important in helping to explain zonal distribution of species at any site.

Physiography is known to be an important factor in explaining many zonation patterns in mangrove swamps (Clarke and Hannon, 1969) and these patterns are generally well correlated with frequency and duration of tidal immersion (Watson, 1928; Chapman, 1944; Macnae, 1968, in particular), as elevation above mean sea level, river floods and microtopography of any area largely determine tidal flooding patterns.

Many patterns of zonation of species in this survey area often broadly follow the patterns described by Macnae (1966, 1968). However, as Bunt (1978) and Bunt *et al*, (1982) commented, the approach by Macnae is a gross simplification of an exceedingly complex problem and in this area of study there are numerous examples of patterns of zonation differing from those given in the literature.

Tidal characteristics exert their influence on patterns of zonation and species associations through many intermediate factors such as salinity of surface and soil water and degree of soil saturation (Mogg, 1963; Giglioni and Thornton, 1965; Thom, 1967; Macnae, 1968; Clarke and Hannon, 1970; Cintron *et al*, 1978, among others) and with this in mind, considerable attention was given to seasonal variations of soil and water salinities at sites in this survey area.

It is the purpose of this chapter primarily to report the distributions of various mangrove species recorded in this survey and to discuss possible reasons for such distributions. Also reported are various associations formed by the species, their occurrences in different regions, particular habitat preferences and strategies of establishment and regeneration. Information on peak dry season soil and water salinities is also provided for most species.

For meaningful discussion of the distributions of the species in this survey area, it is first necessary to examine distributions of each of these species throughout Australia and also throughout their various geographical ranges in the Indo-Pacific region.

2.2 METHODS

Each of the 110 tidal waterways in this survey area were systematically examined, often on a number of occasions, using five-metre work boats between 1975 and 1979. Frequent land excursions were made into the mangrove swamps at each site. Mangrove species were identified (Section 1.2.2) and lists obtained for each site (Appendix A1).

Water salinities were measured with Autolab (Model 602) salinity temperature bridges and American Optics Refractometers (Model 10419). Soil salinities (salinity of the interstitial water (50 cm deep)) were obtained using American Optics Refractometers.

In the following sections (Sections 2.3.1-2.3.24) species distributions (dot pattern) are not indicative of a locality record for a herbarium specimen (although this may be the case), but rather the specific area of the coastline at which the species has been recorded.

(Amendments 18.9.84).

In this thesis each individual tidal waterway or system is considered a "site".

Data on distributions on the west coast of Cape York result from personal observations on the Nassau, Staaten, Gilbert, Norman Rivers and inspection of aerial photographs.

All tree heights mentioned throughout the thesis are visual estimates.

2.3 RESULTS

2.3.1 ACANTHACEAE

Acanthus ilicifolius L.

GROWTH FORM: Small sparsely branched herb or small shrub 1-2 metres high.

OCCURRENCE: Fairly restricted; found on 49 of the 110 tidal waterways examined.

Acanthus ilicifolius is commonly found colonizing accreting portions of meanders along tidal waterways across the northern coastline of Arnhem Land. On such sites it may form a monospecific understorey within pioneer stands of *Sonneratia alba, Avicennia officinalis* and/or *Avicennia marina*. *Acanthus ilicifolius* occurs amongst the understorey of fringing vegetation along tidal waterways - particularly along portions of waterways that remain brackish for considerable periods of the year. The species is also frequently observed as understorey amongst trees forming the more landward mangrove zones - again particularly in brackish water areas. *Acanthus ilicifolius* tolerates up to 7 months' inundation by freshwater but also commonly colonizes banks of tidal waterways that become hypersaline towards the end of the dry season.

Within the survey area, *Acanthus ilicifolius* occurs in areas inundated by waters of salinity up to 65‰ whereas the highest soil salinity recorded for this species was 73‰.

REGENERATION: The flat seeds are released from a fruit capsule and are dispersed by the tides. Seedling establishment appears more common on unshaded sites, although this is not always true.

PLATE 2.3.1.1
Fruit, a glossy brown capsule (*c*. 2 cm) encloses several seeds.

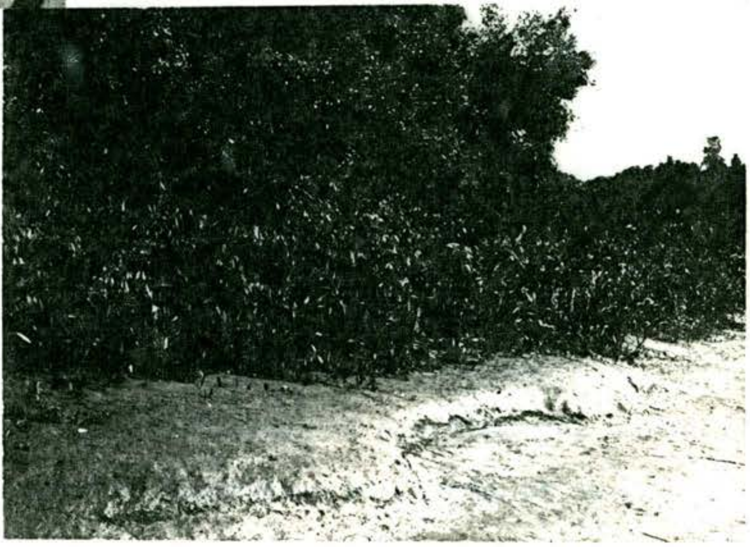
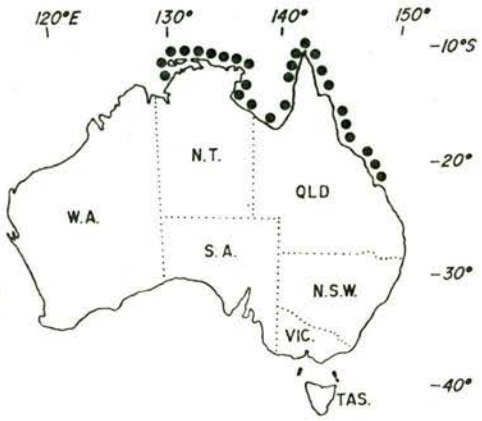


PLATE 2.3.1.2
Acanthus ilicifolius growing at the riverine edge of accreting mudbanks around convex portions of meanders



The southernmost limits of distribution of this species are the Daly River (13°10'S, 130°14'E) on the west coast of the Northern Territory (Wells, 1982) and St Lawrence, Qld (22°15'S) on the east Australian coastline (Jones, 1971a).

Acanthus ilicifolius, although often locally abundant, is discontinuous in occurrence on tidal waterways of the Northern Territory eastwards of the Daly River. The species is particularly uncommon on tidal waterways entering the Gulf of Carpentaria but is more abundant (although still discontinuous in occurrence) along the north-eastern Australian coastline (Bunt, 1978; Duke 1981).

(Amendment 18.9.84).

Avicennia marina

A. eucalyptifolia may be a synonym for *A. marina*. This author is well aware of the nomenclatural difficulties with *Avicennia* that await resolution. In this thesis I have referred to the species as *A. marina* (Forsk.) Vierh. The Australian plant is recognized by some authors as being a distinct variety in which case the correct name would be *A. marina* var. *australasica* (Walp.) Moldenke (1960). This variety is considered synomymous with *A. marina* var. *resinfera* (Forsk) Bakh. *A. eucalyptifolia* Zipp ex Miq. is so called because its leaves are lanceolate. It is similar to *A. marina* but with narrowly lanceolate leaves and with more slender inflorescences.

2.3.2 AVICENNIACEAE

Avicennia marina (Forsk.) Vierh. Syn. *A. eucalyptifolia* Zipp. ex Miq.

GROWTH FORM: Tree up to 25 metres to small shrub 1-3 metres in height.

OCCURRENCE: Widespread; found on all of the 110 tidal waterways examined in the survey area.

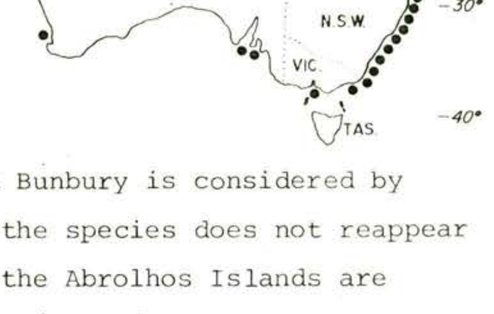
Avicennia marina often forms a monospecific pioneer community on newly accreting mudbanks in estuaries. It may also be found in a mixed pioneer association with either *Sonneratia alba* or *Camptostemon schultzii* or both. *Avicennia marina* forms associations with all mangrove species but it is frequently encountered with *Rhizophora stylosa* and *Camptostemon schultzii* amongst fringing riverside vegetation along tidal waterways in the far north. It also occurs in association with *Ceriops tagal* var. *australis* and *Excoecaria agallocha* in less frequently inundated, more landward sites. It may form a nearly monospecific woodland in the most landward mangrove zone where tidal inundation is infrequent and soil salinities rise to values greater than 70‰ by the middle of the dry season.

The species tolerates a wide range of environmental conditions. It grows in sites that are inundated by freshwater to a depth of over 1 metre for up to 3 months of the year. Within the study area, *Avicennia marina* was found at sites inundated by waters of salinity up to 85‰ whereas the highest soil salinity recorded for this species was 128‰; under these conditions *Avicennia marina* occurred as a shrub less than 0.5 metres in height.

REGENERATION: When the small oval-shaped fruit falls from the tree it swells then splits, letting the seedling break out of the pericarp. The propagule is dispersed by the tide. Seedlings often establish themselves throughout the mangrove forests in the wet season but most die, apparently due to low light intensity on the forest floor. Other seedlings may initially colonize bare mud flats during the wet season but most die during the dry season. Successful seedling colonization is most common on bare muds of accreting banks and within landward mangrove zones.

PLATE 2.3.2.1
Large *Avicennia marina*, erect slender peg-like pneumatophores, emanating from radiating underground cable roots, protrude through the mud.

PLATE 2.3.2.2
Avicennia marina in coppicing habit. Numerous trees growing from a tree trunk that has fallen over in the swamp.



The southernmost limits of distribution of this species are Leschenault Inlet, Bunbury (33°16'S, 115°42'E) on the west Australian coast and at Corner Inlet, Victoria (38°45'S, 146°42'E) on the south-east Australian coast. *Avicennia marina* at Corner Inlet is the southernmost occurrence of any mangrove species in the world.

The occurrence of *Avicennia marina* at Bunbury is considered by Semeniuk *et al.*, 1978, to be an outlier as the species does not reappear along the west Australian coastline until the Abrolhos Islands are reached. Northwards from this point *Avicennia marina* is common at suitable sites around the entire coastline to Corner Inlet in Victoria. Isolated pockets of this species also occur in protected coastal pockets throughout South Australia, Butler *et al.*, 1977).

Avicennia officinalis L.

GROWTH FORM: Shrub to small tree up to 7 metres high.

OCCURRENCE: Restricted; found on only 16 of the 110 tidal waterways examined.

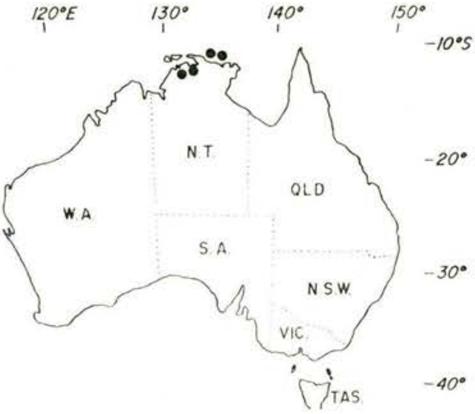
Avicennia officinalis colonizes soft muds along portions of tidal waterways that remain brackish for most of the year. In such habitats it is common on accreting convex portions of meanders where it occurs as a pioneer shrub or small tree, often with *Sonneratia alba*. The species may form a pioneering monospecific band around such convex portions of meanders but this is unusual within the survey area. *Acanthus ilicifolius* and/or *Aegiceras corniculatum* normally provide understorey in this association. *Avicennia officinalis* has not been observed colonizing sites within the landward mangrove zones but occurs only amongst fringing vegetation along the banks of the waterways.

The restricted distribution of this species is difficult to explain. Many river systems in the same latitudinal belt appear to provide suitable habitat for colonization but lack this species. In the few river systems in which *Avicennia officinalis* is found it prefers brackish water sites for colonization but also occurs as fringing vegetation along waterways that become hypersaline by the end of the dry season. Within the survey area, the species was found in areas inundated by waters of salinity up to 63°/oo whereas the highest soil salinity recorded for *Avicennia officinalis* was 66°/oo ; it occurs under these conditions as a shrub less than 2 metres in height.

REGENERATION: Seedlings of *Avicennia officinalis* colonize bare mud on accreting portions of river meanders. Seedlings appear intolerant of shade and have not been observed amongst the understorey of fringing riverside vegetation on any of the tidal waterways examined.

PLATE 2.3.3.1
No trunk buttresses, but masses of adventitious roots serving as pneumatophores are often present.

PLATE 2.3.3.2
Fruit, heart-shaped, slightly flattened, beaked, covered in soft brown tomentum.



The restricted distribution of this species could be a result of its being at the edge of its geographical range in northern Australia.

Avicennia officinalis has not been recorded west of Buffalo Creek, Darwin, NT (12°20'S, 130°57'E) or east of the Glyde River (12°16'S, 135°03'E) in eastern Arnhem Land (Wells, 1982). That *Avicennia officinalis* does not occur in rivers entering the north coast of Melville Island is most unusual as this species is quite widely distributed throughout south-east Asia (Chai, 1973; Chapman, 1975).

Camptostemon schultzii Mas.

GROWTH FORM: Shrub to large tree up to 25 metres high.

OCCURRENCE: Widespread; found on 70 of the 110 tidal waterways examined.

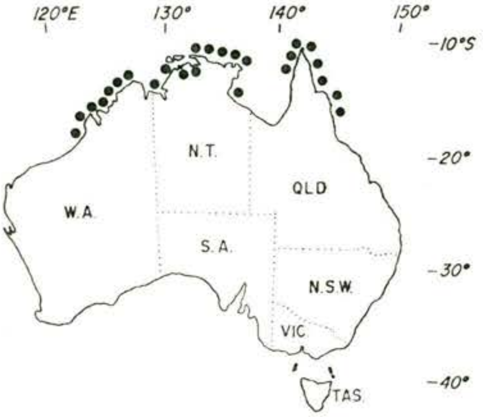
Camptostemon schultzii occurs in association with most mangrove tree and shrub species within the survey area, often on well drained sites. It frequently forms an association with *Rhizophora stylosa* and *Avicennia marina* as fringing vegetation along tidal waterways and attains large tree dimensions along portions of waterways that remain brackish for most of the year.

On accreting mudbanks to seaward, particularly in the Kimberley area of Western Australia, *Camptostemon schultzii* may form a pioneer association with *Sonneratia alba* and/or *Avicennia marina* (height $\leq$8 metres). Such an association is unusual for *Camptostemon*. This species normally prefers to colonize well drained soils on sites that are inundated only by spring high tides. However, on the extensive gently sloping mudbanks of many embayments in the Kimberley region (particularly Port Warrender), the species may be inundated twice per day by tides attaining heights of 8 metres that allow high tide waters to inundate all but the upper portions of the canopy of this association.

It is common as a small tree to shrub in estuarine localities and along the banks of hypersaline waterways. Within the survey area, the species was found in areas inundated by waters of salinity up to $75^{o}/_{oo}$, whereas the highest soil salinity in which *Camptostemon schultzii* was observed growing was $82^{o}/_{oo}$; it occurred under these conditions as a shrub less than 2 metres in height.

REGENERATION: The woolly seeds are dispersed by the tides and seedlings survive below forest canopies in fringing riverside swamps. Within the Kimberley region, seedlings also colonize exposed mudbanks.

PLATE 2.3.4.1
Trunk fluted at the base. Pneumatophores present as thick rounded woody structures above the ground (with characteristic circular white lenticels).



The southernmost limits of distribution of *Camptostemon schultzii* are Cape Bossut (18°43'S, 121°38'E) on the west Australian coastline (Semeniuk *et al.*, 1978) and the Pascoe River, Qld (12°31'S) on the east Australian coastline (Duke, 1981). The species is common from Cape Bossut to Gove (12°13'S, 136°42'E) in the Northern Territory, excluding the Joseph Bonaparte Gulf region where it is uncommon and the north coast of Melville Island, where it is unrecorded (Wells, 1982). *Camptostemon schultzii* has also not been observed on any tidal waterway entering the western shores of the Gulf of Carpentaria although isolated trees of this species were recorded on the Limmen Bight River (15°06'S, 135°42'E), which enters into the southern portion of the Gulf of Carpentaria. The species is unknown on any other tidal waterway entering the southern shoreline of the Gulf of Carpentaria across to Karumba (Saenger & Hopkins, 1975; Wells, 1982). Olsen (pers.comm.) records isolated trees at Karumba.

Along eastern shores of the Gulf of Carpentaria this species occurs at least as far south as Weipa, Qld (12°40'S, 141°50'E) (Specht *et al.*, 1977). Bunt (1978) describes the distribution of *Camptostemon schultzii* down the east Australia coast as being discontinuous in occurrence from Cape York to Cooktown, Qld. *Camptostemon schultzii* is one of the few mangrove species that comes close to being endemic to Australia. As well as its wide distribution across northern Australia, the species also occurs in tidal waterways entering the Gulf of Papua (Percival & Womersley, 1975; Floyd, 1977).

Lumnitzera littorea (Jack) Voigt

GROWTH FORM: In the survey area it is a shrub to small tree up to 8 metres high. In contrast, this species occurs as a tree up to 25 metres in height in Malaysia and the northern parts of Cape York Peninsula.

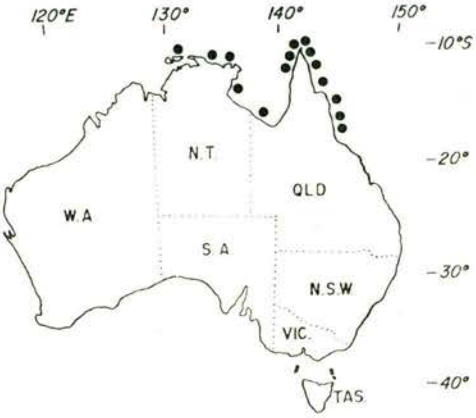
OCCURRENCE: Restricted; found on only 9 of the 110 tidal waterways examined.

Lumnitzera littorea normally is found as a shrub on rock/mud substrates but also colonizes infrequently inundated sites along tidal waterways that attain salinities equal to or greater than seawater by the middle of the dry season. It may also occur as a small tree or shrub in landward mangrove zones that are subject to considerable brackish water inundation, in association with *Bruguiera gymnorhiza; Rhizophora apiculata, Aegiceras corniculatum* and *Excoecaria agallocha*. *Lumnitzera littorea* is often associated with another shrub *Scyphiphora hydrophyllacea* on suitable rock/mud substrates. These two species may have distinct preferences for infrequently inundated well drained soils. Within the survey area, *Lumnitzera littorea* was found in areas inundated by waters of salinity up to 35‰.

REGENERATION: The small woody fruits are dispersed by the tides. Only occasional colonization of sites by seedlings of this species has been observed.

PLATE 2.3.5.1
The narrowly obovate alternate leaves are succulent and brittle in texture. Flowers red, borne in terminal racemes. The fruiting body is *c.* 2 cm long, vase-shaped.

PLATE 2.3.5.2
A bushy shrub of *Lumnitzera littorea* (height 3 metres) on the Woolen River, NT.



Lumnitzera littorea has not been recorded west of the Johnston River (11°18'S, 131°10'E) on Melville Island. Distribution of the species across the northern portion of Arnhem Land is discontinuous and it has not been recorded south of the Rose River (14°17'S, 135°44'E) on the western shore of the Gulf of Carpentaria (Wells, 1982).

Saenger & Hopkins (1975) record *Lumnitzera littorea* at Tarrant Point (17°23'S, 139°25'E) in the south-eastern portion of the Gulf of Carpentaria and Woolston (1973) also records the species at Mornington Island.

Along the eastern shore of the Gulf of Carpentaria, *Lumnitzera littorea* occurs at least as far south as Weipa (Love, pers. comm.). On the east Australian coast this species is recorded south to the Herbert River, Qld (18°32'S) (Jones, 1971a), although it has a discontinuous distribution throughout this area (Bunt, 1978; Duke & Bunt pers. comm.).

Lumnitzera littorea only occurs as a shrub to small tree <6 metres in the Northern Territory (Wells, 1982). On Cape York Peninsula this species often attains tree heights to 25 metres (Bunt, 1978).

Lumnitzera racemosa Willd.

GROWTH FORM: Shrub to small tree up to 5 metres high.

OCCURRENCE: Widespread; found on 84 of the 110 tidal waterways examined.

Lumnitzera racemosa normally colonizes the more landward, less frequently inundated mangrove zones. It occurs amongst fringing riverside vegetation along portions of tidal waterways that remain fresh or slightly brackish for the greater part of the year. It sometimes forms nearly monospecific stands on the landward fringe of mangrove forests - particularly in areas where the landward fringe merges into a sedge swamp. *Lumnitzera racemosa* also commonly occurs in association with *Ceriops tagal* var. *australis*, *Excoecaria agallocha*, *Avicennia marina* and *Aegialitis annulata* on consolidated muds in areas that are infrequently inundated.

The species withstands considerable periods of inundation by freshwater. In seasonally flooded areas, it grows in a mallee habit. *Lumnitzera racemosa* also can tolerate extremely saline conditions (e.g. areas inundated by waters of salinity up to 78‰). Being common in infrequently inundated zones, its salinity tolerance would probably be much higher than the 78‰ recorded here. The highest soil salinity in which the species was observed growing was 87‰; it occurs under these conditions as a shrub less than 1.5 metres in height.

REGENERATION: The small woody seeds are dispersed by the tides and may be deposited along the banks of tidal waterways in large numbers. Successful seedling establishment has been observed at open sites only. Seedlings are intolerant of shade.

PLATE 2.3.6.1
Lumnitzera racemosa grows in a 'mallee' habit in areas totally inundated by fresh or brackish waters for most of the year.

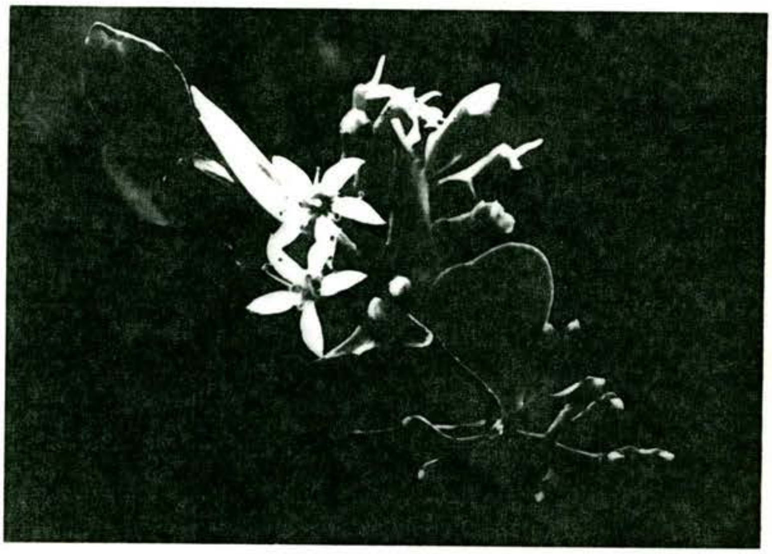
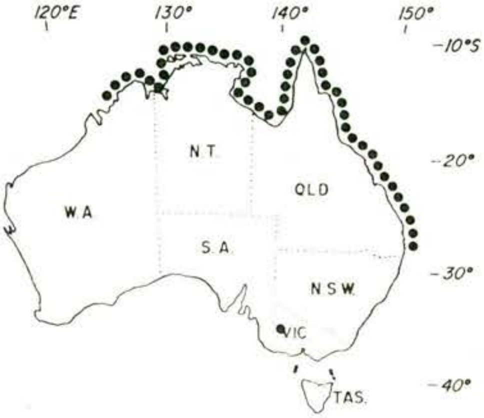


PLATE 2.3.6.2
The small white flowers are borne in axillary racemes. Fruit, small, sessile, crowned at the apex by five erect calyx lobes.



The southernmost limits of distribution of *Lumnitzera racemosa* are Beagle Bay ($16^{\circ}56'$S, $122^{\circ}32'$E) on the west Australian coast (Semeniuk *et al.*, 1978) and Moreton Bay, Qld ($27^{\circ}30'$S) on the east Australian coast (Dowling, 1979).

Excluding the Kimberley area of Western Australia, where the species is uncommon, *Lumnitzera racemosa* is widespread throughout the remainder of its range.

2.3.7 EUPHORBIACEAE

Excoecaria agallocha L.

GROWTH FORM: Shrub to large tree up to 10 metres high.

OCCURRENCE: Widespread; found on 106 of the 110 tidal waterways examined.

Excoecaria agallocha frequently occurs in association with *Ceriops tagal* var. *australis*, *Avicennia marina* and *Lumnitzera racemosa* on consolidated muds in the more landward, less frequently inundated zones. It also occurs as tall trees amongst fringing riverside vegetation along portions of tidal waterways that remain brackish for the greater part of the dry season.

Excoecaria agallocha in association with *Avicennia marina* is a noticeable component of fringing riverside vegetation on all upstream portions of tidal waterways in the north-west Kimberleys (WA) and the Ord (WA) Victoria and Fitzmaurice rivers in the Northern Territory. This association is inundated only by spring high tides. The large tidal range and rapidly increasing land gradients back from the river banks that occur here may be responsible for the lack of suitable sites for colonization by other mangrove species. Most mangrove species may be unable to tolerate the high soil salinities towards the end of the dry season at sites colonized by the *Excoecaria/Avicennia* association; hence, the occurrence of this association as fringing riverside vegetation in these areas may result from complex interactions of several environmental factors.

Excoecaria agallocha tolerates long periods of inundation by freshwater. Within the survey area, the species was found at sites inundated by waters of salinity up to 85‰ whereas the highest soil salinity recorded for this species was 90‰; it occurred under these conditions as a shrub less than 1 metre in height.

REGENERATION: The small seeds are dispersed by the tide. Seedlings are often found in peripheral localities at the landward edge of mangrove swamps - particularly in areas abutting saltpans and appear tolerant of low light levels.

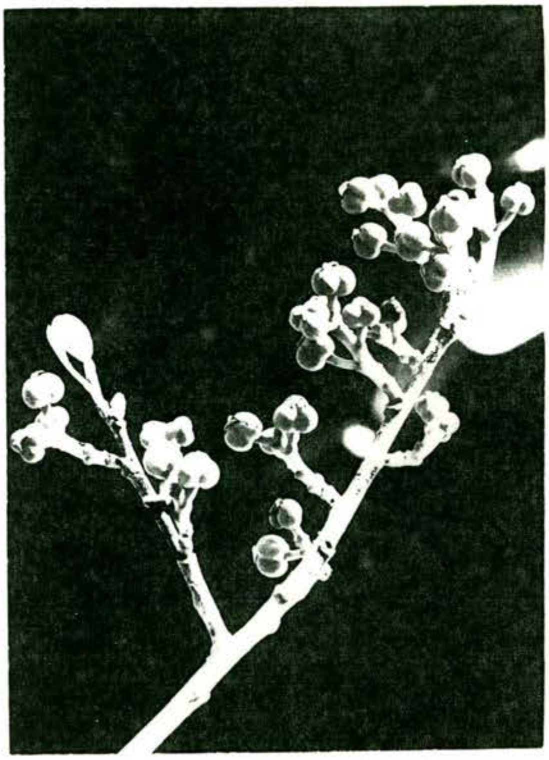
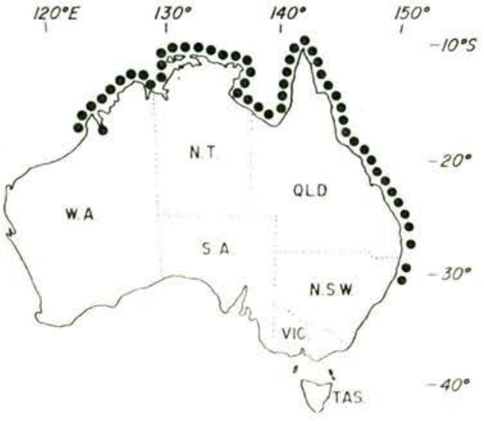


PLATE 2.3.7.1
Male and female flowers in axillary racemes. Female flowers much shorter. Fruit (shown) a small tri-lobed capsule which explodes releasing three seeds.

PLATE 2.3.7.2
Excoecaria agallocha occurs as a shrub in the inner mangrove zones. (Lenticels on surface roots allow these roots to function as pneumatophores.)



The southernmost limits of distribution of *Excoecaria agallocha* are at Thangoo Station (18°16'S, 122°10'E) on the west Australian coast (Semeniuk *et al*, 1978) and Laurieton NSW (31°39'S, (31°39'S, 152°48'E) on the east Australian coast (W.G. Allaway, pers.comm). *Excoecaria agallocha* is fairly abundant throughout its range except at sites along the NSW coastline, where it is discontinuous in occurrence.

It occurs on most tidal waterways particularly in association with *Avicennia marina*, *Ceriops tagal* var. *australis* and *Lumnitzera racemosa* on consolidated muds in the more landward, less frequently inundated zones.

(Amendment 18.9.84).

Xylocarpus spp.

After extensive examination of *Xylocarpus* spp. in S.E. Asia and northern Australia there still exists confusion in nomenclature. The correct name for *Xylocarpus* species is in doubt. C.A. Gardner (1923) and R.L. Specht (1958) refer to it as *X. granatum* Koen, Noamesi (1958) considers it to be *X. moluccensis* (Lamk) Roem., while recent workers have preferred the name *X. mekongensis* Pierre (Dr. Tomkinson per N. Duke, pers. comm.). The material in the N.T. Herbarium comes closest to that of *X. australasicus* Ridley which was described from northern Queensland. Additionally material from the Kimberleys in W.A. held at the W.A. Herbarium matches the type specimens of this species held at the Royal Botanic Gardens, Kew (Kenneally, pers. comm.).

2.3.8 MELIACEAE

Xylocarpus australasicus Ridl.

GROWTH FORM: Shrub to large tree up to 14 metres high.

OCCURRENCE: Widespread; found on 91 of the 110 tidal waterways examined.

Xylocarpus australasicus is frequently represented amongst fringing riverside vegetation along north Australian tidal waterways. In portions of rivers that remain brackish for long periods of the dry season, *Xylocarpus australasicus* occurs as the dominant tree species in association with *Diospyros ferrea* var. *humilis*, *Bruguiera parviflora* and *Rhizophora stylosa*. The most extensive forest types of this nature occur on Andranangoo Creek, Melville Island and the Koolatong River (Blue Mud Bay, NT). *Xylocarpus australasicus* has not been observed as a pioneering species and colonizes sites that are infrequently inundated. The species can withstand long periods of inundation by freshwater (up to 8 months) and also tolerates limited periods of hypersaline conditions. Within the survey area, the species was found in areas inundated by waters of salinity up to 76‰ whereas the highest soil salinity recorded for *Xylocarpus australasicus* was 84‰; it occurred under these conditions as a shrub less than 1 metre in height.

REGENERATION: The large angular seeds of *Xylocarpus australasicus* are widely distributed by the tide but many fail to germinate. Many are attacked by boring insects. Seedlings are frequently encountered on consolidated muds amongst fringing riverside vegetation. Seedlings appear to be able to tolerate low light levels.

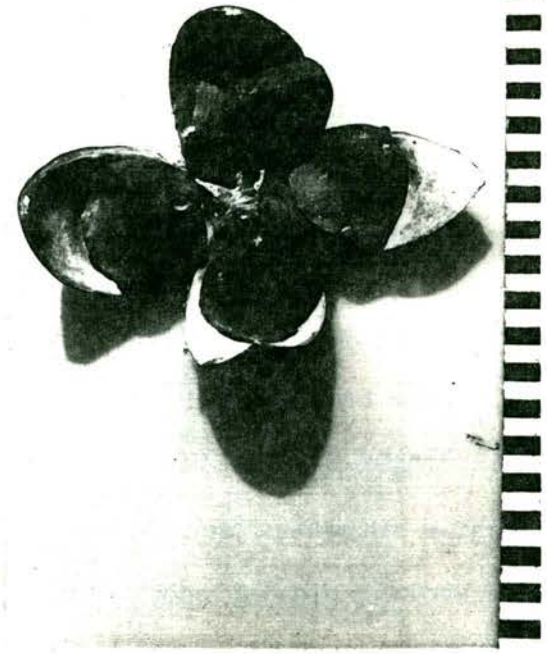


PLATE 2.3.8.1
Fruit, round, 8-9 cm diameter - encloses several irregularly shaped pithy shells, each of which encloses a single seed (side scale in cm).

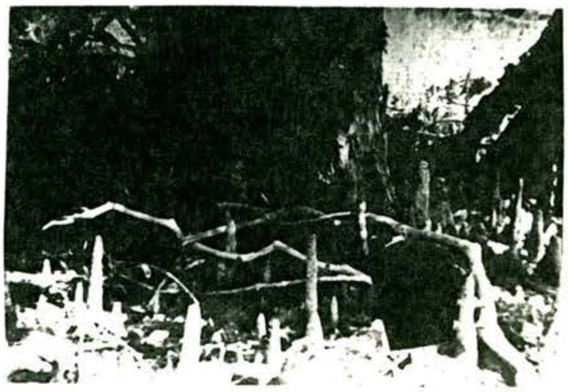
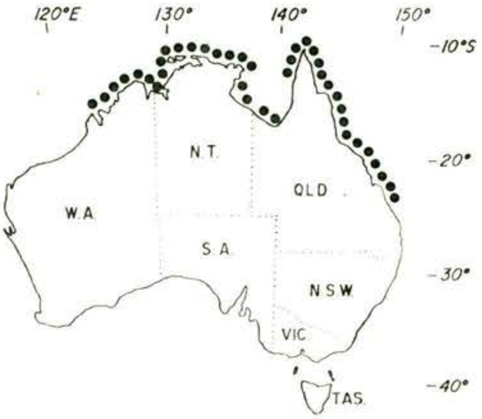


PLATE 2.3.8.2
Pneumatophores (thick wood, conical knobs) rise, from underground cable roots, through the mud around the base of the tree.



The southernmost limits of distribution of *Xylocarpus australasicus* are King Sound, Derby (17°19'S, 123°38'E) on the west Australian coast (Semeniuk *et al*, 1978) and Gladstone, Qld (23°50'S) on the east Australian coast (Saenger & Robson, 1977).

Throughout this area *Xylocarpus australasicus* commonly occurs as isolated trees amongst fringing vegetation along tidal waterways. In portions of tidal waterways that remain brackish for long periods, *Xylocarpus australasicus* may occur as a dominant tree species typically in association with *Diospyros ferrea* var. *humilis*, *Bruguiera parviflora* and *Rhizophora stylosa* on suitable substrates.

Xylocarpus granatum Koen.

GROWTH FORM: Shrub to small tree up to 9 metres high.

OCCURRENCE: Restricted; found on only 3 of the 110 tidal waterways examined.

Xylocarpus granatum occurs on various substrates, in particular, consolidated muds. It is often associated with *Rhizophora apiculata, Bruguiera gymnorhiza, Xylocarpus australasicus* and the mangrove fern *Acrostichum speciosum* within the survey area. The species can withstand considerable periods of inundation by freshwater but on the three tidal waterways on which it has been observed, it shows a preference for sites that are infrequently inundated by brackish waters. In waters approaching seawater salinity *Xylocarpus granatum* occurs as a small shrub (height ≤ 2 metres). Within the survey area, the species was found at sites inundated by waters of salinity up to 34‰.

REGENERATION: The large angular seeds are dispersed by the tides and successful establishment of seedlings occurs beneath overlying tree canopies. Seedlings appear extremely shade tolerant.

PLATE 2.3.9.1
The large round 'cannonball' fruit often 10-12 cm in diameter, has a thick rind which splits into four parts and contains 10-18 irregularly shaped pithy shells, each of which encloses a single seed.

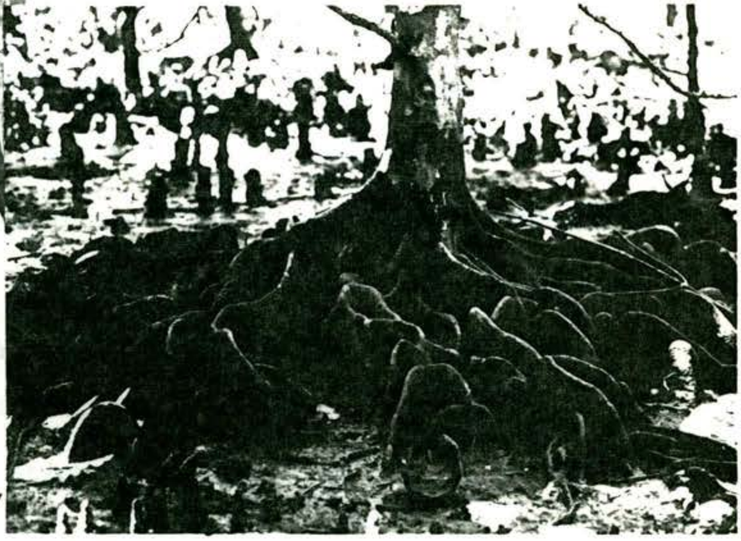
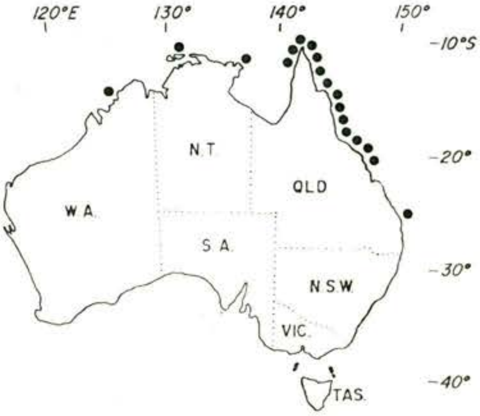


PLATE 2.3.9.2
Deep plank roots meander away from the base and form narrow, ridged, plate-like pneumatophores.

The southernmost limits of distribution of *Xylocarpus granatum* are the Prince Regent River ($15^{O}27$'S, $125^{O}03$'E) on the west Australian coast (Wells, 1981) and Frazer Island, Qld ($25^{O}30$'S) on the east Australian coast (Dowling and McDonald, 1982).



In the Northern Territory *Xylocarpus granatum* occurs on Andranangoo Creek, Melville Island ($11^{O}21$'S, $130^{O}51$'E) and on the Gove Peninsula (Yirrkala) (Specht, 1958). Waddy (pers.comm.) reports the species on Groote Eylandt.

The species has not been recorded on any other tidal waterway in the Northern Territory (Wells, 1982). Saenger and Hopkins (1975) report the species at Tarrant Point, Qld ($17^{O}23$'S, $139^{O}25$'E) in the south-eastern portion of the Gulf of Carpentaria. The writer considers this record is most probably *Xylocarpus australasicus* as this species has been observed growing at Karumba ($17^{O}28$'S, $140^{O}50$'E) a little distance away from Tarrant Point under an equally seasonally arid climate.

Specht *et al.* (1977) record *Xylocarpus granatum* at Weipa and the species is fairly abundant in the Port Musgrave area north of Weipa (Messel *et al.* 1981). Distribution of this species along the remainder of the western shores of Cape York Peninsula is unknown. *Xylocarpus granatum* is particularly common amongst fringing vegetation in tidal waterways down the east Australian coastline (Bunt, 1978; Duke, 1981).

2.3.10 MYRSINACEAE

Aegiceras corniculatum (L.) Blanco.

GROWTH FORM: Shrub up to 5 metres high.

OCCURRENCE: Widespread; found on 103 of the 110 tidal waterways examined.

Aegiceras corniculatum commonly forms an understorey in fringing riverside tree associations along tidal waterways. The species colonizes consolidated muds and may also form groves at the landward edge of swamps - particularly along portions of rivers that remain brackish for long periods during the dry season. In upstream areas of tidal waterways that become hypersaline by the end of the dry season, *Aegiceras corniculatum* may form an association with *Sonneratia alba* on soft unconsolidated muds. In such situations, impenetrable thickets of *Aegiceras* occur beneath the *Sonneratia* tree canopy.

Aegiceras corniculatum forms associations with most mangrove species. It is a plant extremely tolerant to a wide range of environmental conditions, and can withstand up to 9 months' continual freshwater inundation. It occurs as a small shrub (height ≤2 metres) throughout the fringing vegetation of most hypersaline waterways.

Within the survey area, the species was found at sites inundated by waters of salinity up to 67‰, whereas the highest soil salinity recorded for this species was 73‰; it occurred under these conditions as a shrub less than 1 metre in height.

REGENERATION: The fruit is cylindrical, curved with a sharp point. The embryo pierces the pericarp after the enlarged fruit has fallen. Dense crops of seedlings are often observed under mature shrubs fringing tidal waterways. The seedlings appear intolerant of heavy shade, but odd shrubs may occupy sites within the inner mangrove zones if the canopy is broken. Seedlings often establish along the inner margins of mangrove swamps where there is considerable light.

PLATE 2.3.10.1
The small curved, horn-like fruits are distributed by the tides.

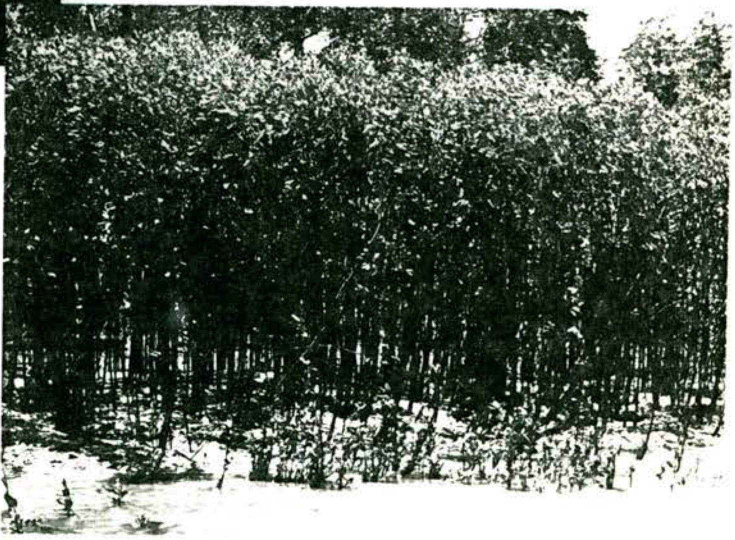
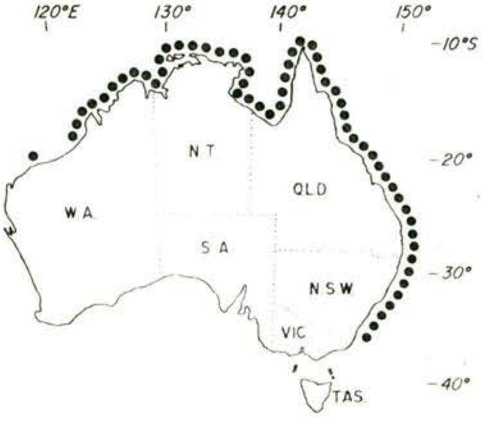


PLATE 2.3.10.2
A monospecific grove of *Aegiceras corniculatum*, Darwin Harbour, NT.



The southernmost limits of distribution of *Aegiceras corniculatum* are at Cossack (20°41'S, 117°12'E) on the west Australian coast (Semeniuk *et al.*, 1978) and Merimbula, NSW (36°53'S, 149°55'E) on the south-east coast of NSW (P. Weate, pers. comm.).

Throughout this area *Aegiceras corniculatum* is fairly abundant, particularly as a shrub understorey to fringing vegetation along tidal waterways.

Osbornia octodonta F.v.M.

GROWTH FORM: Shrub to small tree up to 6 metres high.

OCCURRENCE: Widespread; found on 85 of the 110 tidal waterways examined.

Osbornia octodonta occurs as a small tree or shrub on rocky headlands and in peripheral locations bordering many sand beaches within estuaries. It is common also along cutaway (concave) portions of meanders on waterways that become hypersaline by the middle of the dry season and often forms groves in such localities. It may also be represented throughout *Ceriops*-dominated thickets and amongst mangrove species colonizing the less frequently inundated inner zone. In the Kimberley area of Western Australia, *Osbornia octodonta* is also common as a closed shrub community bordering saline mudflats.

The species colonizes sites that are inundated by waters of seawater salinity or greater on a wide range of substrates as long as such sites do not receive more than 60 days inundation by freshwater per year. Within the survey area, the species was found at sites inundated by waters of salinity up to 56‰. In the latter half of the dry season, shrubs of *Osbornia octodonta* (1-2 metres in height) are commonly found growing in areas where the soil salinity varies between 42-45‰.

REGENERATION: The small capsule is dispersed by the tides. Seedlings have been infrequently observed although they do occur amongst fringing vegetation in estuaries. Seedlings have also been observed successfully colonizing landward mangrove zones as isolated plants upon clay soils that are infrequently inundated and that would be of high soil salinity by the end of the dry season. Seedlings appear intolerant of shade.

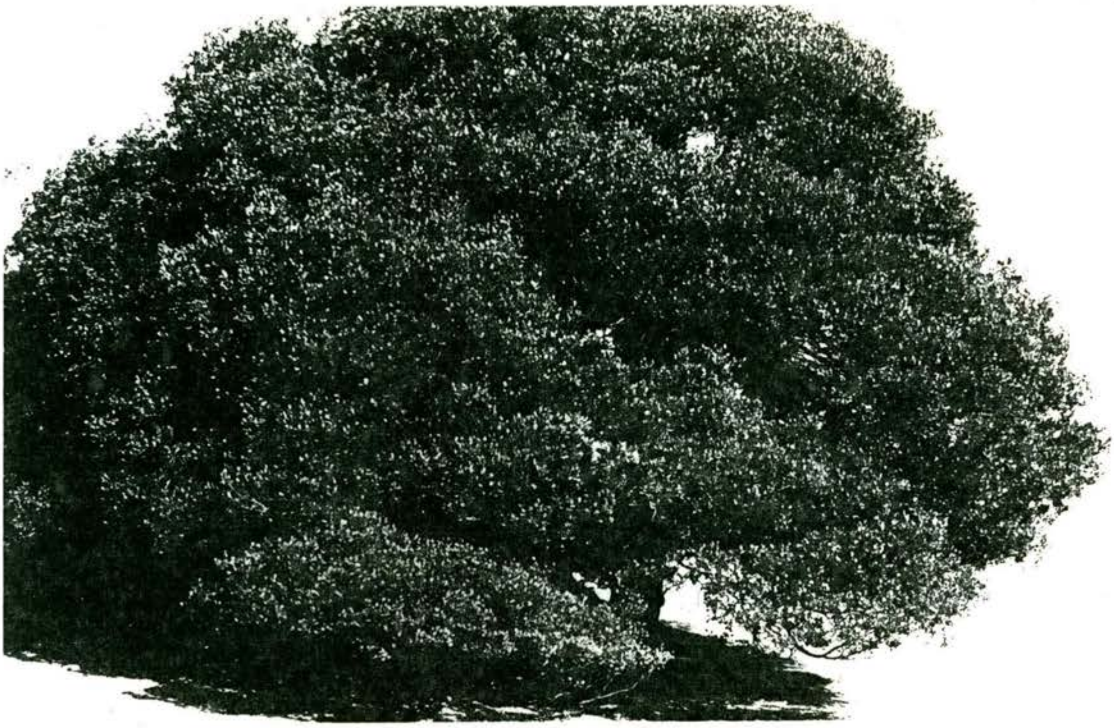
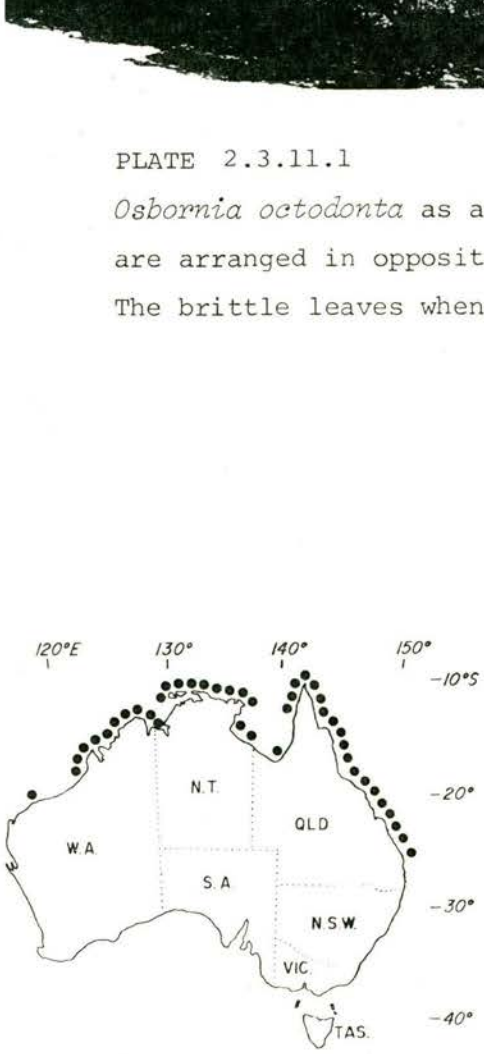


PLATE 2.3.11.1
Osbornia octodonta as a shrub. The small obovate leaves are arranged in opposite pairs on the four-angled branchlets. The brittle leaves when crushed have an aromatic scent.



The southernmost limits of distribution of *Osbornia octodonta* are at Cossack (20°41'S, 117°11'E) on the west Australian coast (Semeniuk *et al.*, 1978) and Tin Can Bay, Qld (25°30'S) on the east Australian coast (Dowling and McDonald 1982).

Distribution of *Osbornia octodonta* is discontinuous around the coastline, particularly in the Gulf of Carpentaria. Specht *et al.* (1977) record this species at Weipa, Qld (12°40'S, 141°50'E), although Saenger and Hopkins (1975) did not record it at Tarrant Point in the south-eastern portion of the Gulf of Carpentaria. Wells (1982) records *Osbornia octodonta* from over half the tidal waterways of the Kimberley region of Western Australia and the Northern Territory. Bunt (1978), Duke (1981) and Dowling (pers.comm.) record this species as being fairly common at estuarine sites along the east coast of Queensland.

Aegialitis annulata R. Br.

GROWTH FORM: Herb or small shrub up to 3 metres high.

OCCURRENCE: Widespread; found on 104 of the 110 tidal waterways examined.

Aegialitis annulata is frequently observed on rock/mud substrate in estuarine locations, particularly around headlands. It occurs also amongst understorey in various fringing riverine tree associations which are inundated by waters of salinity at least equal to seawater at the end of the dry season. It is common as a shrub in mixed associations of *Avicennia marina, Excoecaria agallocha, Lumnitzera racemosa* and *Ceriops tagal* var. *australis* in the landward, less frequently inundated zones. It may occur as a monospecific community principally on sand/mud substrates within estuaries.

Aegialitis annulata often forms a carpet-like understorey beneath *Sonneratia alba* on consolidated muds in the Kimberley area (WA) and within Darwin and Bynoe Harbours (NT). It is abundant as understorey amongst fringing riverside vegetation in tidal waterways that become hypersaline by the end of the dry season. It is also often observed as a stunted shrub (height ≤0.5 metres) in peripheral locations around saltpans.

Aegialitis annulata appears intolerant of long periods of inundation by freshwater and normally occurs only on substrates that are inundated by highly saline waters for most of the year. It attains its greatest height of ≤3 metres in waters that oscillate in salinity between 20-30‰ for most of the year. Within the survey area, the species was found in areas inundated by waters of salinity up to 85‰, whereas the highest soil salinity recorded for this species was 90‰; it occurred under these conditions as a low shrub 0.5-1 metre in height.

REGENERATION: Propagules are dispersed by the tides. Seedlings colonize sites with high light intensities. Seedlings appear intolerant of shade.

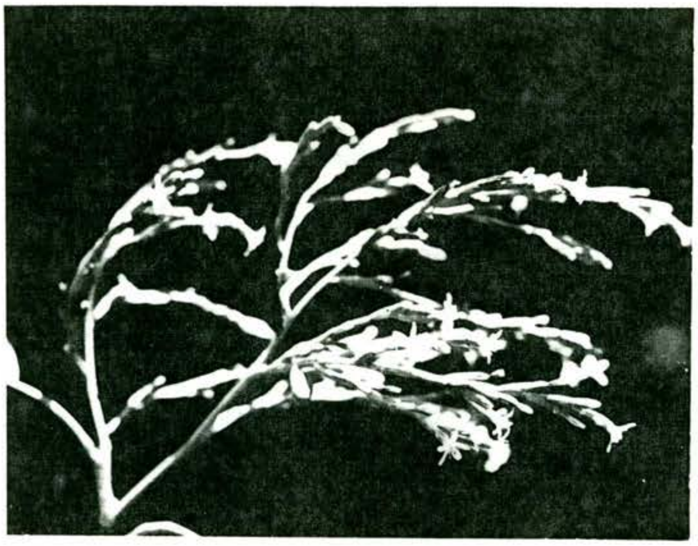
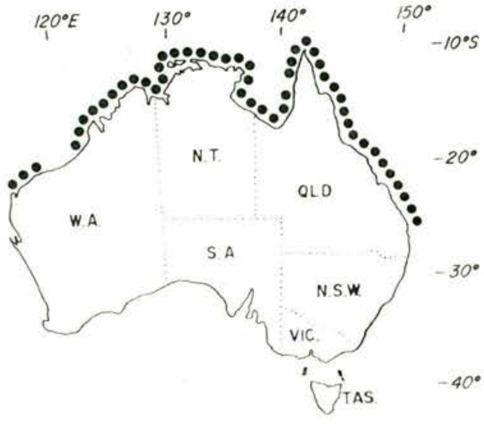


PLATE 2.3.12.1
Flowers, white; borne in axillary panicles - each small flower within a bract.

PLATE 2.3.12.2
Grove of *Aegialitis annulata*. Note the stem tapering to a broad base. Pneumatophores are absent in this species



The southernmost limits of distribution of *Aegialitis annulata* are at Exmouth Gulf ($21^{\circ}53$'S, $114^{\circ}22$'E) on the west Australian coast (Semeniuk *et al.*, 1978) and Frazer Island, Qld ($25^{\circ}30$'S) on the east Australian coast (Jones, 1971a).

Throughout its range *Aegialitis annulata* is fairly abundant.

Bruguiera exaristata Ding Hou

GROWTH FORM:	Shrub to tall tree up to 12 metres high.
OCCURRENCE:	Widespread; found on 88 of the 110 tidal waterways examined.

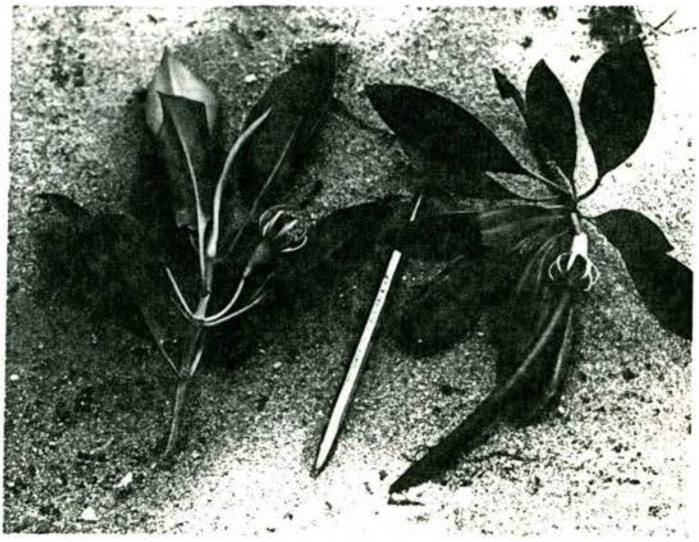
In the northernmost parts of its range in Australia, *Bruguiera exaristata* is frequently observed in mixed associations with most other mangrove species amongst the fringing vegetation. The species sometimes occurs in monospecific stands but more commonly forms associations with *Bruguiera parviflora, Bruguiera gymnorhiza, Ceriops tagal* var. *australis, Avicennia marina, Rhizophora stylosa* and *Camptostemon schultzii*. It is sparsely represented in *Ceriops*-dominated thickets as a shrub (height ≤4 metres).

Bruguiera exaristata normally colonizes sites which are reasonably well drained but inundated by spring high tides. It tolerates long periods of inundation by freshwater and attains greatest girth and height in areas that are inundated by brackish waters for most of the year. The species is also tolerant of hypersaline conditions but under such conditions occurs as a shrub (height ≤2.5 metres). Within the survey area, the species was found in areas inundated by waters of salinity up to 72‰, whereas the highest soil salinity recorded for the species was 78‰; it occurred under these conditions as a low shrub less than 2 metres in height.

REGENERATION: The light, small propagules are dispersed easily by tides or floods. They quickly establish on muds throughout mangrove forests in the wet season but many seedlings within the forest die, probably due to the low light intensities on the forest floor. Only a small proportion of the seedlings that become established throughout the fringing forests in the wet season survive the ensuing year. Crabs (Sesarmidae) eat a high proportion of these seedlings.

PLATE 2.3.13.1
Monospecific stand of *Bruguiera exaristata* (height <8 m), Hutchinson Strait, NT.

PLATE 2.3.13.2
Leaves are sharply acuminate - narrow elliptic in outline 7-10 cm long and 4-5 cm broad, collected in opposite pairs at the ends of the branchlets. Flowers solitary in the leaf axils. Fruiting body distinctly ribbed, calyx lobes 8-10. Hypocotyl 7-10 cm, green and slender.



The southernmost limits of distribution of *Bruguiera exaristata* are at Cossack (20°41'S, 117°11'E) on the west Australian coast (Semeniuk *et al.*, 1978) and Port Clinton, Qld (22°30'S) on the east Australian coast (Saenger, pers.comm). The species is fairly well represented amongst fringing vegetation along tidal waterways throughout these limits except along the west Australian coastline where it is infrequently observed.

(Amendment 18.9.84).

Re: spelling of *Bruguiera gymnorhiza*.

Although spelt in Kewensis as *B. gymnorrhiza* the spelling on the original specimen (described by Linnaeus) is *B. gymnorhiza*. However, Prof. Tomlinson (Harvard) considers that *B. gymnorrhiza* is perhaps appropriate due to an initial spelling mistake on the label of the original specimen.

Bruguiera gymnorhiza (L.) Lamk.

GROWTH FORM: Shrub to large tree up to 18 metres high.

OCCURRENCE: Relatively widespread; found on 39 of the 110 tidal waterways examined.

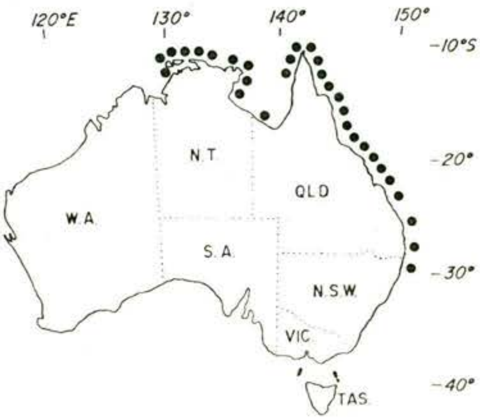
Bruguiera gymnorhiza frequently is observed in backswamp areas inundated by spring high tides. The species occurs in association with most mangrove species but in particular with *Rhizophora stylosa, Rhizophora apiculata, Bruguiera exaristata, Lumnitzera racemosa, Camptostemon schultzii, Xylocarpus australasicus, Avicennia marina* and a strand plant, *Diospyros ferrea* var. *humilis*.

Bruguiera gymnorhiza often is abundant amongst the fringing vegetation along portions of tidal waterways that remain brackish for considerable periods of the year. *Bruguiera gymnorhiza* attains its greatest girths and heights here. It occurs on rock/mud substrates and on well drained soils with a high sand content. It also may occur on poorly drained soils and can tolerate considerable inundation (9 months) by freshwater. In estuaries *Bruguiera gymnorhiza* may occur towards the landward edge of mangrove swamp, particularly in areas that receive considerably freshwater seepage throughout the year. Within the survey area, *Bruguiera gymnorhiza* was found in areas inundated by waters of salinity up to 37‰, whereas the highest soil salinity recorded for the species was 42‰; it occurred under these conditions as a low shrub less than 2 metres in height.

REGENERATION: The propagules are dispersed easily by the tides and the shade-tolerant seedlings frequently regenerate throughout less frequently inundated zones of mangrove forests. Within the survey area, seedlings of *Bruguiera gymnorhiza* have not been observed colonizing sites beneath the canopy of mature trees of its own species.

PLATE 2.3.14.1
Calyx frequently red 10-13 calyx lobes. Extruded hypocotyl 15-25cm, green, stout, dark green, flushed deep purple.

PLATE 2.3.14.2
Tree buttressed at the base with inverted knee-shaped pneumatophores. Soil washed away from root system.



Bruguiera gymnorhiza has not been recorded west of Darwin, NT (12°25'S, 130°48'E) (Wells, 1982).

Although discontinuous in occurrence the species occurs eastwards of this point as far south as the Roper River, NT (14°17'S, 135°44'E) in the Gulf of Carpentaria. *Bruguiera gymnorhiza* has not been observed on any other tidal waterway of the Northern Territory entering into the southern portion of the Gulf of Carpentaria.

Saenger and Hopkins (1975) have recorded the species at Tarrant Point (17°23'S, 139°25'E) in the south-eastern portion of the Gulf of Carpentaria. On the eastern shores of the Gulf of Carpentaria the species occurs at least as far south as Weipa (12°40'S, 141°50'E) (Love, pers. comm.). Its distribution along the remainder of the tidal waterways entering the Gulf of Carpentaria from Weipa to Karumba is unknown. On the east Australian coastline, *Bruguiera gymnorhiza* has been recorded south to the Clarence River, NSW (29°25'S, 153°21'E) (McCormick, pers. comm.; Floyd, pers. comm.), although this species only occurs as isolated trees in northern NSW.

2.3.15 RHIZOPHORACEAE

Bruguiera parviflora (Roxb.) W. and A. ex Griff.

GROWTH FORM: Shrub to tall tree up to 14 metres high.

OCCURRENCE: Widespread; found on 70 of the 110 tidal waterways examined.

Bruguiera parviflora often forms monospecific stands in mangrove zones that are not frequently inundated. The species often occurs as isolated trees amongst fringing riverside vegetation. It may occur in mixed associations, principally with *Bruguiera exaristata*, *Rhizophora stylosa*, *Rhizophora apiculata*, *Ceriops decandra*, *Camptostemon schultzii* and *Avicennia marina*.

Isolated small trees or shrubs of this species are often found amongst fringing riverside vegetation on tidal waterways that attain salinities between 38-45$^{o}/oo$ by the end of the dry season. Monospecific stands on consolidated mud substrate have been observed at sites mainly inundated by brackish water and also on sites inundated by seawater for most of the year. *Bruguiera parviflora* is tolerant of prolonged inundation by freshwater and within the survey area has been found in areas inundated by waters of salinity up to 66$^{o}/oo$, whereas the highest soil salinity recorded for the species was 72$^{o}/oo$; it occurred under these conditions as a low shrub less than 1 metre in height.

REGENERATION: The propagules are dispersed easily by the tides. This species quickly establishes itself in cleared or open areas of forest or at sites along the riverine margins of the forest where light penetration to the forest floor is high. Seedlings of the species appear to be relatively intolerant of shade.

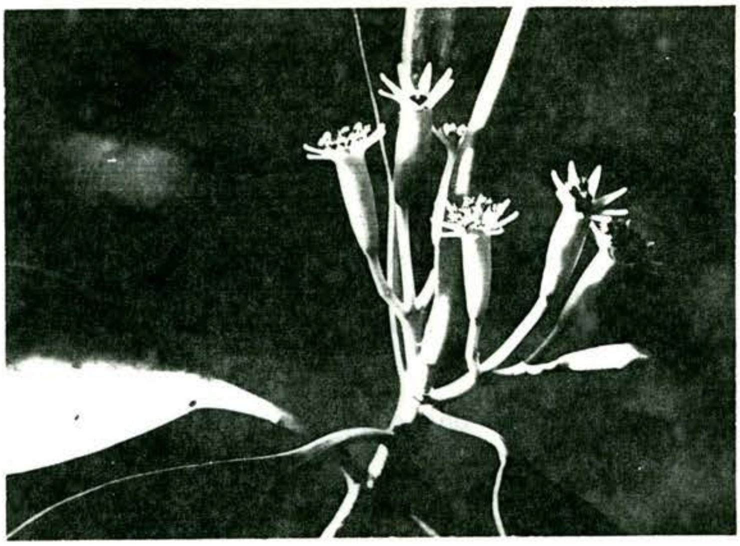


PLATE 2.3.15.1
Flowers in trichotomous cymes. (Hypocotyl green and slender 9-15 cm.) In this species, the emerging cotyledons grow through the bottom of the calyx leaving the remains of the calyx encircling the hypocotyl.

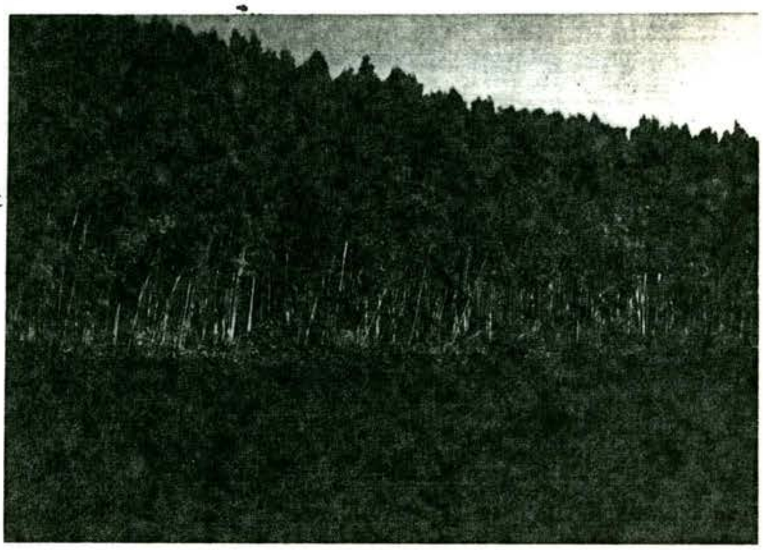
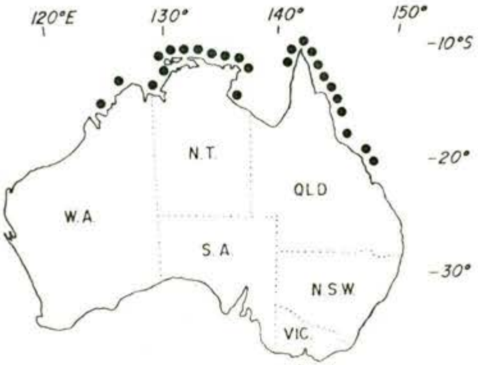


PLATE 2.3.15.2
A monospecific stand of *Bruguiera parviflora* (height <9m), Andranangoo Creek, Melville Island.



The southernmost limits of distribution of *Bruguiera parviflora* are the Sale River (15°57'S, 124°33'E) on the west Australian coast (Wells, 1982) and Proserpine, Qld (20°30'S) on the east Australian coast (Jones, 1971a).

The species is uncommon throughout the Kimberleys and the Joseph Bonaparte Gulf region of Western Australia and the Northern Territory. Distribution of the species is continuous across the northern coastline of the Northern Territory.

Bruguiera parviflora is rare on tidal waterways entering the western shores of the Gulf of Carpentaria and has not been recorded eastwards of the Limmen Bight River (15°06'S, 135°42'E) in the Northern Territory. *Bruguiera parviflora* recently has been recorded at Port Musgrave (12°00;S, 141°54'E) (Messel *et al.* 1981). The species is fairly common along tidal waterways over the northern portion of the east Australian coast (Bunt, 1978) although it becomes discontinuous in occurrence towards the southern limit of distribution at Proserpine (Duke, 1981).

Bruguiera sexangula (Lour.) Poir.

GROWTH FORM: Tree up to 12 metres high.

OCCURRENCE: Restricted; found on only 2 of the 110 tidal waterways examined.

On the Cato and Peter John Rivers in Arnhem Bay (NT), *Bruguiera sexangula* occurs within the fringing riverside vegetation in mixed association with *Rhizophora stylosa, Camptostemon schultzii, Bruguiera gymnorhiza, Bruguiera parviflora* and *Avicennia marina* on consolidated muds on infrequently inundated sites and on unconsolidated muds inundated by most high tides.

Bruguiera sexangula was found at sites inundated by brackish water at the end of the dry season. It tolerates long periods of inundation by freshwater and within the survey area the species was inundated by waters of salinity up to 33‰.

REGENERATION: The reasonably long (9-12 cm) and thick hypocotyls are dispersed by the tides. Seedlings appear intolerant of high light intensities. The most prolific seedling growth was observed amongst understorey vegetation fringing the rivers.

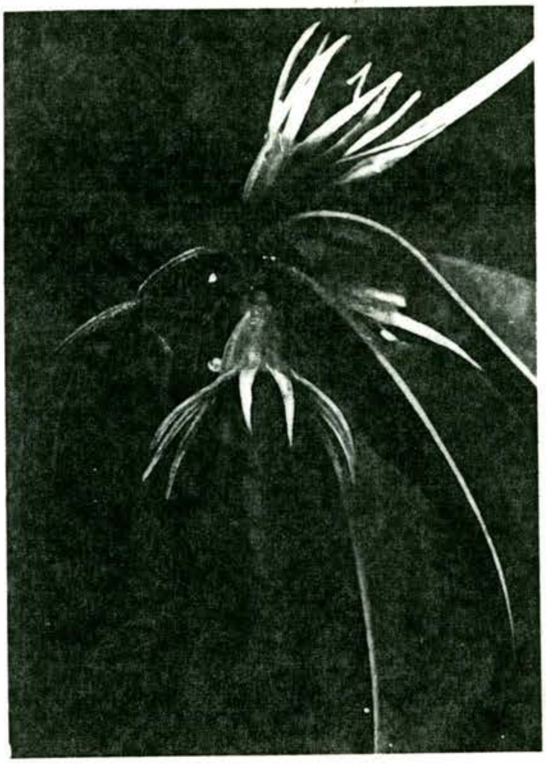
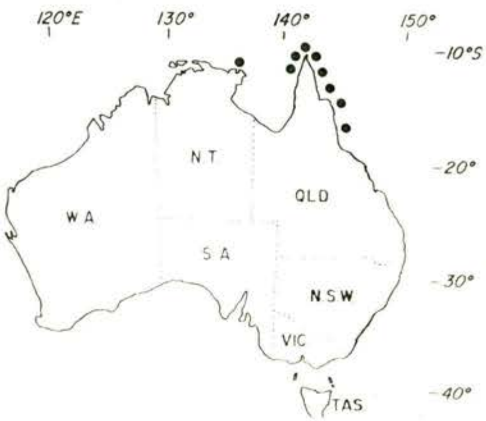


PLATE 2.3.16.1
Pink to green calyx, (10-12 calyx lobes) (flowers, brown). Extruded green hypocotyl 10-20 cm slightly ribbed.

PLATE 2.3.16.2
Base of trunk buttressed often with short stilt roots covered with lenticels. These roots and other inverted 'knee' shaped roots, function as pneumatophores.



Bruguiera sexangula has not been recorded previously from the Northern Territory. It is known from only the Cato and Peter John Rivers in Arnhem Bay, NT (12°15'S, 136°21'E) (Wells, 1982). Waddy (pers.comm.) also reports the species on Groote Eylandt.

On the eastern shores of the Gulf of Carpentaria, *Bruguiera sexangula* has been recorded south to Port Musgrave, Qld. (12°00'S,141°54'E) (pers.obs) while on the east Australian coastline, this species has been recorded south to the Herbert River, Qld (18°25'S) (Duke, 1981). The distribution of *Bruguiera sexangula* down the east Australian coastline is discontinuous (Duke, 1981).

2.3.17 RHIZOPHORACEAE

Ceriops decandra (Griff.) Ding Hou

GROWTH FORM: Shrub to small tree up to 5 metres high.

OCCURRENCE: Fairly restricted; found on 50 of the 110 tidal waterways examined.

Ceriops decandra typically occurs as understorey in various mixed associations of fringing riverside trees (e.g. *Rhizophora stylosa*, *Camptostemon schultzii*, *Bruguiera exaristata* and *Avicennia marina*). *Ceriops decandra* is frequently observed as an understorey plant (mixed with *Aegiceras corniculatum* and *Aegialitis annulata*) on tidal waterways that become hypersaline by the end of the dry season. It appears intolerant of long periods of inundation by freshwater but more tolerant than *Ceriops tagal* var. *australis* or *Ceriops tagal* var. *tagal*. Within the survey area, the species was found in areas inundated by waters of salinity up to 67‰, whereas the highest soil salinity recorded for this species was 75‰; it occurred under these conditions as a low shrub less than 1 metre in height.

REGENERATION: The small fluted propagules are easily dispersed by the tide. Seedlings appear intolerant of high light intensities and successful seedling establishment is frequently observed beneath the tree canopy of fringing vegetation along tidal waterways. Crabs, principally Sesarmidae, eat hypocotyls and established seedlings.

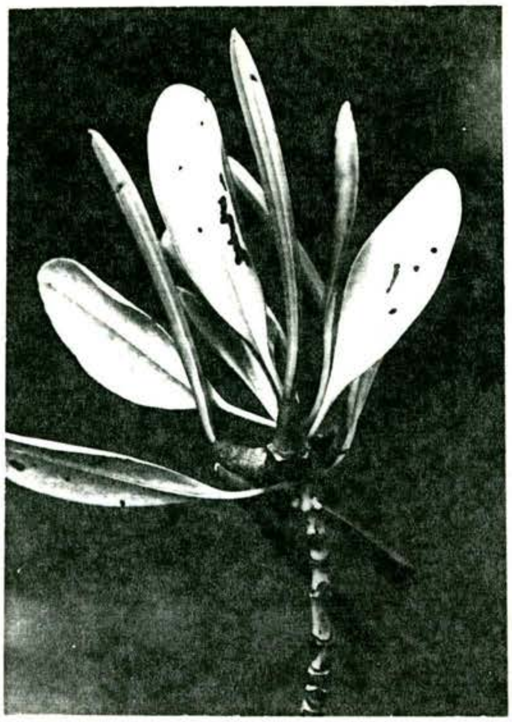


PLATE 2.3.17.1

Fruiting body brown, pear shaped and wrinkled, slightly curved above the calyx. The hypocotyl (14-20 cm) is fluted and broadened at its base and points in many directions due to the arrangement of the fruits on small thick peduncles.

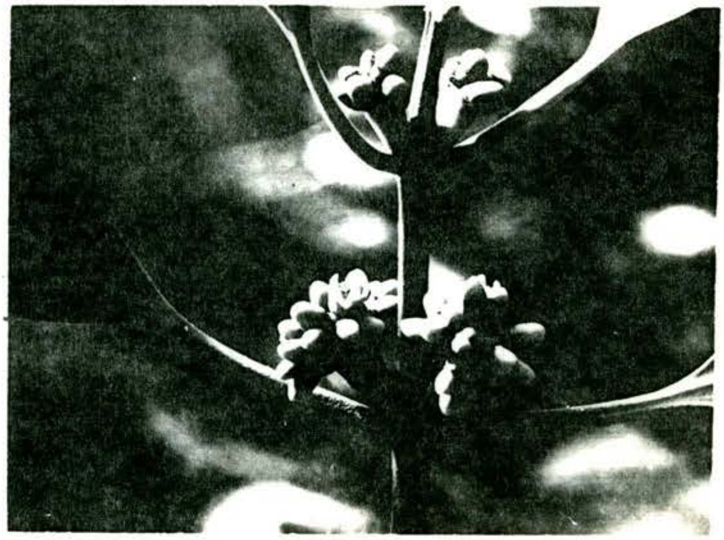
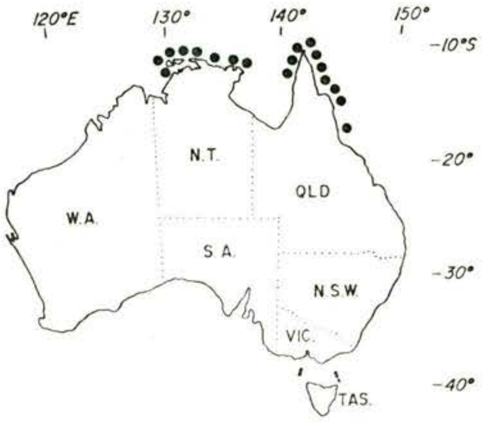


PLATE 2.3.17.2

Flowers white, axillary, clustered on a very short, thick, angular peduncle.



Ceriops decandra has not been recorded west of Darwin, NT (12°25'S, 130°48'E) (Wells, 1982). Its distribution across the northern coastline of the Northern Territory is discontinuous and it has not been recorded on any tidal waterway entering the western or southern shores of the Gulf of Carpentaria. Occurrence of *Ceriops decandra* throughout the Queensland portion of the Gulf of Carpentaria is largely unknown. It may occur at Weipa (Love, pers. comm.). It occurs at least as far south as Port Musgrave (12°00'S, 141°54'E) (pers. obs). On the east Australian coastline the species has been recorded south to the Herbert River, Qld (18°25'S) (Duke, 1981) and is common between Cape York and Cooktown, Qld (Bunt, 1978) and south to Cairns, Qld (16°55'S) (Dowling & McDonald 1982).

Ceriops tagal (Perr.) C.B. Robinson var. *australis* C.T. White

GROWTH FORM: Shrub to small tree up to 12 metres high.

OCCURRENCE: Widespread; found on 102 of the 110 tidal waterways examined.

Ceriops tagal var. *australis* frequently forms monospecific thickets in the landward, less frequently inundated zones. It often dominates a mixed association with tall shrubs of *Excoecaria agallocha*, *Avicennia marina* and *Lumnitzera racemosa*. *Aegialitis annulata* commonly occurs as an understorey in this association. Shrubs of *Osbornia octodonta* and *Bruguiera exaristata* may occur in the mixed *Ceriops*-dominated association, particularly in thickets bordering portions of rivers that become hypersaline by the end of the dry season. *Ceriops tagal* var. *australis* sometimes forms an association with *Bruguiera parviflora* on certain sites.

The species appears intolerant of long periods of freshwater inundation. It normally is found on well drained consolidated clays in less frequently inundated zones of mangrove swamps. Within the survey area, the species was found at sites inundated by waters of salinity up to 72‰, whereas the highest soil salinity in which the species was observed growing was 78‰; it occurred under these conditions as a low shrub less than 1.5 metres in height.

REGENERATION: The narrow, short propagules are dispersed by the tide. Successful seedling colonization only occurs on sites infrequently inundated by tides. Seedlings are moderately shade tolerant. They often colonize bare saltpans during the wet season only to die during the dry season.

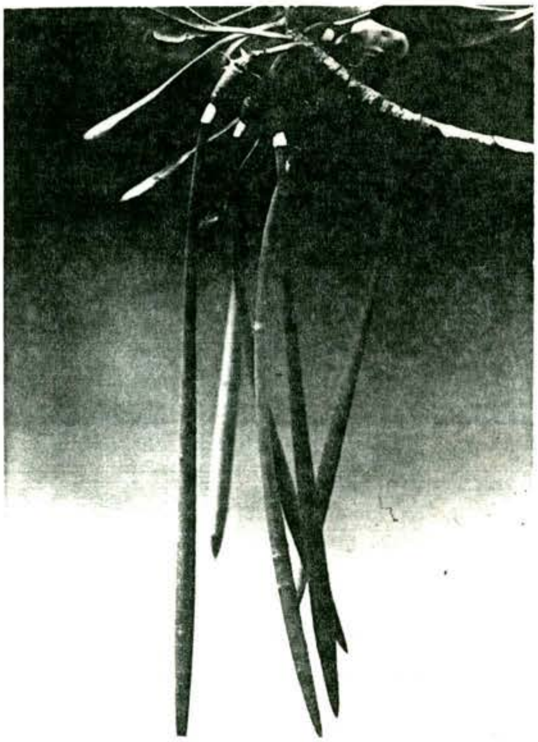
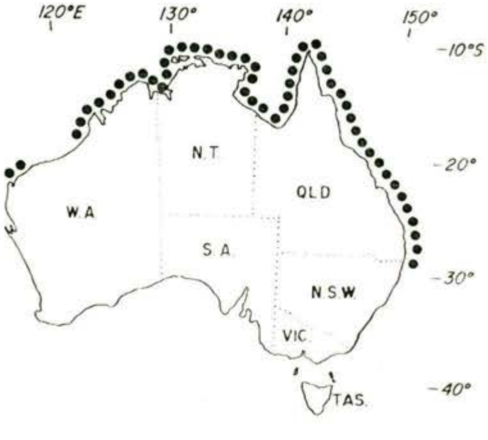


PLATE 2.3.18.1
Fruit brown, pear-shaped. The extruded hypocotyl is slender and smooth - not fluted as in *Ceriops tagal*

PLATE 2.3.18.2
A monospecific stand of *Ceriops tagal* var. *australis*. Broad branching buttresses form around the base but no pneumatophores are present.

The southernmost limits of distribution of *Ceriops tagal* var. *australis* are at Exmouth Gulf (21°53'S, 114°22'E) on the west Australian coast (Semeniuk *et al.*, 1978) and the Tweed River, NSW (28°11'S, 153°32'E) on the east Australian coast (Lear & Turner, 1977). Throughout its range the distribution of this variety is continuous.



2.3.19 RHIZOPHORACEAE

Ceriops tagal (Perr.) C.B. Rob.

GROWTH FORM: Small shrub up to 3 metres high.

OCCURRENCE: Restricted; found only on 11 of the 110 tidal waterways examined.

Ceriops tagal usually occurs as an understorey in certain fringing riverside associations. It was observed with shrubs of *Bruguiera gymnorhiza*, *Ceriops tagal* var. *australis*, *Excoecaria agallocha* and *Avicennia marina*. This variety of the species colonizes consolidated muds or rock/mud substrates. It occurs on sites that are inundated by seawater for most of the dry season. Within the survey area, it was found at sites inundated by waters of salinity up to $36^{o}/oo$.

REGENERATION: The narrow, short propagules obviously are dispersed by the tides. However, this writer finds it largely impossible to distinguish between seedlings of *Ceriops tagal* and *Ceriops tagal* var. *australis* where these two species occur together in the field.

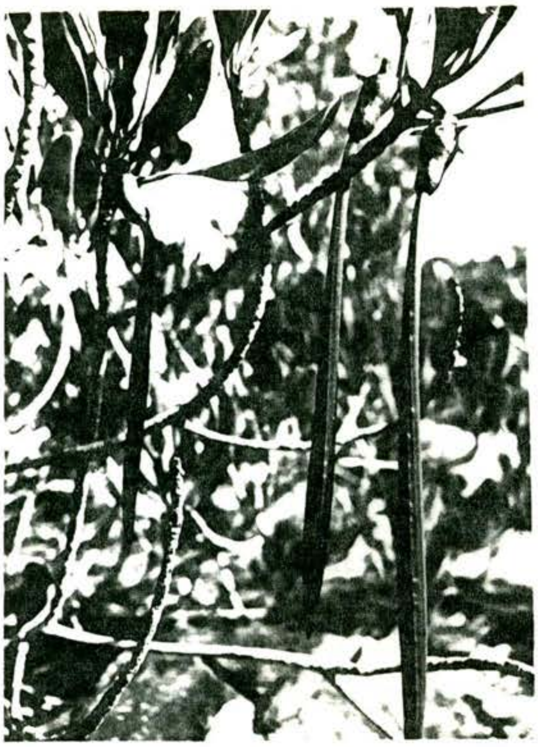
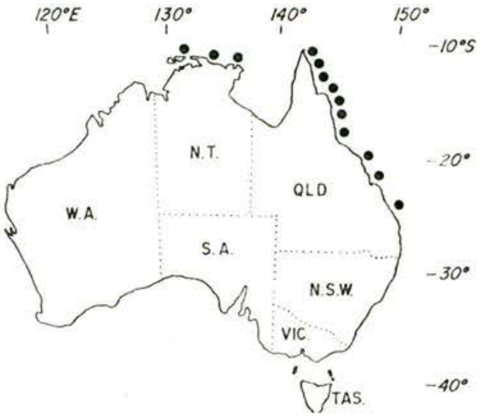


PLATE 2.3.19.1
Fruit brown, pear-shaped. The extruded hypocotyl attains 20 cm in length and is distinctly fluted and broadened towards the base. (A small, slender tree with broad branching buttresses at the base and short knobby pneumatophores rising from the mud about the base.)



Ceriops tagal has not been recorded west of Tinganoo Creek, Melville Island, NT (11°24'S, 131°29'E) or east of the Cato River, NT (12°16'S, 136°21'E) (Wells, 1982).

Distribution of this variety of the species across the northern coastline of the Northern Territory is extremely discontinuous. *Ceriops tagal* has not been recorded on any tidal waterway within the Gulf of Carpentaria.

In eastern Australia, the variety is quite abundant south from Cape York to Cooktown (Bunt, 1978; Duke 1981) and becomes progressively more isolated in occurrence as it approaches the southernmost limit of its distribution at Bustard Head, Qld (24°01'S) (Dowling & McDonald, 1982).

2.3.20 RHIZOPHORACEAE

Rhizophora apiculata Blume

GROWTH FORM: Tall shrub to small tree up to 10 metres high.

OCCURRENCE: Restricted; found on only 13 of the 110 tidal waterways examined.

Rhizophora apiculata colonizes estuarine areas that are inundated frequently, and often is sparsely represented amongst fringing riverside tree associations. *Rhizophora apiculata* normally occurs in mixed association with *Rhizophora stylosa*, *Camptostemon schultzii*, *Bruguiera parviflora*, *Bruguiera gymnorhiza* and *Avicennia marina*.

On Dongau Creek, Melville Island (NT), *Rhizophora apiculata* forms an association with *Rhizophora stylosa*, both species being stunted (height ≤1.5 metres). Soil salinities (36‰) have been recorded at this site by the end of the dry season, but such salinities do not appear to stress tree growth of these species. Imperfect tidal flushing and resultant poor drainage may be responsible for the stunted habit of this association, which has not been observed elsewhere in the survey area.

Rhizophora apiculata is tolerant of long periods of freshwater inundation and usually colonizes sites inundated by seawater or brackish water for most of the year. Within the survey area, the species was found at sites inundated by waters of salinity up to 65‰; it occurred under these conditions as a shrub less than 1.5 metres in height.

REGENERATION: Propagules of *Rhizophora apiculata* are produced in large numbers on mature trees and either embed themselves in mud below the parent tree or are carried by tides to other areas. They appear to be very tolerant of shade. As the propagule is shorter than that of *Rhizophora stylosa*, *Rhizophora apiculata* seedlings are carried into shallower waters and hence can establish themselves on higher ground than *Rhizophora stylosa*.

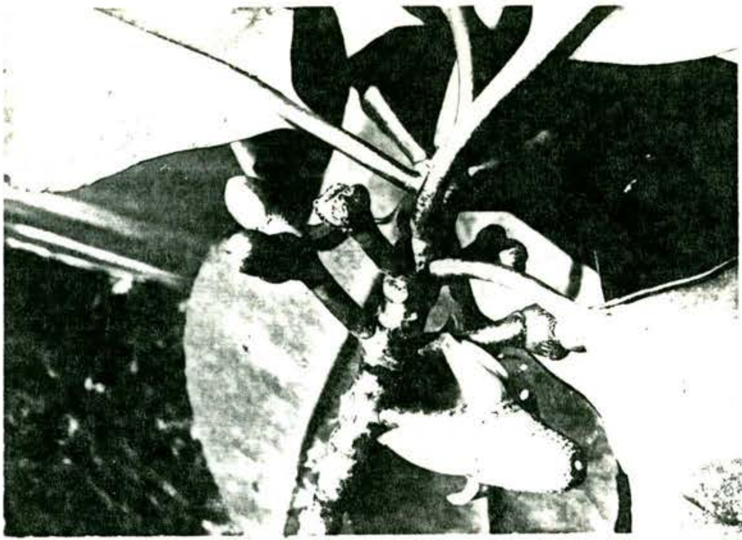
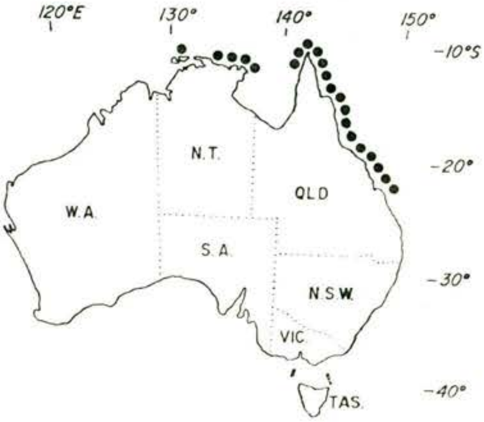


PLATE 2.3.20.1
Cymes with two sessile flowers on a long thick peduncle. Calyx lobes 4. Fruit brown, pear-shaped with the extruded hypocotyl rarely over 30   long.

PLATE 2.3.20.2
A tall tree attaining 12 metres in height. Tall stilt roots. Pendulous roots may descend from the lower branches and long looping bow-shaped pneumatophores extend away from the base as in *Rhizophora stylosa*.



Rhizophora apiculata has not been recorded west of Andranangoo Creek, Melville Island (11^{O}21'S, 130^{O}51'E) or east of Gove (12^{O}13'S, 136^{O}43'E) in the Northern Territory (Wells, 1982). The species is absent from the greater portion of tidal waterways entering into the Gulf of Carpentaria. Specht *et al.* (1977) did not record *Rhizophora apiculata* at Weipa (12^{O}40'S, 141^{O}50'E) although this writer found this species to be common within Port Musgrave (12^{O}00'S, 141^{O}54'E) just 65 km north of Weipa.

On the east Australian coastline *Rhizophora apiculata* has been recorded south to Port Clinton, Qld (22^{O}30'S) (Duke & Bunt, 1979); these authors suggest that this species may occur further south. Duke and Bunt (1979) show that throughout its range along the east Australian coast, *Rhizophora apiculata* is continuous in occurrence.

2.3.21 RHIZOPHORACEAE

Rhizophora stylosa Griff.

GROWTH FORM: Shrub to tall tree up to 20 metres high.

OCCURRENCE: Widespread; found on 104 of the 110 tidal waterways examined.

Rhizophora stylosa is frequently a dominant species along the banks of tidal creeks, which it often overhangs. Monospecific stands are common in estuarine localities and *Rhizophora stylosa* may occur as the seaward pioneering species or alternatively form a band of variable width behind a pioneer community of *Sonneratia alba* or *Avicennia marina*.

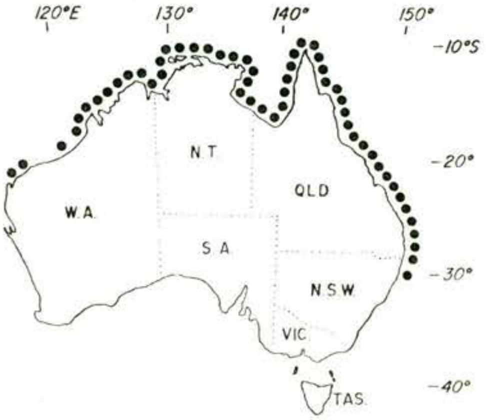
Along tidal rivers and creeks, it often forms a mixed tree association with *Camptostemon schultzii* and *Avicennia marina*. It also is present in other mixed associations, chiefly with *Bruguiera parviflora*, *Xylocarpus australasicus*, *Bruguiera gymnorhiza*, *Bruguiera exaristata*, *Aegiceras corniculatum* and *Ceriops decandra*. In estuarine localities, it colonizes muds frequently inundated by the tides. However, the species is also common on firm, consolidated muds in landward zones which are less frequently inundated.

Rhizophora stylosa grows to a maximum size in portions of tidal waterways that remain brackish for most of the year. The species is tolerant of prolonged inundation by freshwater. Within the survey area, the species was found in areas inundated by waters of salinity up to 74‰, whereas the highest soil salinity in which *Rhizophora stylosa* has been observed growing was 81‰; it occurred under these conditions as a shrub less than 1.5 metres in height.

REGENERATION: The propagules are dispersed by the tides. The great length and unwieldiness (of *Rhizophora* spp of the hypocotyls), compared to many of the smaller-fruited mangroves, as discussed by Rabinowitz, (1978) may retard their landward dispersal by water within swamps. Seedlings of *Rhizophora stylosa* appear intolerant of low light levels.

PLATE 2.3.21.1
Leaves are opposite on the branchlets, thick and brittle in texture. (Flowers in cymes branching in pairs. Fruit brown, pear-shaped.) The long, narrow hypocotyls are dotted with numerous lenticels.

PLATE 2.3.21.2
Several stout stilt roots support the tree base and long looping bow-like stilt roots which function as pneumatophores extend away from the tree. On some trees, long aerial prop roots descend from the lower branches.



The southernmost limits of distribution of *Rhizophora stylosa* in Australia are at Yardie Creek (22°20'S, 113°51'E) on the west Australian coast (Semeniuk *et al*., 1978) and Corindi Creek, NSW (30°03'S, 153°12'E) on the east Australian coast (Floyd, pers. comm.). Floyd notes that this species was previously recorded as far south as the Richmond River, NSW (28°31'S) (Jones, 1971a) however this record referred to an old Herbarium specimen. *Rhizophora stylosa* does not occur on the Richmond River now and, except for the collection made at Corindi Creek in 1979, the species was not known to have occurred in recent times south of Cudgera Creek on the Tweed River, NSW (Floyd, pers.comm).

2.3.22 RUBIACEAE

Scyphiphora hydrophyllacea Gaertn.

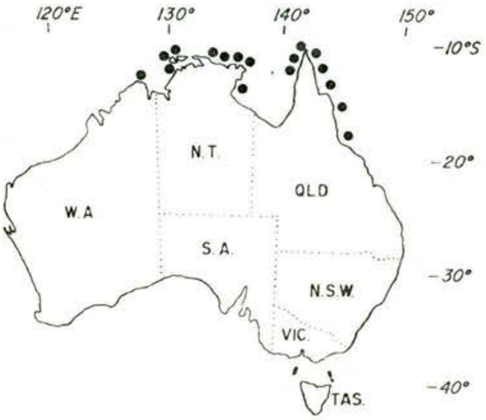
GROWTH FORM: Shrub up to 4 metres high.

OCCURRENCE: Restricted; found on only 21 of the 110 tidal waterways examined.

Scyphiphora hydrophyllacea occurs on mud/rock substrates, often forming a shrub layer along the banks of tidal waterways that attain salinities between 35-40‰ by the middle of the dry season. It also occurs amongst mangrove species colonizing the more landward zones. The species normally occupies sites that are inundated infrequently; it appears fairly intolerant of lengthy periods of inundation by freshwater. The rock/mud substate on which *Scyphiphora hydrophyllacea* occurs appears unsuitable as a site for colonization by most other mangrove species. Within the survey area, the species was found in areas inundated by waters of salinity up to 63‰; it occurred under these conditions as a shrub less than 2 metres in height.

REGENERATION: The small ribbed fruits are dispersed by the tides. Seedlings of *Scyphiphora hydrophyllacea* appear intolerant of shade but have only been infrequently observed in the survey area.

PLATE 2.3.22.1
Leaves simple, opposite, obovate, spiny on upper surface. Between each pair of leaves are two broad, interpetiolar stipules which are characteristic of the family. The small cymes of whitish flowers are borne in the leaf axils. Fruits small, grooved or ribbed, crowned at the apex by a translucent, short calyx tube.



To the west in its Australian distribution, *Scyphiphora hydrophyllacea* occurs at Cape Londonderry (13°48'S, 126°46'E), the most northerly point of Western Australia (Semeniuk *et al.*, 1978).

The species has not been recorded throughout the remainder of the Joseph Bonaparte Gulf and reappears again in Bynoe Harbour (12°34'S, 130°31'E) near Darwin in the Northern Territory. *Scyphiphora hydrophyllacea* has a discontinuous distribution across the remainder of the northern coastline of the Northern Territory and has been recorded as far south as the Rose River, NT (14°17'S, 135°44'E) on the western shores of the Gulf of Carpentaria (Wells, 1982). The species has not been observed on any other tidal waterway of the Northern Territory entering into the southern portion of the Gulf of Carpentaria. Saenger and Hopkins (1975) did not record this species at Tarrant Point (17°23'S, 139°25'E) in the south-eastern portion of the Gulf of Carpentaria.

Specht *et al.* (1977) record the species as far south as Weipa, Qld (12°4°'S, 141°50'E) on the eastern shore of the Gulf of Carpentaria. However, occurrence of this species down the remainder of this shore to Karumba is unknown. On the east Australian coast this species occurs as far south as Townsville, Qld (19°12'S), although again it is discontinuous throughout this region (Jones, 1971a; Duke, 1981).

(Amendment 18.9.84).

Work is currently underway at the Australian Institute of Marine Science describing several new *Sonneratia* species and their respective distributions.

Sonneratia alba J. Sm. (petalous form).

GROWTH FORM: Shrub to tall tree up to 12 metres high.

OCCURRENCE: Widespread; found on 68 of the 110 tidal waterways examined.

Sonneratia alba often occurs in monospecific stands or in mixed association with trees of *Rhizophora stylosa*, *Camptostemon schultzii* and/or *Avicennia marina* on accreting mudbanks to seaward. Although a pioneering species, it occupies sites that are largely protected from strong wave action.

In some tidal waterways of the Kimberleys (WA), *Aegialitis annulata* forms a short carpet-like understorey beneath trees of *Sonneratia alba* (Messel *et al.*, 1977). *Sonneratia alba* occurs far upstream on some waterways that do not receive a substantial freshwater input after commencement of the dry season (e.g. South Alligator River). In such saline rivers, it forms a shrub association with *Avicennia officinalis* on accreting mudbanks around convex portions of river meanders; *Acanthus ilicifolius* is often observed as understorey in this association.

Sonneratia alba colonizes sites that are inundated by most high tides. It frequently occurs on consolidating soft muds and appears intolerant of long periods of exposure to inundation by freshwater. Within the survey area, the species was found in areas inundated by waters of salinity up to 44‰, whereas the highest soil salinity recorded for the species was 50‰; it occurred under these conditions as a shrub less than 2.5 metres in height.

REGENERATION: Fruits are dispersed by the tides. Seedlings of *Sonneratia alba* are never common but when they occur they are always on bare, newly-accreting mudbanks. The species was not observed regenerating under tree canopies. Considerable insect attack of the fruits has been observed.

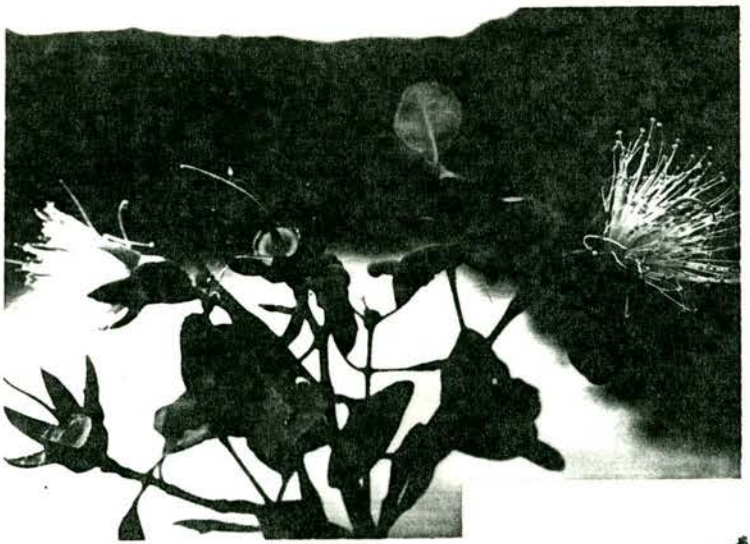
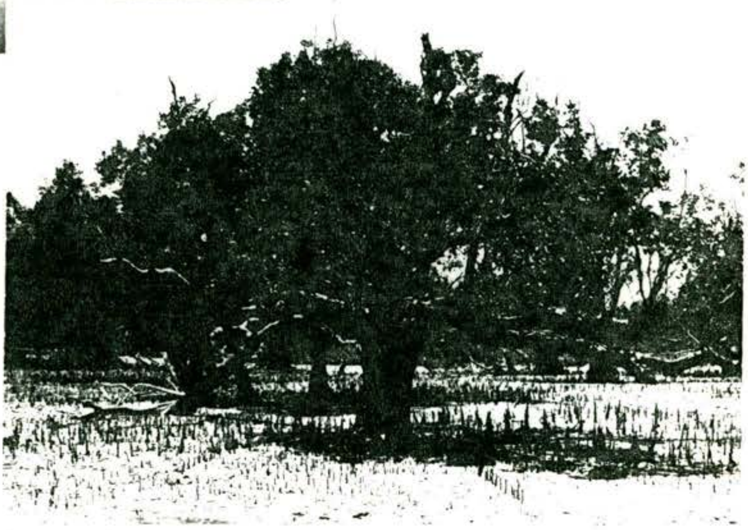
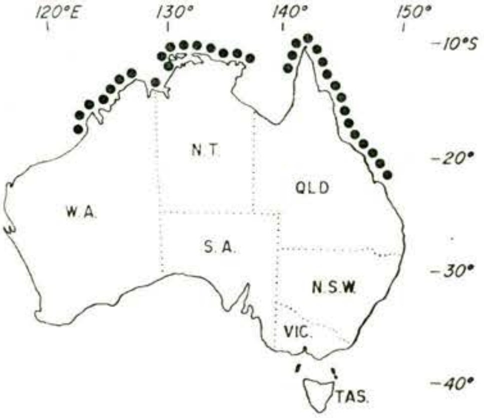


PLATE 2.3.23.1
The large, nocturnal (bat-pollinated), white flowers with red petals are conspicuous in this species. (Fruits are many-seeded.)

PLATE 2.3.23.2
This species frequently colonizes accreting mud-banks in estuaries. Thick, woody pneumatophores are prominently shown.



The southernmost limit of distribution of *Sonneratia alba* on the west Australian coast is at Cape Bossut (18°43'S, 121°38'E) (Semeniuk *et al.*; 1978). The species is common throughout the estuaries of tidal waterways in the Kimberleys (Wells, 1981) but is largely absent from tidal waterways draining into the Joseph Bonaparte Gulf.



The species is nearly continuous in occurrence from Port Paterson, NT (12°34'S, 130°31'E) around the northern coastline to Gove (12°13'S, 136°42'E) in the Northern Territory. The species has not been recorded on any tidal waterway entering the western or southern shores of the Gulf of Carpentaria (Wells, 1982). *Sonneratia alba* occurs at least as far south as Weipa, Qld (12°40'S, 141°50'E) on the eastern shores of the Gulf of Carpentaria (Love, pers. comm.). On the east Australian coast this species occurs as far south as Port Clinton, Qld (22°30'S) (Duke, 1981). Work in progress at the Australian Institute of Marine Science suggests that a whole range of *Sonneratia* spp. occur along the east Australian coast (Duke, pers. comm.).

Sonneratia caseolaris (L.) Engl.

GROWTH FORM: Shrub to tall tree up to 18 metres high.

OCCURRENCE: Restricted; found only on 12 of the 110 tidal waterways examined.

Sonneratia caseolaris occurs as a pioneering species on accreting mudbanks in some rivers that remain fresh or slightly brackish over most of the year. It normally colonizes soft muds but may occur on firmer, more consolidated muds. It is restricted to riverine sites that are inundated by most high tides.

Sonneratia caseolaris may form monospecific stands along riverbanks and may occur throughout the river course on small raised midstream mudbanks. Here, low light levels occur beneath the tree canopy. It often forms mixed associations with other pioneering species such as *Avicennia marina, Avicennia officinalis, Aegiceras corniculatum* and *Acanthus ilicifolius*. In some localities, the species occurs in mixed association with *Sonneratia alba*.

Sonneratia caseolaris is more abundant at sites inundated by brackish waters, but the species can tolerate seawater salinity for a limited period. Within the survey area, the species was found in areas inundated by waters of salinity up to 35‰. In the more saline areas, *Sonneratia caseolaris* is a shrub. It only attains tree dimensions in brackish or predominantly freshwater sites.

REGENERATION: Fruits are dispersed by the tides. This species only regenerates on accreting exposed bare mudbanks. Seedlings appear to be intolerant of shade. Aggregations of seedlings often are observed colonizing mudbanks (concave portions of meanders) that have previously slumped into the river. Seedlings establishing on such sites are normally dislodged and swept away during wet season floods.

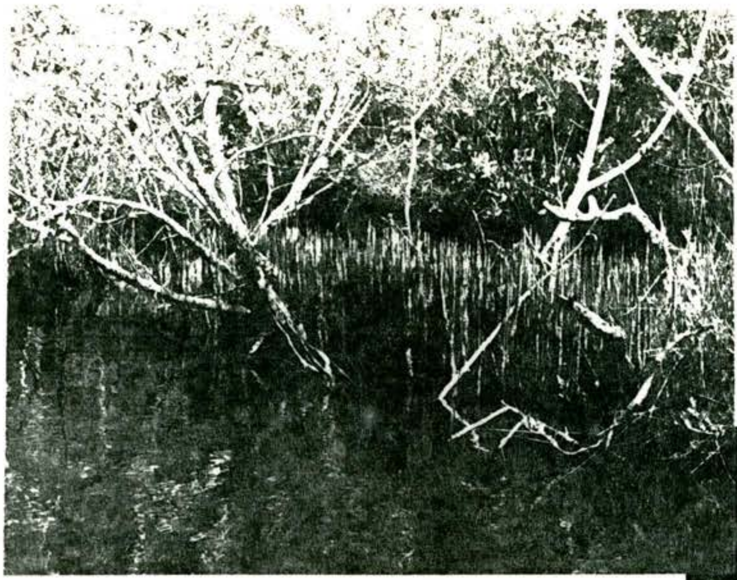
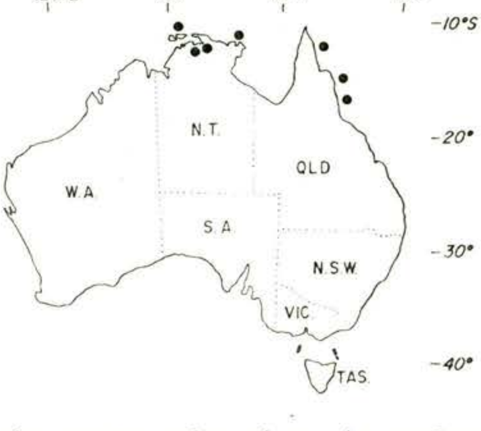


PLATE 2.3.24.1
From the subsurface cable roots, pneumatophores, projectile-like spikes through the mud in radiating lines from the trunk.

PLATE 2.3.24.2
Leaves - narrow elliptic or sublanceolate, apex blunt, base continuing to the petiole so that the leaf appears stalkless. Fruit - 6 cm dark green, depressed above with a persistent style, calyx flattened in fruit; sepals spreading more or less horizontally.



The most westerly occurrence of this species is on Andranangoo Creek, Melville Island, NT (11°21'S, 130°51'E) (Wells, 1982). It is abundant on tidal waterways entering Van Diemen Gulf (NT) and also occurs on certain rivers within Arnhem Bay (NT). Its distribution is discontinuous throughout the northern coastline of the Northern Territory and the species has not been recorded east of the Peter John River in Arnhem Bay, NT (12°15'S, 136°21'E). It also has not been recorded on tidal waterways within the Gulf of Carpentaria. On the east Australian coast it occurs from the Olive River, Qld (12°10'S) to the Murray River, Qld (18°05'S) (Duke, 1981) although its distribution here is again discontinuous.

2.3.25 *Acrostichum speciosum:*
Derris trifoliata
Diospyros ferrea var. *humilis*
Nypa fruticans
Rhizophora lamarckii

None of these species of mangroves was studied in detail although they occur within the survey area: the vine *Derris trifoliata* and the tree *Diospyros ferrea* var. *humilis* are frequently observed within mangrove associations, particularly along portions of tidal waterways along the northern coastline of the Northern Territory that remain brackish for extended periods throughout the year.

The stemless palm mangrove *Nypa fruticans* occurs at only one site in the Northern Territory, Maxwell Creek, Melville Island, a site not investigated during this survey. *Rhizophora lamarckii*, although occurring within the Alligator Rivers complex in the Northern Territory (Hegerl *et al.*, 1979), was not observed by this writer.

2.4 SPECIES ASSOCIATIONS IN THE SURVEY AREA

Within the survey area, three basic categories of mangroves exist:

(a) Pure or monospecific stands

(b) Paired associations

(c) Mixed associations.

2.4.1 ASSOCIATIONS - MONOSPECIFIC STANDS

The following species have been observed in certain circumstances to form monospecific stands in the survey area:

Acanthus ilicifolius

Avicennia marina

Avicennia officinalis

Lumnitzera racemosa
Aegiceras corniculatum

Osbornia octodonta

Aeqialitis annulata

Bruquiera exaristata

Bruguiera parviflora

Ceriops tagal var. *australis*

Rhizophora stylosa

Sonneratia alba

Sonneratia caseolaris

Often these monospecific stands form broad zones or may occur as discrete entities near other associations. Discussion of many of these stands is given under the individual species' headings.

Why certain species form monospecific stands appears to depend on many local environmental factors. The occurrence of *Avicennia marina* in the most landward mangrove zones can normally be ascribed to the fact that soil salinities experienced in such zones at the end of the dry season are apparently above tolerance levels of all other mangrove species. Stands of *Bruguiera parviflora* probably become pure over time through the gradual elimination of other mangrove species due to the low level of light that penetrates through the tall *Bruguiera* canopy to the forest floor. There is little available light to promote seedling development and floors of such forests are practically bare. It appears that *Bruguiera parviflora* out-competes other mangrove species in colonizing these infrequently inundated sites. Regeneration in monospecific stands of this species appears to occur by gradual replacement by seedlings rapidly growing in areas of higher light levels where older trees have died and fallen to the forest floor after teredo-worm attack.

Degree of tidal inundation, soil salinities and type of substrate appear particularly important for establishment of *Sonneratia alba* in lower estuarine localities. The presence of numerous woody pneumatophores also provides this species with certain advantages in colonizing newly accreting mudbanks that are frequently inundated. An ability to tolerate extremely lengthy periods of freshwater inundation is probably a major factor permitting the establishment of extensive monospecific stands of *Sonneratia caseolaris* along certain rivers on the northern coastline of the Northern Territory.

2.4.2 PAIRED ASSOCIATIONS

Paired associations are reasonably common and involve mangrove species from, in many cases, different plant families that colonize, under certain circumstances, quite similar habitats. Local environmental conditions are again most likely to be responsible for these associations but actual reasons for any two species forming such an association are undoubtedly complex. The following paired associations occur in this survey area:

- *Avicennia marina/Sonneratia alba* association - most commonly observed at seaward sites across the northern coastline of the Northern Territory on accreting mudbanks that are inundated by most high tides.
- *Avicennia marina/Aegialitis annulata* association - typically occurs on mud substrates that are infrequently inundated. Along some waterways in the southern portion of the Gulf of Carpentaria, this association may occur as fringing riverside vegetation.
- *Avicennia marina/Camptostemon schultzii* association - occurs as fringing riverside vegetation in the Kimberley region of Western Australia on accreting mudbanks. This association is inundated daily by high tides and during periods of spring

tides (range 11 metres) is inundated nearly to the top of the canopy.

- .*Avicennia marina/Aegiceras corniculatum* association - *Aegiceras* forms the understorey to this association, which is frequently observed as fringing vegetation along many upstream portions of tidal waterways that remain fresh/ slightly brackish for most of the year.
- .*Avicennia officinalis/Acanthus ilicifolius* association - occurs around convex portions of meanders at certain sites across the northern coastline of the Northern Territory, particularly in areas where waters remain brackish for most of the year. This association is inundated by most high tides.
- .*Bruguiera exaristata/Bruguiera parviflora* association - frequently observed on many tidal waterways except those in more arid portions of the survey area. This association often occurs immediately landward of a zone of *Rhizophora stylosa.*
- .*Camptostemon schultzii/Sonneratia alba* association - frequently observed on accreting mudflats to seaward in the Kimberley region of Western Australia. This association is inundated by all high tides.
- .*Rhizophora stylosa/Rhizophora apiculata* association - occurs at several sites along the northern coastline of the Northern Territory but is relatively uncommon. It forms a low closed forest in some estuaries on consolidated muds.
- .*Excoecaria agallocha/Xylocarpus australasicus* association - frequently occurs as fringing riverside vegetation on infrequently inundated mud substrates in upstream portions of tidal waterways in the Kimberley region.

2.4.3 MIXED ASSOCIATIONS

Under the wide variety of physiographic conditions that exist in mangrove-colonized habitats, all mangrove species in the Northern Territory and Kimberley region of Western Australia form mixed associations in certain circumstances. These associations are shown in Tables 2.4.1

and 2.4.2.

The most frequently observed mixed mangrove association in the Northern Territory is of *Rhizophora stylosa, Camptostemon schultzii* and *Avicennia marina.* This association commonly forms fringing forests along tidal waterways.

Even species of quite restricted distribution such as *Sonneratia caseolaris* may, under certain circumstances, form a mixed association with *Sonneratia alba, Rhizophora stylosa* and *Avicennia marina* or with *Lumnitzera racemosa, Acanthus ilicifolius* and freshwater strand species such as *Melaleuca leucadendron.*

The most common types of mixed associations in the Northern Territory are with:

(a) *Rhizophora stylosa* dominant

(b) *Camptostemon schultzii* dominant

(c) *Avicennia marina* dominant

(d) *Ceriops tagal* var. *australis* dominant

(e) *Xylocarpus australasicus* dominant

(f) *Sonneratia caseolaris* dominant

(g) *Avicennia officinalis* dominant

(h) *Bruguiera parviflora* dominant

(i) *Bruguiera exaristata* dominant

Mixed associations dominated by either *Rhizophora stylosa, Camptostemon schultzii* or *Avicennia marina* occur as fringing riverside vegetation on portions of all river and creek systems in the survey area.

Mixed associations dominated by *Ceriops tagal* var. *australis,* principally with *Excoecaria agallocha, Avicennia marina, Bruguiera exaristata, Aegialitis annulata* and *Lumnitzera racemosa* occur on consolidated clay soils at sites inundated only by spring high tides.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Σ
1.	*Acanthus ilicifolius*	m	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	22
2.	*Avicennia marina*	+	m	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	20
3.	*A. officinalis*	+	+	m	+						+	+	+					+	+			+		+	+	11
4.	*Camptostemon schultzii*	+	+	+			+	+		+	+	+	+	+	+	+	+	+	+	+	+	+		+		19
5.	*Lumnitzera littorea*	+						+		+	+	+	+	+	+	+		+		+	+	+	+			14
6.	*L. racemosa*	+	+		+		m	+		+	+	+	+	+	+	+		+	+	+	+	+	+			17
7.	*Excoecaria agallocha*	+	+		+	+	+		+	+	+	+	+	+	+	+	+	+	+	+		+				18
8.	*Xylocarpus granatum*	+						+		+	+				+						+	+				7
9.	*X. australasicus*	+	+		+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+				19
10.	*Aegiceras corniculatum*	+	+	+	+	+	+	+	+	+	m	+	+	+	+	+		+	+	+	+	+		+	+	21
11.	*Osbornia octodonta*	+	+	+	+	+	+	+		+	+	m	+	+		+			+	+	+	+	+	+		18
12.	*Aegialitis annulata*	+	+	+	+	+	+	+		+	+	+	m	+	+	+		+	+	+	+	+	+	+		20
13.	*Bruguiera exaristata*	+	+		+	+	+	+		+	+	+	+		+	+		+	+	+	+	+				17
14.	*B. gymnorhiza*	+	+		+	+	+	+	+	+	+		+	+		+	+	+	+	+	+	+				18
15.	*B. parviflora*	+	+		+	+	+	+		+	+	+	+	+	+	m	+	+	+	+	+	+				18
16.	*B. sexangula*	+	+		+			+		+					+	+		+			+	+			+	11
17.	*Ceriops decandra*	+	+	+	+	+	+	+		+	+		+	+	+	+	+		+	+	+	+				18
18.	*C. tagal* var. *australis*	+	+	+	+		+	+		+	+	+	+	+	+	+		+	m	+		+				16
19.	*C. tagal*	+	+		+	+	+	+		+	+	+	+	+	+	+		+	+		+	+				17
20.	*Rhizophora apiculata*	+	+		+	+	+		+	+	+	+	+	+	+	+	+	+		+		+				17
21.	*R. stylosa*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	m		+		21
22.	*Scyphiphora hydrophyllacea*					+	+					+	+													4
23.	*Sonneratia alba*	+	+	+	+						+	+	+									+		m	+	9
24.	*S. caseolaris*	+	+	+							+						+							+	m	6

TABLE 2.4.1

Occurrence (m) in monospecific stands and joint occurrences (+) in mixed stands between mangrove species in the survey area, each species listed under the same number along the top of the table as it is down the table. (Σ for each species is the total number of other spp. with which it jointly occurs in mixed stands in the survey area).

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Σ
1.	*Acanthus ilicifolius*		+	+			+		+	+														+	+	7
2.	*Avicennia marina*	+			+		+	+			+		+	+	+	+	+	+	+	+	+	+		+	+	17
3.	*A. officinalis*	+									+													+	+	4
4.	*Camptostemon schultzii*		+							+				+	+	+	+	+			+	+		+		10
5.	*Lumnitzera littorea*														+								+			2
6.	*L. racemosa*	+	+					+			+	+	+		+				+							8
7.	*Excoecaria agallocha*		+				+					+	+						+	+						6
8.	*Xylocarpus granatum*	+													+						+	+				4
9.	*X. australasicus*	+			+										+	+		+				+				6
10.	*Aegiceras corniculatum*		+	+			+											+				+		+	+	7
11.	*Osbornia octodonta*						+	+					+						+							4
12.	*Aegialitis annulata*		+			+	+					+						+	+					+		7
13.	*Bruguiera exaristata*		+		+										+	+		+	+			+				7
14.	*B. gymnorhiza*		+		+	+	+		+	+				+			+	+		+	+	+				12
15.	*B. parviflora*		+		+					+				+			+	+	+	+	+	+				10
16.	*B. sexangula*		+		+										+	+					+	+				6
17.	*Ceriops decandra*		+		+					+	+		+	+	+	+			+	+		+				11
18.	*C. tagal* var. *australis*		+				+	+				+	+	+		+		+								8
19.	*C. tagal*		+					+							+	+		+			+					6
20.	*Rhizophora apiculata*		+		+				+						+	+	+			+						7
21.	*R. stylosa*		+		+				+	+	+			+	+	+	+	+						+		11
22.	*Scyphiphora hydrophyllacea*					+																				1
23.	*Sonneratia alba*	+	+	+	+						+		+									+				7
24.	*S. caseolaris*	+	+	+							+															4

TABLE 2.4.2

Joint occurrences (+) common in mixed stands between each species listed under the same number along the top of the table as it is down the table. (Σ for each species is the total number of other spp. with which it commonly jointly occurs in mixed stands in the survey area.)

Ceriops-dominated thickets occur around many of the less frequently inundated concave (cutaway) portions of meanders in sections of tidal waterways that remain around or above seawater salinity (35‰) for most of the year. *Ceriops* thickets also colonize extensive areas immediately landward of *Bruguiera*-dominated forests. *Ceriops*-dominated mixed associations occur in all regions of the survey area.

The mixed association with *Xylocarpus australasicus* dominant occurs on consolidated muds at certain localities - in particular across the northern coastline of the Northern Territory and the western coastline of the Gulf of Carpentaria that are inundated by predominantly brackish waters over most of the year. These forests are only inundated by spring high tides.

The *Avicennia officinalis*-dominated mixed association occurs only at sites across the northern coastline of the Northern Territory. Other species commonly found in this assocaition include *Sonneratia alba*, *Acanthus ilicifolius*, *Aegiceras corniculatum* and, in some instances, *Avicennia marina*. This association colonizes accreting convex portions of meanders along certain rivers that remain brackish for most of the year.

The mixed associations dominated by *Bruguiera parviflora* and *Bruguiera exaristata* are frequently observed at sites across the northern coastline of the Northern Territory where it occurs immediately landward of *Rhizophora stylosa*-dominated mixed associations. Other species commonly encountered in these associations include *Bruguiera gymnorhiza*, *Camptostemon schultzii*, *Avicennia marina*, *Rhizophora stylosa* and *Ceriops decandra*. Forests formed of this association are only inundated by spring high tides.

2.5 PEAK SOIL AND WATER SALINITIES RECORDED FOR SPECIES IN THE SURVEY AREA

The highest soil and water salinities recorded for mangrove species in this survey area are given in Fig. 2.5.1 where species have been arranged in ascending order of the maximum salinity recorded with the occurrence of each species. It is seen for all species that

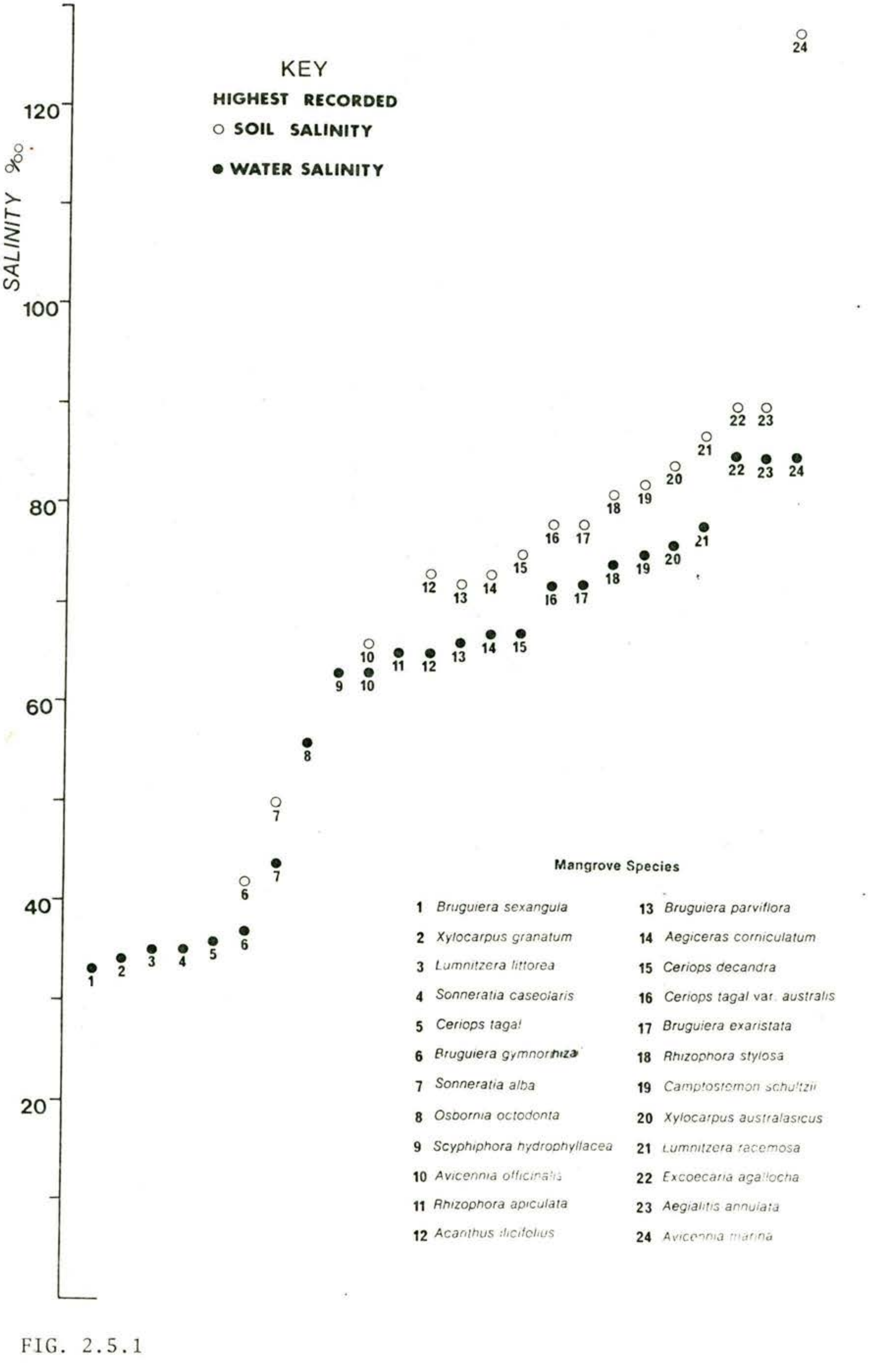


FIG. 2.5.1

Highest recorded soil (interstitial water) and water salinities for mangrove species in the survey area. Arranged in order of increasing salinity.

highest recorded soil salinities are always slightly higher than corresponding high tide water salinities. Carriker (1967) and others have shown that in most estuaries the salinity of pore (interstitial) water at the sediment surface normally slightly exceeds that of the surrounding waters. This confirms the earlier observations of Alexander *et al*, (1932) that water retained in the mud substrate along a tidal waterway at low tide is slightly more saline than the river water itself at equivalent distances from the sea.

Nelson (1962) has shown that in sediments of the upper reaches of a tidal waterway, chlorinity does not change with profile depth whilst in those of the lower, more saline reaches, interstitial chlorinity (and thus interstitial salinity) increases slightly with depth. Paijmans and Rollet (1977) however show for mangrove muds in the Gulf of Papua (New Guinea) that salinity increases markedly below a depth of 4 metres. Wolanski and Gardiner (1981) working in north Queensland swamps point out that at least to a depth of 2 metres salinity in mangrove muds does not vary systematically with depth. Laevastu and Fleming (1959) have also shown that replacement of fresh interstitial water with saline waters (as occurs at different rates in all tidal waterways in this survey area) was rapid, whereas replacement of saline interstitial waters by overlying fresh waters was a much slower process.

Quantitative relationships between the salinity in the substratum and variable salinity of the overlying water are not completely understood although Smith (1956) in particular, has discussed the possibility that density of animal burrows may, by irrigation of these burrows at high tide, profoundly influence the speed of adjustment of interstitial salinities to variations in overlying water salinities.

Numerous workers have commented on the effect of soil and water salinities on floristic composition and resultant structure of mangrove communities and associations. Such studies have most recently been reviewed by Macnae (1968); Walsh (1974) and

Chapman (1976), in particular.

Macnae (1968), in his description of salt flats in Western Australia observed species changes and increasing scrubbiness with increasing soil salinities. He reported dwarfed *Avicennia marina* growing in soils of 90°/oo salinity. More recently, Cintron *et al.* (1978), in their study of mangroves in Puerto Rico and adjacent islands in the Carribean, suggest that mangrove growth is limited by soil salinities higher than 90°/oo and that mangroves were not found at sites possessing soil salinities much in excess of 80°/oo . They also show that tree height was inversely proportional to soil salinity (r = 0.72) between 17-72°/oo and that where soil salinities exceeded 65°/oo that dead tree basal area exceeded live tree basal area.

From observations of soil and water salinities experienced by various mangrove species in this survey area, it would appear (Fig. 2.5.1) that most species, with the exception of *Avicennia marina*, cannot tolerate soil salinities much in excess of 80°/oo for even limited periods of a year.

In Fig. 2.5.1 it is seen that *Avicennia marina* (a salt-excreting species) was recorded **alive** in a soil of salinity 128°/00 (towards the end of the dry season). However, under these conditions it occurs only as a shrub less than 0.5 metres in height. The considerable difference between highest water salinity (85°/oo) and soil salinity (128°/oo) recorded for this species is explicable by the fact that due to mixing of hypersaline waters, it is extremely difficult for water in a tidal situation (of continual mixing) to attain a salinity much in excess of 80°/oo - even in the driest year, whereas the adjacent unvegetated mudflats can easily attain much higher salinities as salt is increasingly concentrated in the soil and each additional high tide inundation of the mudflats will leave more salts to accumulate at a much faster rate in the soil substrate (chiefly due to evaporation) than the surrounding waters during the late dry season.

Previously it was noted that replacement of fresh interstitial water with saline waters in substrates is a much more rapid process than replacement of saline interstitial water by overlying freshwaters (Laevastu and Fleming, 1959). Such a process is to be expected from differences in densities of the two water bodies. This condition appears to be of considerable ecological importance as it permits different mangrove species (within their salinity limits) to penetrate a greater distance upstream than epifauna (such as crabs) of similar osmotic tolerances. Epifauna must naturally migrate with seasonal changes in salinity along a tidal waterway, but mangroves cannot move. However, as the interstitial water salinity (at depth) of many of the mud substrates remains quite saline even when overlain by freshwaters induced by 'wet' season floods, it is now apparent that most mangrove species are not greatly affected by short periods of freshwater flooding. Certain species - in particular, *Acanthus ilicifolius* and *Avicennia officinalis* - have even been observed excreting salt through their leaves after seven months' periodic tidal inundation by freshwaters.

Different mechanisms, as discussed most recently by Mizrachi *et al*, (1980), regulating or excluding salts, operate in different mangrove species. However, there does not seem to be any evidence that "salt-excluding" species are greatly disadvantaged in colonizing sites when compared to "salt-excreting" species. In fact, from Fig. 2.5.1, it is seen that several "salt-excluding" species (i.e., *Excoecaria agallocha, Lumnitzera racemosa* and *Xylocarpus australasicus*) are amongst the most salt-tolerant species, only surpassed by *Aegialitis annulata* and *Avicennia marina* (both "salt-excreting" species.

In Fig. 2.5.1 species such as *Bruguiera sexangula, Xylocarpus granatum, Lumnitzera littorea, Sonneratia caseolaris* and *Ceriops tagal* appear to have the lowest salinity limits, and it is seen in Fig. 2.6.1

that these species also have a low frequency of occurrence in this survey area. Other species, however, which appear to possess the highest salinity limits, invariably show the greatest frequency of occurrence whereas most of those species possessing a percentage frequency of occurrence between 25-75% are seen to be those species in the middle of the range of maximum salinity recorded with their occurrence as shown in Fig. 2.5.1.

It is apparent that an ability to tolerate extremely high salinities, even for quite limited periods of the year, and a wide range of salinities, would provide certain species with advantages in establishment throughout tidal waterways in this survey area. Such species are likely to be more ubiquitous in occurrence than those species that could tolerate salinities only slightly greater than seawater salinity (35$^{\circ}/oo$). Thus, the salinity limits tolerated by the various species may be one important factor in explaining distribution, abundance and structure of different mangrove communities in this survey area. The observational evidence presented here suggests that the upper limit of mangrove growth with respect to soil salinity may be at approximately 2.5 times the concentration of salt in normal seawater and is in agreement with the findings of Cintron *et al.,* (1978) for species in the Carribean.

2.6 DISCUSSION

In attempting to provide plausible explanations for the distributions of mangrove species recorded in this survey area, it is necessary firstly to examine distributions of each of these species throughout their entire geographic ranges in the Indo-Pacific region and secondly to attempt to understand details of their distributional patterns within the survey area.

2.6.1 DISTRIBUTIONS OF SPECIES IN THE INDO-PACIFIC REGION

Numerous studies by various workers on many aspects of mangrove vegetation in the Indo-Pacific region have been published and reference is best directed to Chapman (1976, 1977) on this matter.

Guppy, (1906), Steenis (1958, 1962); Macnae (1968) and Chapman (1975, 1976, 1977) have, in particular, provided overviews together with their own researches on community structure and occurrences of the various mangrove species in the Indo-Pacific region, and interpretation of species distributions in this survey area is greatly facilitated by their studies. More recent work by Percival and Womersley (1975, (New Guinea); Floyd (1977) (New Guinea); Bunt (1978) and Duke and Bunt (1979) (eastern Queensland); Semeniuk *et al.*, (1978) (Western Australia); Johnstone and Frodin (in press); Lin, (1980)(China); and Bunt *et al.*, (1982) (eastern Queensland), in particular, have now largely elucidated distributions of mangrove species in areas outside this survey area that were also largely unknown.

Of particular relevance is the need to examine distributions of mangrove species recorded in this survey area in the context of distributions of these same species throughout south-east Asia and along the east coast of Africa, as shown in Chapman (1977). Using this approach, regions of "geographical" extent, as discussed by Pielou (1975), large enough to be regarded as the most probable source areas from which the complement of species now recorded in this study area have been drawn, both during present and historical times, are included in the discussion.

Certain species, *Aegiceras corniculatum; Aegialitis annulata; Avicennia marina; Bruguiera exaristata; Ceriops tagal* var. *australis, Excoecaria agallocha; Lumnitzera racemosa; Osbornia octodonta; Rhizophora stylosa* and *Xylocarpus australasicus*, are shown in Fig. 2.6.1 as quite ubiquitous throughout the survey area, with overall percentage occurrences greater than 75% for the sites surveyed. Other species, *Acanthus ilicifolius; Bruguiera gymnorhiza; Bruguiera parviflora; Camptostemon schultzii; Ceriops decandra* and *Sonneratia alba* show overall percentage occurrences of between 25-75%, whereas *Avicennia officinalis; Bruguiera sexangula; Ceriops tagal; Lumnitzera littorea; Rhizophora apiculata; Scyphiphora hydrophyllacea; Sonneratia caseolaris*

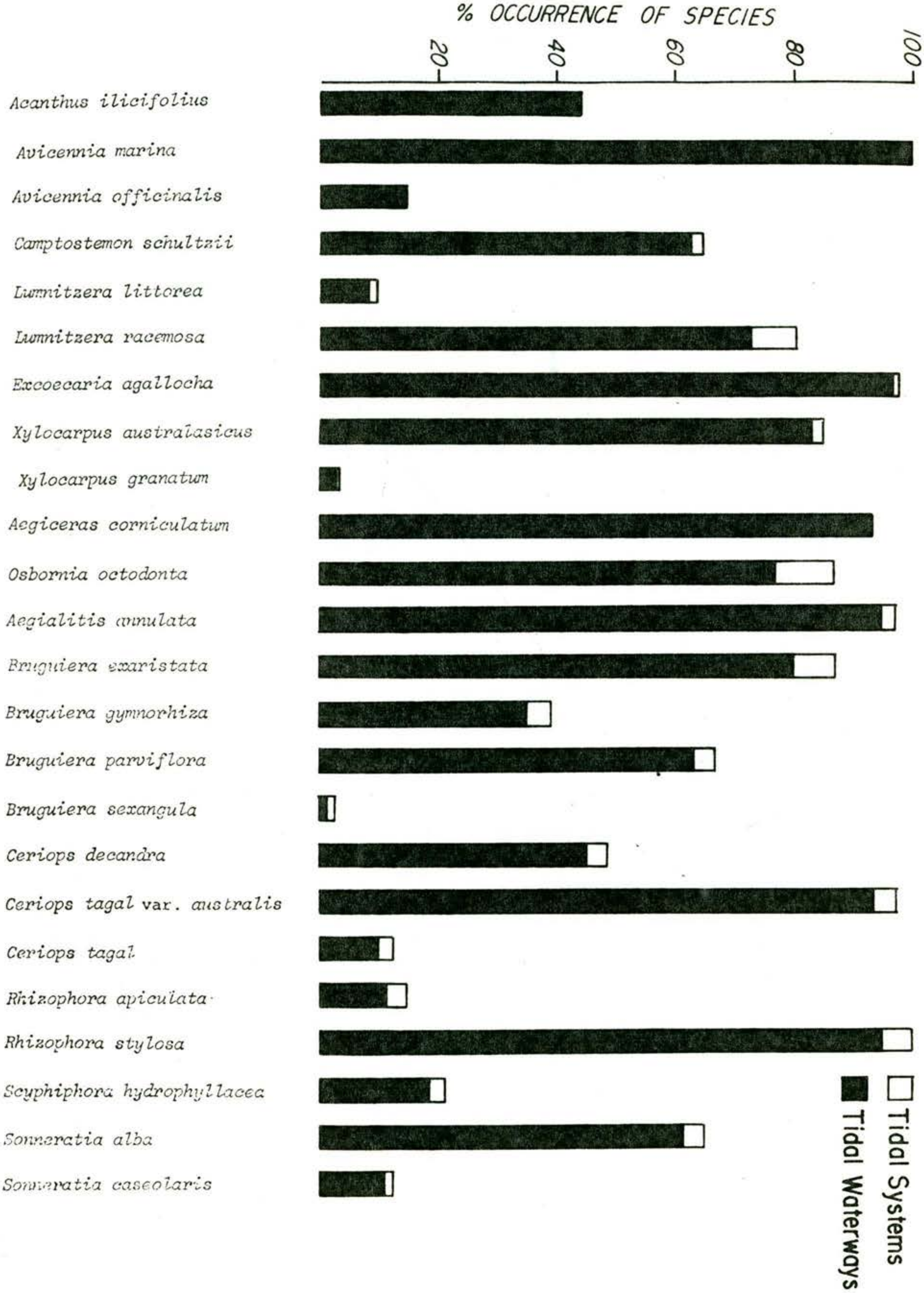
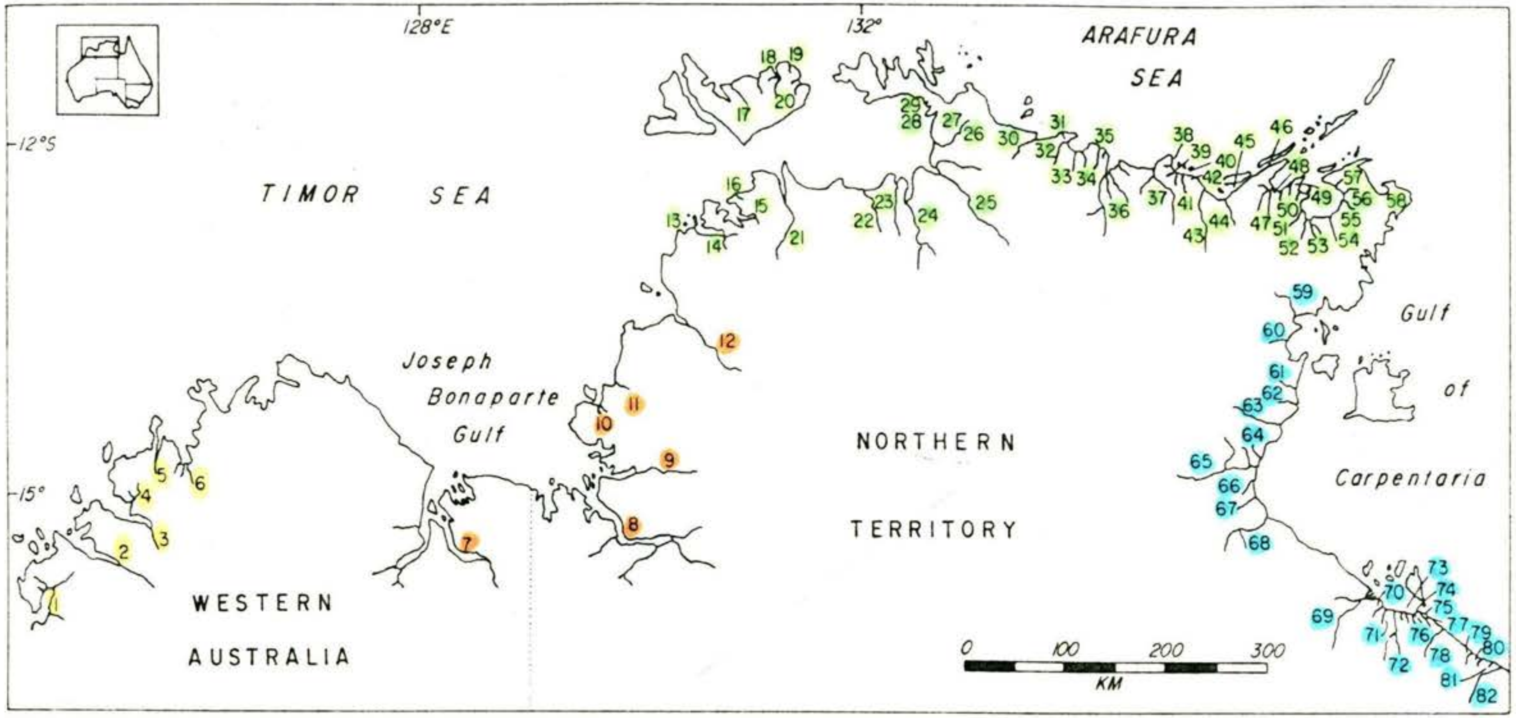


FIG. 2.6.1

Percentage occurrence of mangrove species in tidal waterways and tidal systems in the survey area.



1 GEORGE WATER
2 PRINCE REGENT
3 ROE
4 HUNTER
5 MITCHELL
6 PORT WARRENDER
7 ORD
8 VICTORIA
9 FITZMAURICE
10 PORT KEATS
11 MOYLE
12 DALY
13 PORT PATERSON
14 BYNOE HARBOUR
15 DARWIN HARBOUR
16 BUFFALO
17 ANDRANANGOO
18 JOHNSTON/BATH
19 DONGAU
20 TINGANOO
21 ADELAIDE
22 WILDMAN
23 WEST ALLIGATOR
24 SOUTH ALLIGATOR
25 EAST ALLIGATOR
26 MURGENELLA
27 MINI MINI
28 IWALG
29 ILAMARYI
30 KING
31 ARRLA
32 GOOMADEER
33 WURUGOIJ
34 MAJARIE
35 NUNGBALGARRIE
36 LIVERPOOL/TOMKINSON
37 BLYTH/CADELL
38 NGANDADAUDA
39 DJABURA
40 DJIGAGILA
41 DARBITLA
42 BENNET
43 GLYDE
44 WOOLEN RIVER
45 HUTCHINSON STRAIT
46 CADELL STRAIT
47 BUCKINGHAM/KALARWOI
48 WARAWURUWOI
49 KURALA
50 SLIPPERY
51 DARWARUNGA
52 HABGOOD
53 BARALMINAR/GOBALPA
54 GOROMURU
55 CATO
56 PETER JOHN
57 BURUNGBIRINUNG
58 MELVILLE BAY
59 KOOLATONG
60 WALKER
61 HART
62 MUNTAK
63 ROSE
64 YIWAPA
65 ROPER
66 NAYARNPI
67 TOWNS
68 LIMMEN BIGHT
69 McARTHUR
70 'COULOMB'
71 'FARADAY'
72 WEARYAN
73 'BOHR'
74 'PLANCK'
75 'ARCHIMEDES'
76 'GALILEO'
77 FAT FELLOWS
78 ROBINSON
79 'EINSTEIN'
80 'NEWTON'
81 'PAULI'
82 CALVERT

FIG. 2.6.2

Tidal systems in the four major regions of the survey area.

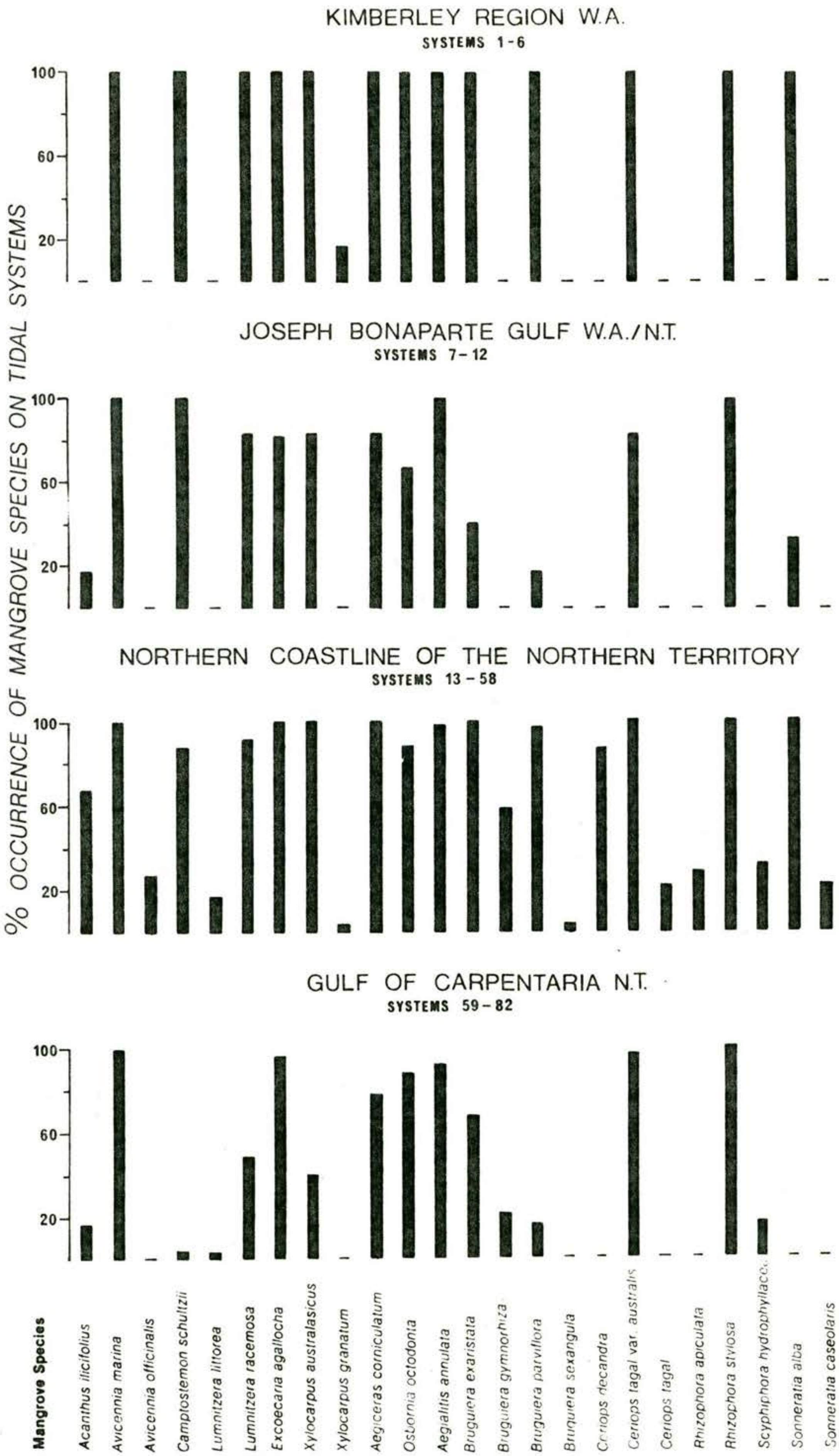


FIG. 2.6.3

Percentage occurrence of mangrove species on tidal systems in the four major regions of the survey area.

and *Xylocarpus granatum* only show overall percentage occurrences of less than 25% for sites in this survey area.

Many of the ubiquitous species *(Aegiceras corniculatum; Avicennia marina; Excoecaria agallocha* and *Lumnitzera racemosa)* across this portion of the north Australian coastline have also been shown, particularly in Chapman (1977) to possess extremely wide geographical ranges throughout the Indo-Pacific region. Other ubiquitous species in this survey area, *Ceriops tagal* var. *australis; Rhizophora stylosa* and *Xylocarpus australasicus*, show only restricted ranges principally in the Australian/New Guinea region; however these species show historical botanical affinities with *Ceriops tagal* (Perr.) C.B. Rob.; *Rhizophora mucronata* Lamk. and *Xylocarpus moluccensis* (Lamk.) Roem. respectively and care must be taken when discussing distributions of these closely related species, which have in all probability speciated away from the core species *Ceriops tagal*, *Rhizophora mucronata* and *Xylocarpus moluccensis* through geographical isolation over considerable geological time.

Distributions of *Aegialitis annulata* (Steenis, 1962) and *Bruguiera exaristata* (in Chapman (1976, 1977)), also show these species as being largely endemic to Australia/New Guinea and this is also true for *Osbornia octodonta* which, however, extends slightly more northward, occurring locally at sites to Sabah, east Malaysia (Fox, 1970) and into the Philippines (Pancho, 1978). *Aegialitis annulata* has a most perplexing geographical range. It is only recorded at sites around the southern margins of Indonesia (Chapman, 1976); West New Guinea and the Gulf of Papua (Percival and Womersley, 1975) and Australia (Saenger *et al.*, 1977; Bunt, 1978; Duke, 1981; Wells, 1983, in particular). *Aegialitis annulata* is absent from the remainder of south-east Asia, although a closely related species, *Aegialitis rotundifolia* Roxb. occurs as Blasco, (1975) shows in the northern hemisphere (Burma, India). These species now occur solely in seasonally dry regions in both hemispheres, and an intolerance of high, well distributed rainfall throughout the year, as occurs at many sites in south-east Asia, may be largely responsible for the non-occurrence of either of these species there. Absence of any overlap in the geographical ranges of these two species today is remarkable. Fossil pollen of *Aegialitis* was found in Tertiary deposits in north-western Borneo by Muller (1964).

Of the mangrove species with overall percentage occurrences of between 25-75% (Fig. 2.6.1), *Acanthus ilicifolius, Bruguiera gymnorhiza, Bruguiera parviflora, Ceriops decandra* and *Sonneratia alba* all have quite extensive geographical ranges in the Indo-Pacific region - this is particularly so for *Bruguiera gymnorhiza* and *Sonneratia alba* (Chapman, 1975, 1976, 1977; Fosberg, 1975). *Camptostemon schultzii* provides the exception and is largely endemic to Australia and the southern coastline of New Guinea (Percival and Womersley, 1975) and overlaps in range with a closely related species *Camptostemon philippinense* (Vidal) Becc. on Ambon Island in the Moluccas (Chapman, 1976).

For species with overall percentage occurrences of less than 25% in this survey area they appear to require specific habitats and their disjunct distributions most probably result from variations in the degree of seasonal aridity experienced in different portions of the survey area. Several problems, however, exist to this plausible hypothesis being totally accepted.

This group of species was only infrequently recorded at sites in this survey area, but also possess some members - *Ceriops tagal* and *Xylocarpus granatum* - that have extremely large geographical ranges from the east coast of Africa to the Pacific Ocean, whereas *Avicennia officinalis, Bruguiera sexangula, Lumnitzera littorea, Rhizophora apiculata, Scyphiphora hydrophyllacea* and *Sonneratia caseolaris* are largely confined within south and south-east Asia (Chapman, 1977, in particular) with some species extending to sites in the northern portion of Oceania (Hosokawa *et al*., 1977; Fosberg, 1947, 1975).

It is apparent from the previous discussion and in Chapman (1975, 1976, 1977) that though a particular mangrove species has a wide geographical distribution it may not be abundant or even occur at all tidal wetland sites within that range. Conversely, just because a species has a restricted geographical range does not imply that this species will be rarely encountered within its range. Successful establishment of any species at any site then within its range is considered as Saenger *et al*, (1977) so aptly put it, "to depend on the complex inter-relation of historical, environmental, biological and chance factors".

It is also important to emphasize that, as Macnae (1968) and Chapman, (1976) show, floristic diversity of mangrove swamps decreases with increasing latitude in both hemispheres away from the Equator - illustrating the tropical nature of the vegetation. However it appears that local climatic conditions and the presence/absence of suitable intertidal substrates in the various coastal regions of the continents may determine present diversity. In this regard, even though suitable edaphic conditions may exist for a species to become established at sites within its geographic range, actual colonization of these sites will not occur in the presence of unfavourable climatic conditions.

In undertaking this survey of one of the least studied regions of mangrove species distributions in the entire Indo-Pacific, it was originally felt that the delimitation of species distributions in this area of northern Australia, marking as it does a boundary of the Indian Ocean, Timor and Arafura Seas, might throw considerable light onto the distributions of many mangrove species. In this, the study has only been partially successful and the findings reiterate the complexity of the distributional problem and the need to examine many species distributions individually.

2.6.2 DISTRIBUTIONS OF INDIVIDUAL SPECIES IN SURVEY AREA

Bruguiera gymnorhiza in this survey area (Section 2.3.14) is seen not to be recorded at any site in Western Australia or Joseph Bonaparte Gulf and only shows sporadic occurrences throughout the Gulf of Carpentaria. From an examination of local climatic conditions (Section 1.3) this species only appears to occur in areas that are not subjected to high levels of seasonal aridity. Also, throughout most other parts of its range, such as in Kenya (Dale, 1958); Mozambique (Macnae and Kalk, 1962); South Africa (Ward and Steinke, 1982); Madagascar and south-east Asia (Chapman, 1975, 1976, 1977); New Guinea (Percival and Womersley, 1975) and the east coast of Queensland (Macnae, 1966; Jones, 1971a; Bunt, 1978), *Bruguiera gymnorhiza* shows a preference establishing at sites where brackish water influence is considerable and climatic conditions could best be described as humid tropical (Beard, 1977).

The Kimberley coastline of Western Australia in this survey area, although quite seasonally arid, still receives between 1,000-1,500 mm of rainfall per year (Fig. 1.3.4) with some 97% of this precipitation falling during December-May during the 'wet" season (Kuri Bay, Climatic Averages, Western Australia, 1975). Many suitable sites for establishment of this species are considered by this writer to occur on substrates abutting the steep riverine sandstone gorges where freshwater seepage into substrates from surrounding water tables occurs for most of the year. It is at such protected sites that local climatic conditions are considerably ameliorated. However, *Bruguiera gymnorhiza* has not been recorded at any of these sites despite extensive searches.

Inspection of the Indo-Pacific distribution of this species shows that it occurs down the east African coast to around latitude 33°S (Chapman, 1975, 1976, 1977; Ward and Steinke (1982), is absent from the west Australian coast but shows considerable attentuation to 29°S on the east Australian coast (Jones, 1971a; Wells, 1983). Thus, latitudinal distributions of *Bruguiera gymnorhiza* down the humid east coasts of Africa and Australia are closely parallel. It is at this point that this species' distribution at sites along the Red Sea (Zahran, 1975) must be examined.

Zahran shows that *Bruguiera gymnorhiza* occurs at Suakin ($19^{\circ}15'$N) in the Sudan and at Mersa Halaib (22°N) on the border of Egypt and the Sudan. However, Suakin receives on average only 149 mm of rainfall per year, although the amount is known to fluctuate between 33 mm (1953) and 617 mm (1896). It is seen then that *Bruguiera gymnorhiza* is established at several sites along the Red Sea that are subjected to levels of aridity much higher than at those areas within western and northern Australia from which it is not recorded. Thus, the argument that the absence of *Bruguiera gymnorhiza* from the coastlines of Western Australia, Joseph Bonaparte Gulf and most of the Gulf of Carpentaria is totally due to high levels of seasonal aridity is not entirely convincing and other factors may well be involved. One such factor could be direction of surface sea currents (Section 1.3.7) during the 'wet' season when *Bruguiera gymnorhiza* fruits are dispersed (Table 5.1). Currents during this portion of the year are considered largely unfavourable to a westward extension of the range of this species down the Western Australian coastline.

Historically, Churchill (1973) in his palynological study in the south-west of Western Australia shows that members from the Rhizophoraceae *(Rhizophora, Ceriops);* Sonneratiaceae; Nypaceae and Avicenniaceae once extended during the early Tertiary period down to Perth. However, although Churchill did not identify *Bruguiera* pollen it is not to say that it was absent from the Tertiary mangrove flora here, although the findings of Beard, (1977) of probable aridity in the Kimberley region, even in the pre-Tertiary, could imply that *Bruguiera* spp. were even then absent from the west Australian coastline.

In this regard the statement by Fosberg (1975) that pollen of *Bruguiera* is extremely difficult to distinguish from *Rhizophora* may also be the causal factor in the non-identification of *Bruguiera* pollen from Tertiary deposits in the south-west of Western Australia.

The present high latitude distributions of *Bruguiera gymnorhiza* on the east African (33°S) and east Australian (29°S) coastlines contrasts with its absence from the west Australian coast, only being recorded now at sites north of 13°S latitude on the west coast of the Northern Territory (Wells, 1983). As indicated above, this contrast in its distributions on opposite sides of the Indian Ocean cannot be ascribed to particular factors, but it is possible that different populations of this species in different regions within its geographic range now possess different physiological adaptations to seasonally arid conditions, however no studies to test this hypothesis have been undertaken.

In the distribution of *Camptostemon schultzii* in Australia (Section 2.3.4), it is seen that this is the only mangrove species that attenuates further down the west (18°S) rather than the east (12°S) Australian coastline (Wells, 1983). Although, within this survey area, *Camptostemon schultzii* colonizes a wide variety of habitats along the northern coastline of the Northern Territory, it appears most commonly in sites infrequently inundated by brackish waters for most of the year.

However, in the Kimberleys of Western Australia, a coastline that is seasonally quite arid (Section 1.3), *Camptostemon schultzii* commonly forms an association with *Avicennia marina* and/or *Sonneratia alba* in the most seaward pioneer zone (Wells, 1981). In fact, *Camptostemon schultzii* occurs in most mangrove associations in the Kimberleys and is, with *Rhizophora stylosa* and *Avicennia marina*, a frequently encountered species.

Camptostemon schultzii is largely absent, however, from most sites within Joseph Bonaparte Gulf and the Gulf of Carpentaria (Fig. 2.6.3, Appendix Al). Even at those localities where it occurs (Victoria, Daly, Fitzmaurice and Limmen Bight Rivers and Karumba (Olsen, pers.comm.), only a few small, usually straggly, trees or shrubs are observed.

The immediate problem is the ability of *Camptostemon schultzii* to establish at seasonally arid sites in the Kimberleys but not at other highly seasonally arid regions in this survey area (viz. Joseph Bonaparte Gulf; Gulf of Carpentaria). The only noticeable difference in the habit of this species concerns variations in leaf shape. Along the northern coastline of the Northern Territory leaves are largely narrowly elliptic (mean length $\bar{x}$ = 10.85 cm, S.D = 1.16 cm; mean width $\bar{x}$ = 3.67 cm, S.D = 0.70 cm; N = 40) whereas leaves of *Camptostemon schultzii* in the Kimberley region for an equivalent sample size (N = 40) are narrowly lanceolate (mean length $\bar{x}$ = 8.44 cm; S.D = 0.65 cm; mean width $\bar{x}$ = 1.69 cm; S.D = 0.23 cm). Inspection shows no significant differences in length between leaves from these two areas, although widths are significantly slightly narrower in the sample from the Kimberleys.

In the Kimberleys, *Camptostemon schultzii* is largely shielded by high sandstone cliffs of the Mitchell Plateau. It is plausible to suggest that deflection of much of the hot, dry south-east trade winds that blow across the deserts occurs due to this plateau and that these winds do not affect to a great extent most mangrove associations here during the 'dry' season - in the most seasonally arid portion of the year. However, as these south-east trade winds, blowing across central Australia, and northern central Queensland are not deflected or interrupted by any coastal mountain ranges along the Gulf of Carpentaria or throughout most of Joseph Bonaparte Gulf, the virtual absence of *Camptostemon schultzii* from these regions as opposed to its presence in the Kimberleys could largely be a response to increased seasonal aridity along these shorelines. Certainly on the Limmen Bight, Fitzmaurice and Victoria Rivers, *Camptostemon schultzii* is only observed as an occasional small tree or shrub at sheltered sites beneath rocky gorges and is not observed at any wind-exposed sites in these areas.

That *Camptostemon schultzii* was not recorded at any site along the north coast of Melville Island is most unusual. This species occurs at Ambon Island (Moluccas) (Chapman, 1976, 1977) immediately north of Melville Island and the overall presence of favourable surface sea currents (Soegiarto and Birowo, 1975) during the period of fruiting suggests that *Camptostemon schultzii* could easily reach those shores. Surface currents around the northern coastline of the Northern Territory (Fig. 1.3.7) during the period of its fruiting (Table 5.1) are, however, largely unfavourable for establishment of *Camptostemon schultzii* along the northern coastline of Melville Island. However, fruits and the woolly covered seeds from populations of this species in the Kimberley region have an ideal opportunity (during the period of fruiting), because of favourable surface currents in this region, at this time of year, to reach and establish on the north Melville Island coastline. That suitable habitat exists at sites along this coastline is not doubted and the reason as to why *Camptostemon schultzii* is absent from these shores is just not known. Perhaps it relates to the time the seed can remain immersed in saltwater and remain viable.

In its eastern distribution, Percival and Womersley (1975) and Floyd (1977) describe *Camptostemon schultzii* as being abundant throughout most of the Gulf of Papua and note that the species does not occur on the north-eastern shores of New Guinea. In Australia Jones (1971a) described this species as occurring on Cape York and more recently Bunt (1978) and Duke (1981) have amplified its distribution as being discontinuous in occurrence from Cape York Peninsula to the Pascoe River (12°31'S) on the east Australian coastline.

That *Camptostemon schultzii* does not occur further down this coastline is now known (Duke, 1981) and may be related to the surface sea currents present down the north-east coastline during its period of fruiting. As shown in Chapter 5, the fruiting periods of *Camptostemon schultzii* vary in different longitudes. On the east Queensland coast fruiting is said to occur in November-December (Jones, 1971a), although this is not supported in observations by this writer. Floyd (1977) states that this species fruits during April in the Gulf of Papua and from an examination of the surface sea currents available for transport of fruits and seeds during April in this region, it is seen (Vol. III, Australia Pilot, p.16-17) that currents present can only allow the species to colonize those sites in New Guinea (viz. only around the Gulf of Papua) and along the north-east Queensland coast where *Camptostemon schultzii* is now known to occur. It is plausible to suggest then that surface sea currents available for transport of fruits/seeds during its period of fruiting are largely responsible for the present distribution of this species in this region and its lack of attenuation down the east Australian coast, as occurs in other mangrove species' distributions. However the anti-clockwise rotation of New Guinea away from Queensland during the Pliocene when the Australian and Asian plates collided (Balgooy, 1976) could also provide an historical reason for present distribution of the species.

The 'atypical' occurrence of *Xylocarpus granatum* (Section 2.3.9) in the Prince Regent River (Kimberleys, Western Australia) is another example of a species occurring in an 'unsuitable' region due to the localized presence of suitable habitat. This species, although occurring down the east African coastline to Madagascar (24°S) (Chapman, 1976, 1977) and to 25°S on the east Australian coastline (Dowling and McDonald, 1982; Saenger; pers.comm.) has only been recorded at one site on the west Australian coast (Wells, 1981).

On the Prince Regent River, *Xylocarpus granatum* occurs upstream of km63 in a narrow fringing band (width normally not exceeding 6 metres) abutting steep sandstone cliffs. The species is more abundant along the north bank of this joint-controlled stream. Sheltered beneath these cliffs, which rise steeply to between 30-50 metres, *Xylocarpus granatum* is not exposed to any dry desiccating south-east trade winds that blow across the continent and is also largely shielded from the sun, which from its declination throughout most of the year relative to the position of this river, rarely shines directly onto the stands of this species there.

It appears then that even though the Prince Regent River lies in a seasonally arid portion of this survey area (Section 1.3), amelioration of climatic conditions and the presence of considerable quantities of freshwater entering the upstream tidal portion of the Prince Regent River throughout most of the year (Messel *et al.*, 1977; Burbidge and Messel, 1979) results in suitable edaphic habitat for this species.

It is likely that *Xylocarpus granatum* at this site is a relict occurrence. However, as it occurs near the most westward portion of this survey area, any fruits produced should have the ability once flushed out of the Prince Regent River and St. Georges Basin, during 'wet' season floods, to colonize sites further north towards Darwin. The surface sea currents occurring along this coastline during the 'wet' season (Fig. 1.3.7) are considered ideal to allow colonization at other sites along the Kimberley and west coasts of the Northern Territory. That *Xylocarpus granatum* has not been recorded from any other sites in the Kimberleys or Joseph Bonaparte Gulf (refer to Appendix A1) is considered to be a result of this species' inability to tolerate any considerable amount of seasonal aridity.

This argument is also considered plausible in explaining the non-occurrence of *Xylocarpus granatum* at sites in the southern portion of the Gulf of Carpentaria as it is seen from the prevailing sea surface currents in the Gulf of Carpentaria during the 'wet' season (Fig. 1.3.7) that fruits of this species, especially from its occurrence at Gove (Specht, 1958; this survey), could be easily carried to sites around the Gulf. The isolated occurrence of *Xylocarpus granatum* at Tarrant Point, given by Saenger and Hopkins (1975), may be one example of such chance establishment and is not a relict occurrence as the Gulf is an emergent coastline.

The discontinuous distribution of *Scyphiphora hydrophyllacea* (Section 2.3.22) also deserves special mention. The species occurs from India, throughout south-east Asia, northern Australia and into the Pacific (Chapman, 1976, 1977). It occurs at Cape Londonderry (Semeniuk *et al.*, 1978), the northernmost point of Western Australia, is not recorded throughout Joseph Bonaparte Gulf (Appendix Al) and reappears at Bynoe Harbour near Darwin. Non-occurrence of this species in Joseph Bonaparte Gulf and also at most sites in the Gulf of Carpentaria (Fig. 2.6.3, Appendix Al) appears primarily due to high seasonal aridity experienced in these regions.

That *Scyphiphora hydrophyllacea* does not occur though, throughout the Kimberleys is most unusual. In this survey area, the species shows a habitat preference for rocky, well drained sites that are infrequently inundated by waters near seawater salinity for most of the year. Such sites occur throughout the Kimberleys and sufficient of those sites are considered to be adequately protected from the harsh dry south-east trade winds that blow across the central deserts of the Australian continent during the 'dry' season.

Acanthus ilicifolius and *Lumnitzera littorea* (Sections 2.3.1 and 2.3.5) are other species that occur from India through south-east Asia into the Pacific region (Chapman, 1976, 1977, in particular). They have not been recorded in Western Australia and only *Acanthus ilicifolius* has been infrequently observed in Joseph Bonaparte Gulf whereas both species occur at some sites in the Gulf of Carpentaria. Non-occurrence of these species at most sites in these regions may be related to the degree of seasonal aridity experienced on these coastlines and also to the fact that their fruiting periods (Table 5.1) occur mainly during the wet season - the period when adverse surface sea currents work against westward establishment.

Excoecaria agallocha, Lumnitzera racemosa and *Xylocarpus australasicus* (Sections 2.3.7, 2.3.6, 2.3.8) are, however, quite abundant at sites within this survey area (Figs. 2.6.1 and 2.6.3, Appendix A1) and also within their geographic ranges in Australia. All these species are shown in their respective distributions to attenuate much further down the east than the west Australian coastlines. For most mangrove species, increased levels of aridity on the west coast of Australia are given as a plausible hypothesis in explaining non-occurrence of species, however *Excoecaria agallocha, Lumnitzera racemosa* and *Xylocarpus australasicus* are species all able to tolerate considerable seasonal aridity and their absence from higher latitudes down the west Australian coast is perplexing and suggests that other historical environmental factors must be involved.

Bruguiera parviflora (Section 2.3.15) is most commonly observed at sites across the northern coastline of the Northern Territory in this survey area (Fig. 2.6.3., Appendix A1) and forests (often nearly monospecific), dominated by *Bruguiera parviflora* are most extensive and attain greater heights in the higher more evenly distributed rainfall areas of Melville Island and Arnhem Bay, in particular (refer Fig. 1.3.3). This is in agreement with Watson's (1928) Malaysian findings and those of Macnae (1966) although Bunt (1978) shows that north of Cooktown *Bruguiera parviflora,* while still attaining heights to 20 metres or more, tends not to occur in monospecific stands but forms an association with *Rhizophora* spp. in particular.

In more arid regions of this survey area, *Bruguiera parviflora* forests are practically non-existent and individual trees become much smaller in stature. In the Kimberley region Wells (1981) shows that although this species was recorded on all tidal waterways studied, its abundance is extremely low, and that this is also the case at sites in Joseph Bonaparte Gulf and along the southern shores of the Gulf of Carpentaria. The infrequent occurrence of *Bruguiera parviflora* in these regions is considered to reflect an inability of this species to establish in any degree at sites subjected to considerable seasonal aridity.

Bruguiera sexangula (Section 2.3.16) is distributed from India and throughout south-east Asia (Chapman, 1976, 1977, in particular). It is considered the rarest species and has only been recorded in this survey from Arnhem Bay. Here it occurs at sites that are inundated by brackish waters and are not subjected to any real degree of seasonal aridity for most of the year.

Ceriops decandra (Section 2.3.17) and *Ceriops tagal* (Section 2.3.19) within this survey area also occur commonly only at sites, across the northern portion of the Northern Territory, that are influenced by 'mild' seasonal aridity. Present distributions of these species within their geographic ranges (Chapman, 1975, 1976, 1977) also illustrate the tendency for establishment to occur only at sites not subjected to any high degree of seasonal aridity.

Ceriops tagal var. *australis* (Section 2.3.18) is largely endemic to the Australian/New Guinea region. Throughout its range in the survey area (Figs. 2.6.1., 2.6.3), and within Australia in general, this variety of the species is quite abundant, often forming distinct zones particularly in more seasonally saline soils that are infrequently inundated. Along portions of the north-east coastline of Queensland where rainfall is high and well distributed throughout the year, the variety's importance in mangrove swamps diminishes.

Ceriops tagal var. *australis* is quite abundant at sites subjected to considerable seasonal aridity. In fact, throughout this survey area, *Ceriops* thickets are of greater areal extent in the lower than in higher rainfall regions and appear to largely replace *Bruguiera* forests occurring in regions of higher rainfall. This is particularly so in the Kimberley region and at sites within the Gulf of Carpentaria. It appears probable that in the not too distant past, *Ceriops tagal* var. *australis* diverged from *Ceriops tagal*, with *Ceriops tagal* var. *australis* better tolerating harsher climatic and edaphic conditions.

Rhizophora apiculata and *Rhizophora stylosa* (Sections 2.3.20; 2.3.21) occur from India and Malaysia, respectively, then at sites in south-east Asia and into the Pacific Ocean (Chapman, 1976, 1977, in particular). Within the survey area, *Rhizophora apiculata* occurred in abundance only at sites across the northern coastline of the Northern Territory that receive reasonably high rainfall, the majority of which receive some precipitation in each month of the year. The species was not recorded in the Kimberleys, Joseph Bonaparte Gulf or Gulf of Carpentaria, regions that are subjected to high levels of seasonal aridity. That *Rhizophora apiculata* was not observed in the Kimberleys - in suitably protected habitats - is considered unusual, however extensive searches failed to locate this species in any of the mangrove associations in this region. On the east Australian coastline Duke and Bunt (1979) show its distribution as being nearly continuous to Port Clinton (22°30'S).

In Malaysia, Watson (1928); Macnae (1968) and Chai (1973, 1975), in particular, show that *Rhizophora apiculata* is very abundant, establishing particularly in brackish water habitats, however this is not always the case in Australia and within the survey area this species is often observed in mixed associations at sites inundated predominantly by waters of seawater salinity. It is also shown in Fig. 2.5.1 that this species may establish at sites subjected to high soil and water salinities for limited periods at the end of the 'dry' season, but in such situations *Rhizophora apiculata* occurs only as a small shrub less than 1.5 metres in heihgt.

Rhizophora stylosa, however, occurs throughout most of the survey area and is quite abundant throughout most of its range in Australia (Semeniuk *et al.*, 1978; Duke and Bunt, 1979; Wells, 1983). The virtual absence of this species from the Daly River, Northern Territory, is considered to result from considerable quantities of freshwaters entering the tidal portion of this river throughout the year and its non-occurrence at many upstream sites in the Kimberley region in particular, as discussed by Wells, 1981, and the Ord River (Thom *et al.*, 1975), is considered to result from lack of suitable sites for establishment of the species due to rapid changes in land gradients.

In south-east Asia, *Rhizophora stylosa* is extremely rare and shows a distinct preference to establish on coral shingle (Hou, 1958; Chapman, 1976, 1977) and sand (Steenis, 1962). In Australia, *Rhizophora stylosa* colonizes a wide variety of habitats often occurring in different growth forms at sites according to the frequency of tidal inundation. It appears that *Rhizophora stylosa* is quite well adapted to establishing on seasonally wet/dry coastlines and perhaps avoids 'everwet' sites such as occur throughout much of south-east Asia. In fact, its preference to establish on coral shingle - a porous substrate - in Malaysia and Indonesia may reflect an inability to survive at sites greatly affected by excessive freshwater inundation.

Within Australia, the distribution of *Sonneratia alba* (Section 2.3.23) is not greatly extended down the east as opposed to the west Australian coastline. This can be related to a lack of suitable sites for establishment along the Ninety Mile Beach in Western Australia. However, when examining the distribution of *Sonneratia alba* down the east African coastline (Dale, 1958; Macnae, 1968; Chapman, 1975, 1976, 1977), it is seen that this species does not occur further south than 19°S (at the Zambezi River). Thus the latitudinal distribution of *Sonneratia alba* is roughly equivalent on the east African coast (19°S), and on the east (22°S) and west coasts of Australia (18°S).

Churchill (1973) records fossil *Sonneratia* pollen from palynological studies of the Tertiary mangrove flora in the south-west of Western Australia and he considers, as do Saenger *et al*, (1977) and Semeniuk *et al*, (1978), that there has been a loss of this species from such higher latitude regions since the Eocene. (It is important to stress here that during the Eocene period, this portion of southern Australia was some 15° further south in latitude than its present latitude.)

The absence of *Sonneratia alba* at sites within most of the Gulf of Carpentaria and Joseph Bonaparte Gulf is considered by this writer to relate to an inability of this species to successfully establish at sites subjected to high levels of seasonal aridity and exposure to hot, dry, desiccating south-east trade winds that blow into these regions from across the interior of the continent. That *Sonneratia alba* occurs quite abundantly throughout the Kimberley region (Wells, 1981), an equally seasonally arid area, is considered to result from the protection afforded to this species by the steep cliffs that deflect most of the trade winds up and away from the extremely narrow bands of mangrove vegetation abutting these cliffs.

Sonneratia caseolaris is discontinuous throughout its geographic range, which extends from India through south-east Asia, northern Australia and New Guinea into the Pacific Ocean (Chapman, 1976, 1977, in particular). *Sonneratia caseolaris* (Section 2.3.24) only occurs across the northern coastline of the Northern Territory at a few sites that receive considerably higher and more evenly distributed rainfall than most other regions in the Northern Territory (Fig. 2.6.3, Appendix A1).

The distribution of *Sonneratia caseolaris* is considered to reflect its inability to occur at sites subjected to high levels of seasonal aridity together with its preference in colonizing sites that are frequently inundated by fresh/brackish waters for most of the year. Although, in answer to Steenis (1968), this species is present in the Northern Territory it does not occur at what are considered to be quite suitable habitats at other sites across the northern coastline of the Northern Territory and reasons for its non-occurrence in the Blyth/Cadell, Liverpool/Tomkinson and Glyde Rivers, in particular, are not known.

In the Alligator Rivers region it appears that the damage caused by the introduced water buffaloes (*Bubalus bubalis*) to the surrounding grassplains (Stocker, 1977) have now also altered fringing riverside vegetation to such an extent that the continued presence of *Sonneratia caseolaris* in this region is in doubt. Even now, only a few small trees of *Sonneratia caseolaris* remain on the East Alligator River and these are considered as the remnant of an association dominated by this species that undoubtedly fringed most of the upstream tidal portions of this river as little as seventy years ago. It is also considered that the tidal waterways in this region are probably now permanently altered through erosion through over-grazing and trampling of the surrounding grasslands and browsing upon the mangrove vegetation by buffaloes.

The non-occurrence of even occasional trees of *Heritiera littoralis* at any site in Western Australia or the Northern Territory is a complex problem. This species has a geographic range from 24°S on the east African coastline, occurs throughout most of south-east Asia and extends eastwards to Saipan in the Pacific Ocean (Chapman, 1976, 1977, in particular). In Australia, *Heritiera littoralis* has only been recorded from mangrove swamps in Queensland (Jones, 1971a;

Saenger *et al.*, 1977; Bunt, 1978; Messel *et al.*, 1980; Duke, 1981; Bunt *et al.*, 1982). That the species occurs at sites like Saipan, separated by considerable oceanic distances, illustrates as Fosberg, (1975) comments, that the floating fruit capsules may be widely dispersed and in this regard at least some establishment of this species at sites within the survey area might be expected to occur. The non-occurrence of *Heritiera littoralis* along the north coast of Melville Island and within Arnhem Bay, sites which are considered to provide suitable habitat and favourable climatic conditions for successful establishment, can not be explained by this writer. Such non-occurrence is even more perplexing when one compares absence of *Heritiera littoralis* from the northern coastline of the Northern Territory in a geographical sense with the species' latitudinal distributions to 24°S on the east African (Chapman, 1976, 1977) and 22°S latitude on the east Australian (Jones, 1971a) coastlines.

The present geographical range of *Nypa fruticans* extends from India throughout south-east Asia to northern Australia and to islands in the Pacific Ocean (Chapman, 1976, 1977). Lin (1980) now shows this species extending to Hainan Island near southern China. In Australia, it occurs at Port Musgrave on the west coast of Cape York (Messel *et al.*, 1980) and discontinuously from the Claudie River to the southern end of Hinchinbrook Channel (18°31'S) on the east Queensland coastline (Jones, 1971a, Bunt, 1978; Duke, 1981).

Nypa fruticans has only been recorded at one site in the Northern Territory - Maxwell Creek on Melville Island (Dunlop, pers. comm.). This isolated occurrence of *Nypa fruticans* on Melville Island poses a number of distributional problems which should be viewed from both quite recent historical (19th century) and old (Eocene period) records.

Churchill (1973) recognized *Nypa*-type pollen (as described by Muller (1964) and Erdtman (1969)) from the Kings Park shales of the Perth basin, W.A., and Hos (pers. comm.) now confirms its occurrence there. However Churchill (1973) erroneously referred these shales to the Eocene: more recent work of Quilty (1974) showed, on foram evidence, the formation to be largely Palacocene. It is also known from the palaeomagnetic studies of Irving (1967) and Weissel and Hayes (1972) that this portion of southern Australia was located at about 60°S latitude, as opposed to its present position of 33-35°S. The absence of large streams draining into the sea in this region during the last Palaeocene, in particular the noticeable absence of siltation, provided suitable conditions for establishment of close inshore coralline reefs. Evidence provided by Teichert (1967) on Eocene coralline reefs near Perth and the examination by Quilty of the fauna and lithology of this period show a consistency of warm water deposition of a coast of negligible drainage. Truswell and Harris (1982) concede that there is overwhelming evidence for high humidity, which *Nypa* requires, at all Eocene sites. However, the other environmental conditions provide no clues as to the occurrence of a suitable habitat for *Nypa* which grows in sites inundated with warm (20-30°C) brackish - i.e., estuarine - water in wet/humid tropical conditions.

It is only with a later suggestion by Quilty (1974) during the Late Palaeocene-Early Eocene (60-50 million years BP) of a significant Swan River flowed westwards from Walyunga (in the Perth region) into a deep embayment that evidence appears of a warm, muddy, brackish water habitat that would have been favoured by *Nypa*. The occurrence of *Nypa* in the Perth region is then considered not extensive during the

Late Palaeocene/Early Eocene due principally to a lack of many suitable sites for establishment.

It is now evident that during most of the Palaeocene, Australia and Antarctica were joined and lay in high southern latitudes. Sea surface temperatures were relatively high and as Truswell and Harris (1982) have shown, there is no evidence for Antarctic ice. During this period, *Nypa* probably occurred sporadically at suitable habitat sites along the fused west Australian/ Antarctic coastline.

During the Eocene, Australia and Antarctica were separated by a widening gulf (Weissel and Hayes, 1972), water temperatures were high (20°C) and it appears that *Nypa* spread eastwards with the intrusion of warm Indian Ocean waters into the numerous basins of southern and south-eastern Australia. Evidence for Antarctic ice development during this period is meagre. *Nypa*-type pollen has been recorded from Early Eocene deposits in the Gippsland Basin, Victoria, by Stover and Partridge, (1973); quoted by Truswell and Harris (1982) and from (most probably) similar geological assemblages of Eocene age in western Tasmania (Cookson and Eisenack, 1967).

Nypa disappears from the fossil record by the middle Eocene in the Gippsland Basin, although it persisted to the Late Eocene in the Perth region (Truswell and Harris, 1982; Hos, pers. comm.), suggesting that warmer water temperatures occurred for a slightly longer period in western, as opposed to eastern, Australia. *Nypa* has not been recorded from any Oligocene deposits in western, southern or south-eastern Australia and during this period there is considerable evidence for pronounced drops in air and water temperatures and an initiation of ice rafting near Antarctica (Truswell and Harris, 1982). For the Miocene, the marine record suggests the development of a major Antarctic icecap - a feature that, although subject to considerable fluctuations in areal extent, persists to the present day.

With the gradual retreat of warmer seas back towards present day tropics since the Oligocene, it is now known that *Nypa* has disappeared from what were most probably only sporadic occurrences along the western, southern and south-eastern coasts of Australia and its isolated presence today on Melville Island may represent a relict occurrence.

Alternatively, the presence of *Nypa fruticans* on Melville Island may be more recently related to the British occupation of Fort Dundas during the years 1824-29. Crosby (1975) and Letts (1977) have discussed the introduction of buffaloes to this settlement from Timor and other close by Indonesian islands. Whether *Nypa* fruits were included in ships' cargoes is not known. However, they may have been included to establish a plantation for roofing thatch (as is used throughout the Indonesian islands), to provide plants from which to produce Arrack (a potent liquor) from the sap, or just to provide a food source (the inner nut is edible - like coconut).

It is considered by this writer that the only way to establish whether the isolated occurrence of *Nypa fruticans* is an introduction to the area since 1825, or some other relatively recent geological period or whether it represents a relict occurrence emanating from this species' previous distribution down to Perth on the west Australian coastline will be by a detailed palynological investigation.

CHAPTER 3

Classification of tidal waterways in the survey area based upon seasonal variations in salinity signatures.

Seasonal variations of salinity in tidal waterways of the survey area.

Distribution of bankside vegetation and variations in high tide water salinities on selected tidal waterways.

3.1 INTRODUCTION

High and low tide water salinity profiles for tidal waterways in the survey area (Fig. 1.2.1) have been reported by Messel *et al.*, (1977), Burbidge and Messel (1979) and Messel *et al.*, (1979-1982) in a series of monographs concerning the distribution of saltwater crocodiles in northern Australia. Seasonal changes in vertical and horizontal stratification of water salinity are well known for many temperate tidal waterways (Carriker, 1951, 1959; Rochford, 1951; Day, 1964 and Bayly, 1975), among others, however, only limited information is available on tropical tidal waterways (Rodriguez, 1975; Nelson-Smith, 1977).

Superimposed on salinity gradients that often exist from mouths to heads of tidal waterways is a series of salinity oscillations of varying duration and amplitude. Among major factors determining these gradients, rates of intrusion of saline waters and fluctuations in salinity at any particular time in the survey area are:

1. Geomorphology and area of the drainage basin
2. Quantities of freshwater that enter tidal portions of of waterways from the catchment area
3. Physico-chemical conditions of the waterway
4. Climatic conditions - in particular the amount of precipitation falling on to a catchment area in any year and the rates of evaporation
5. Amplitudes and periodicity of daily and lunar tide cycles
6. Shape and depth of the tidal waterway and its estuary
7. Composition of the bottom substrate
8. Degree of stream meandering (affecting, in particular, rates of flow and evaporation)

9. Surrounding land gradients
10. Structure and height of vegetative cover fringing a waterway or occurring throughout intertidal land
11. Amount of intertidal land devoid of vegetative cover.

Various schemes have been proposed to classify portions of tidal waterways according to salinity. These schemes have been reviewed by Segerstrale (1959), Hawkes (1975) and Reid and Wood (1976). Emphasis has been placed on positive or 'true' estuarine areas in which freshwater flow exceeds evaporation (Pritchard, 1967); neutral estuarine areas in which neither evaporation nor freshwater inflow dominates (Carriker, 1961) and inverse estuarine areas in which evaporation exceeds freshwater inflow and waters become hypersaline (Day, 1964; Hedgpeth, 1967). Messel *et al*. (1979-1982) have also followed such criteria in classifying waterways.

Within the survey area, tidal waterways are arranged, according to seasonal variations in their salinity signatures, into five distinct types based on broad types of estuarine areas discussed by Carriker, (1961), Day, (1964) and Pritchard, (1967). Characteristics of each of these five types are consistent from year to year, although irregular large flushes of freshwater in climatic events such as cyclonic disturbances and resultant rain depressions over any particular catchment area, cause minor fluctuations in time and rate of repenetration of saline waters into a tidal waterway.

The importance of salinity variations for both animals and plants living within the tidal environment has been shown in the classic studies of Day, (1951), Macnae, (1966) and Carriker, (1967). These authors, among others, emphasize that distribution of any organism inhabiting an estuarine area cannot be attributed to any single factor of the environment but that a complex of periodically changing physico-chemical factors act to limit colonization to a number of organisms having either restricted or wide ranges of ecological adaptations.

3.2 METHODS

High and low tide salinity/temperature profiles were undertaken at 2.5 or 5 km intervals along 110 tidal waterways in the survey area. Measurements were made at the surface, midwater and bottom using Autolab (Model 602) salinity/temperature bridges. American Optics refractometers were used to measure surface salinity only during 1979.

High tide measurements, collected as being the water salinities that actually inundate the mangrove zones, are reported on this chapter. On many waterways, salinity profiles were measured at a number of different times in the year in order to ascertain seasonal and annual salinity fluctuations.

Distributions of plant species occurring as bankside vegetation and measures of abundance were collated from transects carried out at 2.5 km intervals along both banks of tidal waterways. Figs. 3.3.11-3.3.14, showing seasonal changes in high water salinity profiles upstream and annual/seasonal variation of high water salinities at specific 'stations', have been drawn from the original data collected by the Department of Environmental Physics, University of Sydney, in its Crocodile Research Programme. Figs. 3.3.25-3.3.27, showing the amplitude and periodicity of variations in salinity at selected 'stations' on certain well studied waterways, have been drawn using all available high tide water salinity readings and known times of the first rainfall at the start of the wet season on the catchment areas. Where data are lacking for a particular point, a rate of change of salinity has been calculated based on previous salinity profile changes in that river.

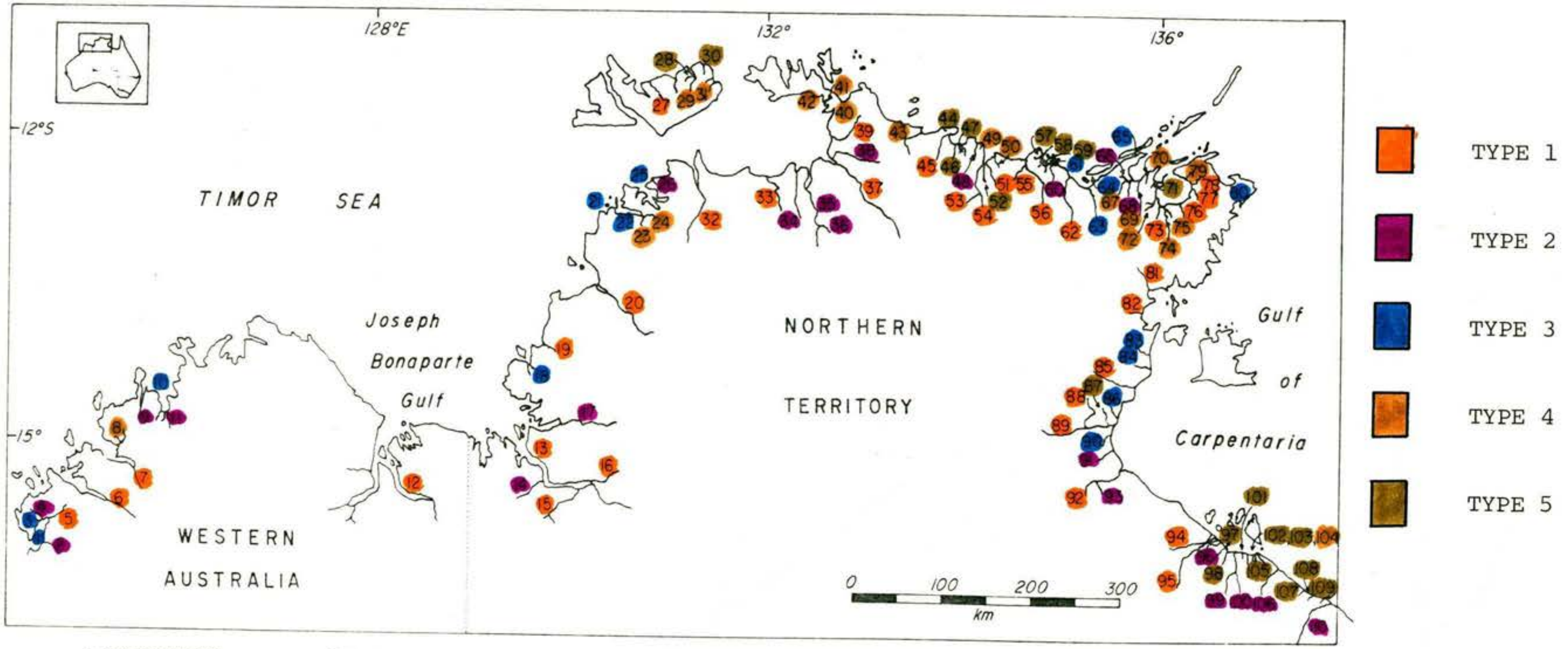
From an examination of all data available, tidal waterways in the survey area were then each classified into one of five types based upon their seasonal variations in water salinity, and an idealized diagram of seasonal variation in water salinity in each of the five types was drawn (Figs. 3.3.2-3.3.6).

Unless indicated otherwise, salinities shown in the figures in this chapter are for waters throughout the profile. In many instances no vertical stratification exists. All data on depths at which measurements were made are obtainable through perusal of records of the Crocodile Research Programme. Catchment areas of various river systems have been taken from Anonymous (1967) Drainage Basins and Divisions, and from calculations made using dot area grids on 1:100,000 topographic maps.

3.3 RESULTS AND DISCUSSION

Within each tidal waterway of the survey area there are daily cycles of tides, currents, salinity and water temperature. Other cycles such as rainfall, which have periods of much longer duration, also superimpose upon daily cycles. In respect of salinity, these waterways are extremely dynamic. During most 'wet' seasons, freshwater input from upstream catchment areas results in most, if not all, saline waters being flushed seawards. During following 'dry' seasons, when freshwater input into tidal portions of a waterway diminishes, saline waters again penetrate upstream.

Within the survey area, each tidal waterway is unique, although on the basis of their seasonal variations in salinity signatures, they can be grouped into five distinct types (Figs. 3.3.1-3.3.6). Waterways having considerable freshwater inflow from areas of upstream drainage (Fig. 3.3.2) and depicted as 'Type 1' in Fig. 3.3.1 are in many instances waterways possessing extensive catchment areas (c.f. Victoria



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102 'PLANCK' CK.
103 'ARCHIMEDES' CK.
104 'GALILEO' CK.
105 FAT FELLOWS CK.
106 ROBINSON R.
107 'EINSTEIN' CK.
108 'NEWTON' CK.
109 'PAULI' CK.
110 CALVERT R.

FIG. 3.3.1

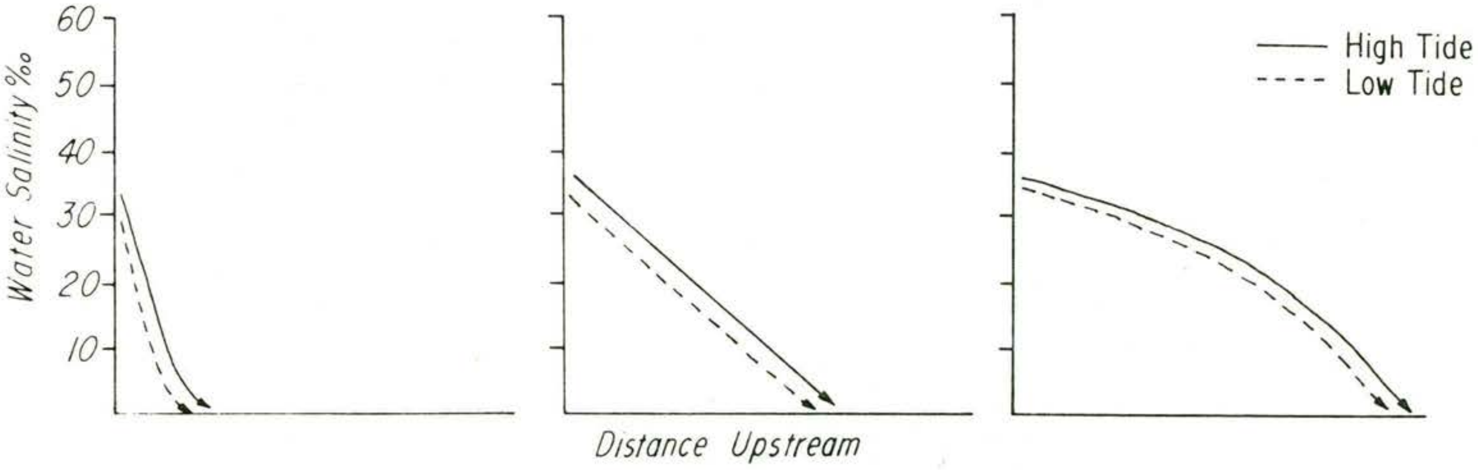
Tidal waterways in the survey area divided into five types depending on seasonal variations in salinity.

River (77,700 km^2); Daly River (51,800 km^2); Roper River (81,300 km^2)). Catchment areas of the Adelaide (7,600 km^2), Wildman (4,770 km^2), Liverpool/Tomkinson (8,300 km^2) and Goomadeer (5,700 km^2) Systems are representative of 'Type 1' waterways possessing medium-sized catchment areas whereas the drainage basins of Andranangoo Creek (367 km^2); Goromuru River (600 km^2) and Habgood River (550 km^2) are examples of 'Type 1' systems draining extremely small catchment areas.

Although in many cases 'Type 1' waterways possess extremely large catchment areas, it is seen that this is not a definitive factor and local geomorphology of a drainage basin, shape of an estuary and changes in land gradients coupled with local climatic conditions are considered among factors influencing river type as classified through salinity signatures.

'Type 1' waterways shown in Fig. 3.3.1 are distributed throughout the survey area and not only occur in regions that experience high annual rainfall (Figs. 1.3.3 and 1.3.4). Certain 'Type 1' systems such as the Ord, Victoria, Roper, Limmen Bight and McArthur Rivers occur in seasonally arid regions that only receive between 500 - 1,000 mm of rainfall per annum, whereas other 'Type 1' systems such as the Glenelg River in the Kimberleys, Andranangoo Creek on Melville Island and the Habgood, Goromuru, Cato and Peter John Rivers in Arnhem Bay receive between 1,500-1,750 mm of precipitation per annum.

'Type 2' waterways discussed in Fig. 3.3.3 and shown in Fig. 3.3.1 also occur throughout the survey area and show no grouping towards any particular climatic region. Intrusion of saline waters into such waterways is a gradual process during the 'dry' season but even though they remain of brackish salinity for a considerable proportion of the year, cessation of freshwater inflow into tidal portions of these waterways by the mid 'dry' season results in an increase in the rate of saline waters moving upstream.



WET SEASON
Nov - March

During this season all saline waters may be flushed from a waterway although saline wedges normally occur in mouth regions.

Rains may cause extensive flooding and freshwaters may occur seaward of river mouths.

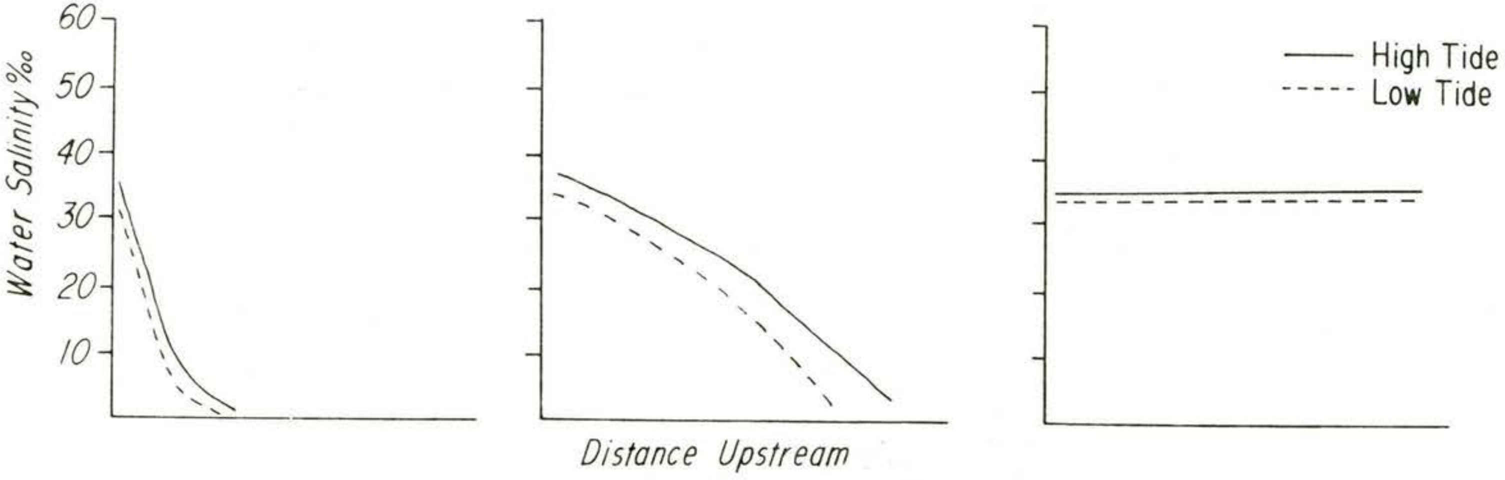
MID DRY SEASON
April - July

Saline waters again gradually move upstream as freshwater input into the tidal portions of a waterway decreases. Low tide salinity values always remain below high tide values at any particular point along a waterway.

PEAK DRY SEASON
August - Nov.

Only a negligible quantity of freshwater now enters the tidal portions of a waterway. However, the intrusion of saline waters upstream is slowed down by the often extensive bodies of freshwaters in upstream tidal reaches. As distance upstream increases, salinities decrease with high tide salinities always remaining above low tide readings.

FIG. 3.3.2 Seasonal water salinity variation in 'Type 1' tidal waterways in the survey area.



WET SEASON
Nov – March

During this season, saline waters are normally flushed from the waterway, although a saline wedge may exist in the mouth region.

MID DRY SEASON
April – July

With the onset of the dry season, saline waters penetrate further upstream although the considerable quantities of freshwaters still entering the tidal portions of the waterway from areas of upstream drainage will result in low tide salinities being always less than salinity measurements made at high tide at any point along a waterway.

PEAK DRY SEASON
August – Nov.

With the cessation of freshwater inflow, saline waters up to seawater salinity (35⁰/oo) penetrate up to limits of tidal influence.

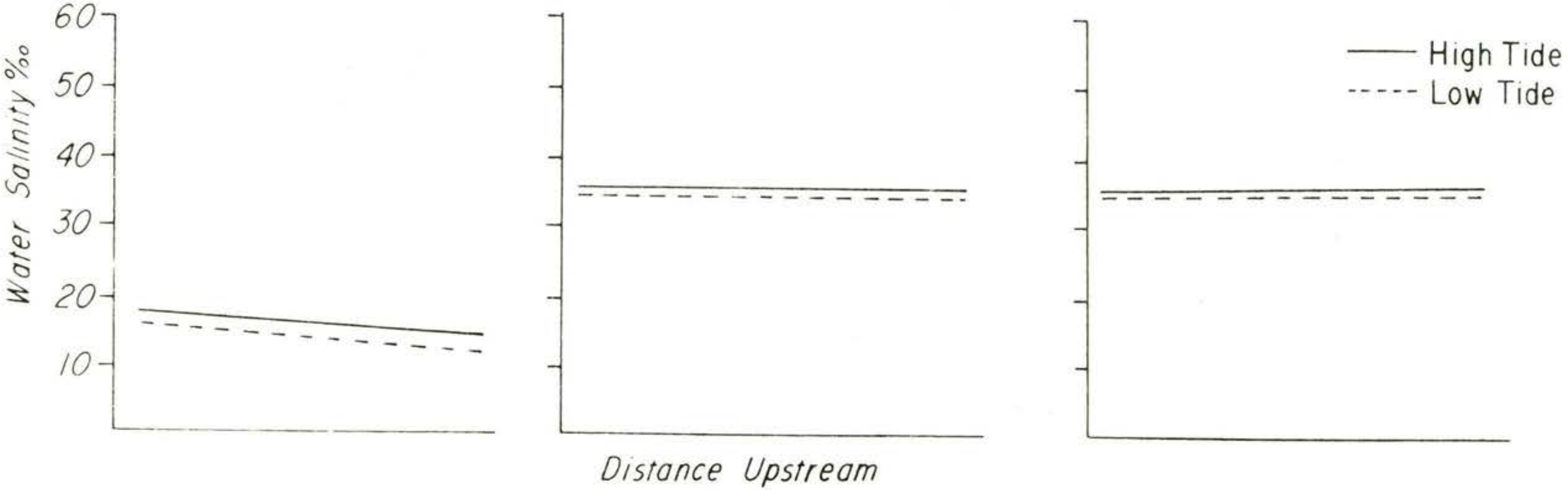
FIG. 3.3.3 Seasonal water salinity variation in 'Type 2' tidal waterways in the survey area.

By the peak of the dry season, seawater salinities ($35^{o}/oo$) usually occur throughout these waterways. Certain 'Type 2' waterways such as the South Alligator (11,700 km^2), Mitchell (3,193 km^2) and Calvert (10,600 km^2) Rivers drain quite extensive catchment areas, however the cessation of freshwater inflow into tidal reaches of these waterways during the mid 'dry' season results in their quite saline condition towards the end of the 'dry' season.

'Type 3' waterways (Fig. 3.3.4) comprise coastal embayments such as Port Warrender, Port Paterson, Darwin and Bynoe Harbours, coastal straits such as Hutchinson and Cadell Straits and short coastal creeks which possess extremely small drainage basins such as Muntak, Yiwapa and Nayarnpi Creeks. They occur throughout the survey area (Fig. 3.3.1) and remain under near continual influence of waters of seawater salinity for most of the year.

'Type 4' waterways (Fig. 3.3.5) are short coastal inlets draining relatively small catchment areas. They also occur throughout the survey area (Fig. 3.3.1). Cessation of freshwater inflow into tidal portions of these waterways occurs relatively soon after commencement of the 'dry' season and this results in a fairly rapid intrusion of saline waters to the limits of tidal influence by the mid 'dry' season. Towards the peak of the 'dry' season flushing of high tide waters, that have inundated surrounding intertidal lands, brings back extra salts into the waterways. Although mixing of these hypersaline waters with seawater is quite evident, by the peak of the 'dry' season, salinities throughout 'Type 4' waterways are still only slightly above seawater salinity. This condition is maintained by continual seawater intrusion and reasonable flushing characteristics of these waterways.

'Type 5' waterways (Fig. 3.3.6) also possess extremely small catchment areas and receive no freshwater input from areas of upstream drainage after commencement of the 'dry' season. Intrusion of saline waters to the limits of tidal influence is then quite rapid. 'Type 5'



WET SEASON
Nov – March

Salinities normally below seawater.

Salinity wedges may oscillate up and down estuaries depending on tidal flows.

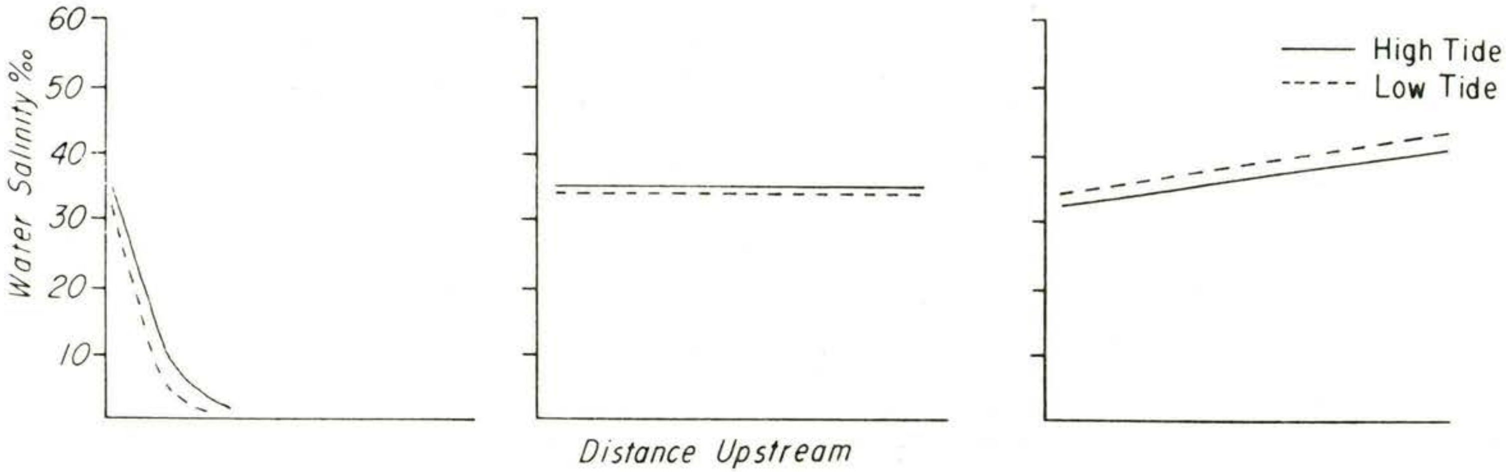
MID DRY SEASON
April – July

Tidal waterways now experiencing seawater salinities.

PEAK DRY SEASON
August – Nov.

Tidal waterways continuing to remain at seawater salinities (≐ 35‰). High tide salinity readings slightly above low tide readings.

[illegible] Seasonal water salinity variation in 'Type 3' tidal waterways in the survey area.



WET SEASON
Nov - March

MID DRY SEASON
April - July

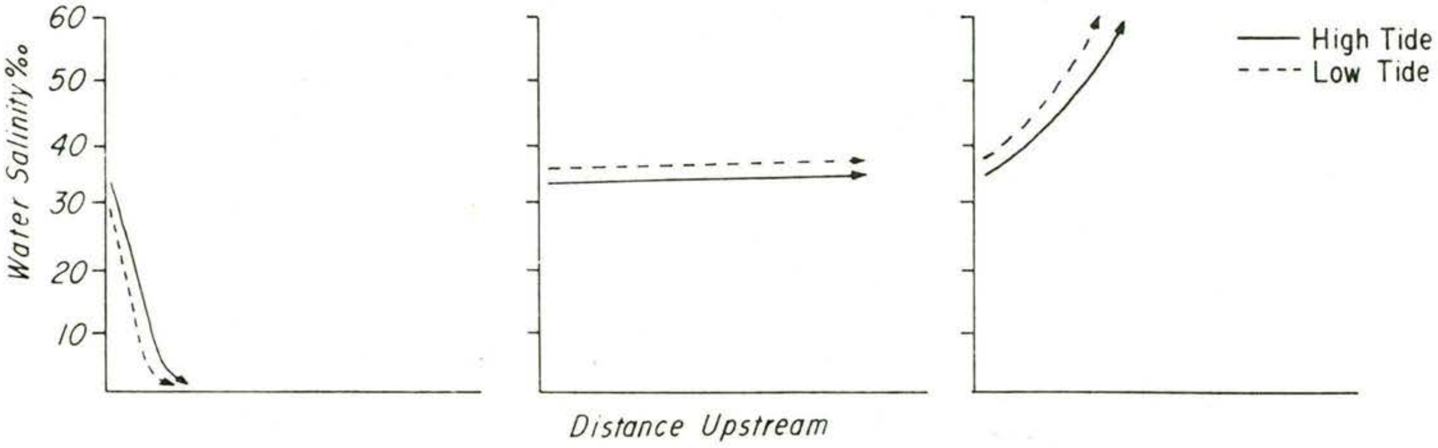
PEAK DRY SEASON
August - Nov.

During this season saline waters are flushed out of the system, although a saline wedge may exist in the mouth of a tidal inlet.

With the onset of the 'dry' season, saline waters penetrate further upstream to the limits of tidal influence but never exceed seawater salinity. This intrusion of saline waters accelerates with cessation of freshwater inflow into the tidal portions of the waterways.

During this period successive high tide inundation of the surrounding intertidal lands results in previously crystallized salts being flushed back into a waterway. Although the influx of seawaters is continually mixing with these slightly hypersaline waters, by the peak of the 'dry' season water salinity is normally between 38 - 42‰.

FIG. 3.3.5 Seasonal water salinity variation in 'Type 4' tidal waterways in the survey area.



WET SEASON
Nov-March

During the wet season most, if not all, saline waters are flushed from the waterways by freshwaters entering from the small catchment areas.

MID DRY SEASON
April-July

Due to the limited catchment area, freshwater inflow into the tidal portions of these waterways ceases with the end of the wet season.

Saline waters intrude upstream to the limits of tidal influence. Due to previously crystallized salts being flushed back into a waterway from surrounding bare intertidal lands, low tide salinity profiles remain above high tide values.

PEAK DRY SEASON
August-Nov.

As distance upstream increases, salinities increase often to values exceeding 70 - 80°/oo (- twice that of seawater).

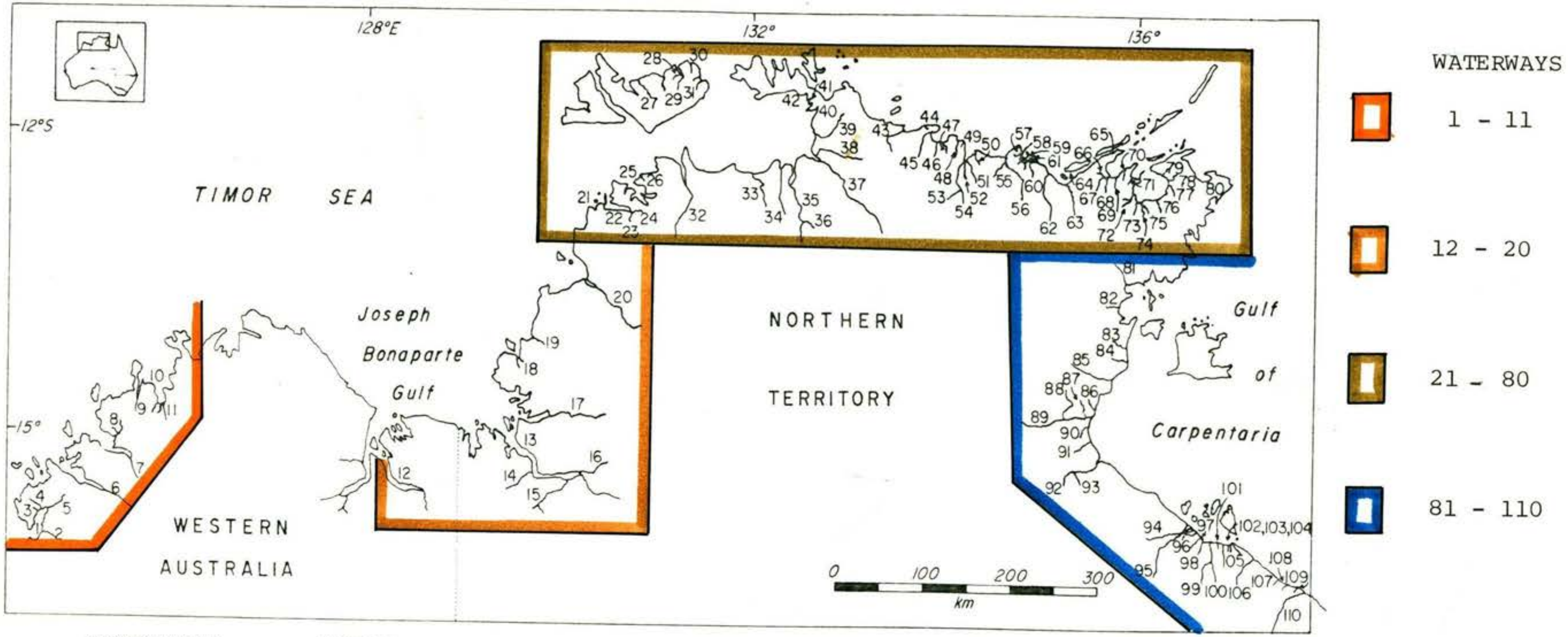
Low tide salinity profiles are always more saline than high tide profiles due to salt-laden waters draining back into the waterways during low tide.

FIG. 3.3.6 Seasonal water salinity variation in 'Type 5' tidal waterways in the survey area.

waterways are shown in Fig. 3.3.1 and 50% of these waterways occur on seasonally arid portions of the coastline (Figs. 1.3.4 and 1.3.5) in the survey area - in particular along the southern portion of the Gulf of Carpentaria. Other hypersaline waterways are scattered along the northern coast of Arnhem Land (Fig. 3.3.1).

In these waterways, often having little fringing vegetative cover, high tides inundate surrounding tidal flats and salts are deposited on these flats through evaporation. As the 'dry' season progresses further high tides repeat this salt-depositing process but at the same time flush increasingly saline waters back into the waterways. As these waters flush from the intertidal areas during low tide periods, very little of these hypersaline waters ever flush from the waterway into the open sea during the dry season as by the time they reach the mouth the next high tide pushes these highly saline waters back upstream with relatively little mixing. Many 'Type 5' waterways such as Arrla and Mungardobolo Creeks attain salinities up to 70°/oo by the peak of the 'dry' season whereas waterways entering into the southern portion of the Gulf of Carpentaria - in extremely arid areas - must attain salinities considerably in excess of 100°/oo . This is shown by waterways such as 'Bohr' Creek having salinities of 52°/oo in May, just after commencement of the 'dry' season (Messel *et al.*, 1980).

Examination of floristic diversity of mangrove species from a regional perspective (Figs. 3.3.7 and 3.3.8) shows that throughout the five types of tidal waterways identified in this survey area certain trends are evident. From Fig. 3.3.8 sites occurring across the northern coastline of the Northern Territory in all types of waterways record negligible differences in numbers of species recorded. For sites within the Gulf of Carpentaria however, it is seen that 'Type 1' waterways are, in most instances, more floristically diverse than 'Types 2, 3, 4 or 5', whereas in the Kimberley and Joseph Bonaparte Gulf regions, there is



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109 'PAULI' CK.
110 CALVERT R.

FIG. 3.3.7

Tidal waterways in different regions of the survey area described in Fig. 3.3.8.

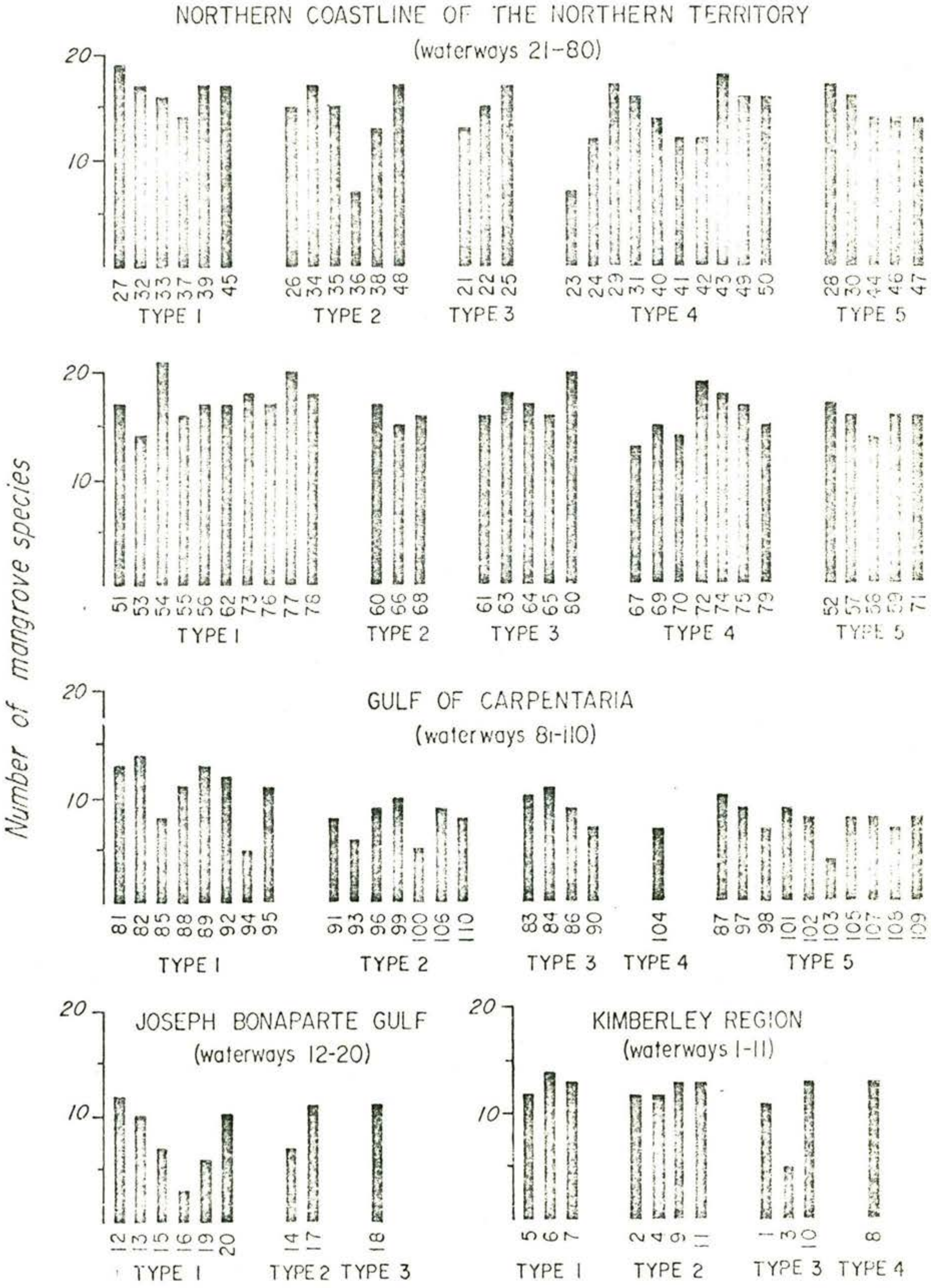


FIG. 3.3.8

Number of mangrove species recorded in the five types of tidal waterways recognised in different regions of the survey area.

no discernible variation. Overall, it is shown in all types of tidal waterways across the northern coastline of the Northern Territory that they are considerably more diverse in mangrove species than equivalent types of tidal waterways occurring throughout the Kimberley region of Western Australia and the two Gulf regions (Joseph Bonaparte and Carpentaria).

Information on distribution of species establishing as bankside vegetation and seasonal variations in high tide water salinities on selected tidal waterways is provided in Figs. 3.3.9-3.3.20. Universal to all waterways are gradients in species distributions which appear to relate to the percentage time of year that a species at any site is influenced by waters of varying salinity. In many waterways peak dry season high tide water salinities vary slowly over considerable upstream distances (e.g., Roper, Adelaide, Liverpool, Blyth Rivers) resulting in a smooth convex curve and distributional limits of particular species are laterally extended due to a greater range of suitable edaphic habitat. Conversely a tidal waterway where saline intrusion does not extend for any great distance upstream results in lateral compression of a species distribution.

In Figs. 3.3.9-3.3.20 many strand species that are not generally regarded as 'mangroves' establish at sites mostly inundated by freshwaters with some species (viz. *Pandanus aquaticus*, *Barringtonia acutangula*, *Melaleuca dealbata*) preferring nearly perennially freshwater inundation.

In water movement at certain periods of a year, and disregarding the reciprocating movement of the tides, a net circulation is set up along tidal waterways in which movement of freshwaters seawards (at the surface) is to some extent balanced by intrusion of saline waters upstream (along the bottom). Such patterns are shown in Figs. 3.3.9-3.3.20. These saline intrusions are often termed 'salt wedges' and within waterways of the survey area are most sharply delineated in the mouth regions of inlets during and immediately following the 'wet' season (e.g., Fig. 3.3.9 - Liverpool River). In several waterways, saline waters never penetrate upstream to the limit of tidal influence and included in this category are the Daly and Roper Rivers (Fig. 3.3.18 and 3.3.19 respectively), where saline waters do not occur upstream of km40 and km100, even though tidal penetration occurs to at least km90, respectively, on these rivers.

On most waterways, considerable partial mixing of waters of different salinities occurs during the 'dry' season up to the limits of tidal influence. By the mid 'dry' season stratified vertical and horizontal salinity profiles occur at both high and low tides, but the degree of stratification lessens as the peak (final phase) of the 'dry' season approaches. In many instances, vertical salinity stratification disappears by the peak of the 'dry' season and well mixed waters of equal salinity occur throughout a profile at any particular point along a waterway. Changes in vertical and horizontal saline stratification is shown in many of the seasonal high tide profiles for various tidal waterways in Figs. 3.3.9 - 3.3.20.

Some writers (e.g., Nelson-Smith, 1977) state that vertical salinity stratification cannot occur in tidal waterways experiencing large tidal ranges with either narrow or wide channels. This conclusion is not supported by recent studies in the Kimberely region of Western Australia - an area experiencing semi-diurnal tides with amplitudes of 8-11 metres, where it is shown by Messel *et al.* (1977) and Burbidge and Messel (1979) that considerable vertical stratification of salinity exists at any point along many tidal waterways at either high or low tide. Here, in the Glenelg, Prince Regent and Roe Rivers, waterways having extremely turbulent tidal flows, different densities of fresh, brackish and sea waters results in bodies of water of varying salinities remaining in a stratified sequence down a profile at any point along the waterways. In fact, it appears that these bodies of water just oscillate up and down a waterway depending on the state of the tide. Towards the peak of the 'dry' season, when freshwater input into tidal portions of these waterways ceases, a greater degree of mixing occurs and vertical salinity stratification gradually disappears, and here the rate of mixing of waters of different salinities during the dry season almost certainly affects rates of intrusion of saline waters upstream.

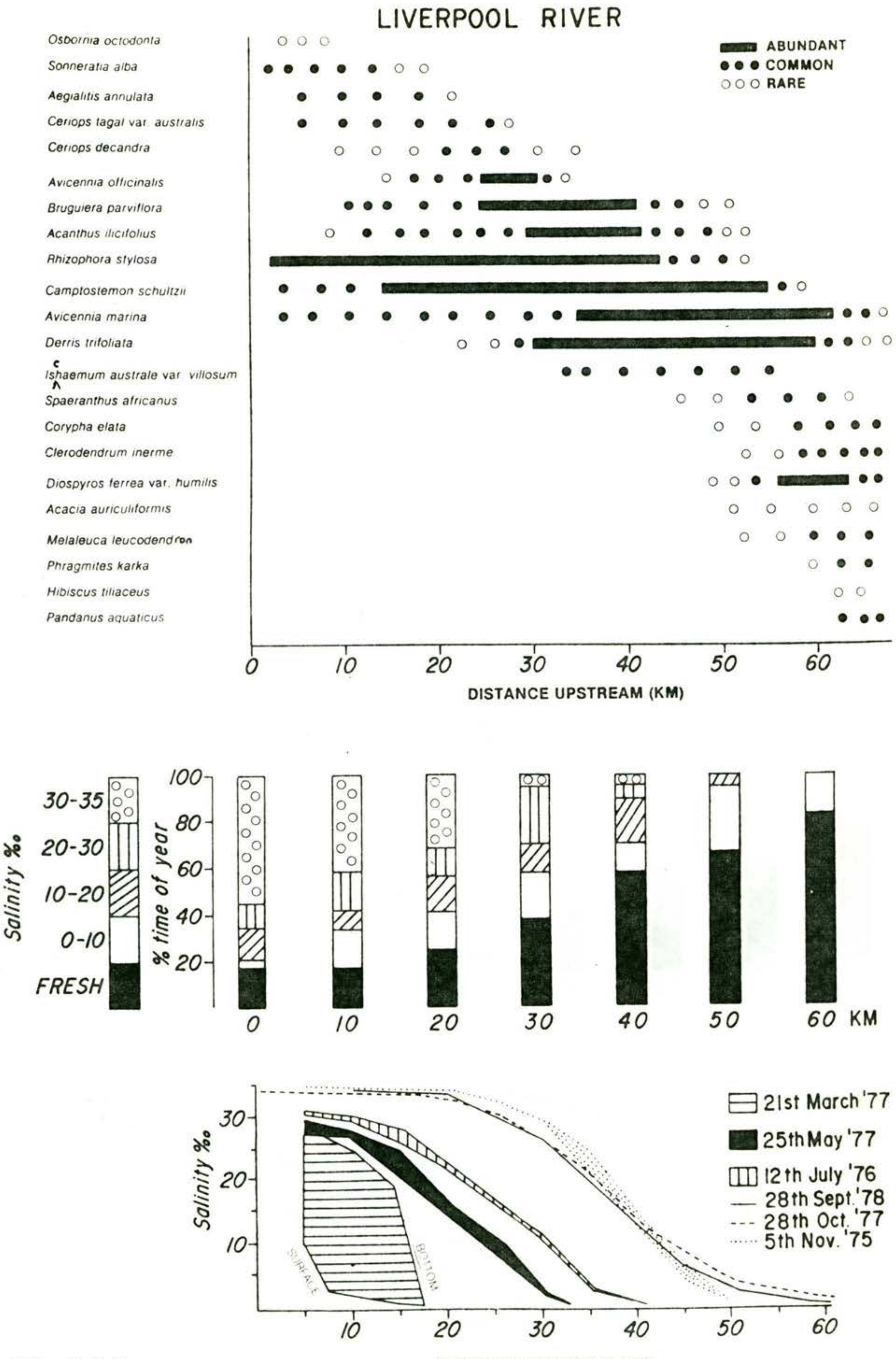


FIG. 3.3.9

Seasonal variations in high tide water salinities and the percentage time of year that such changes would affect plant species establishing as bankside vegetation along the Liverpool River, N.T. (Type 1 waterway).

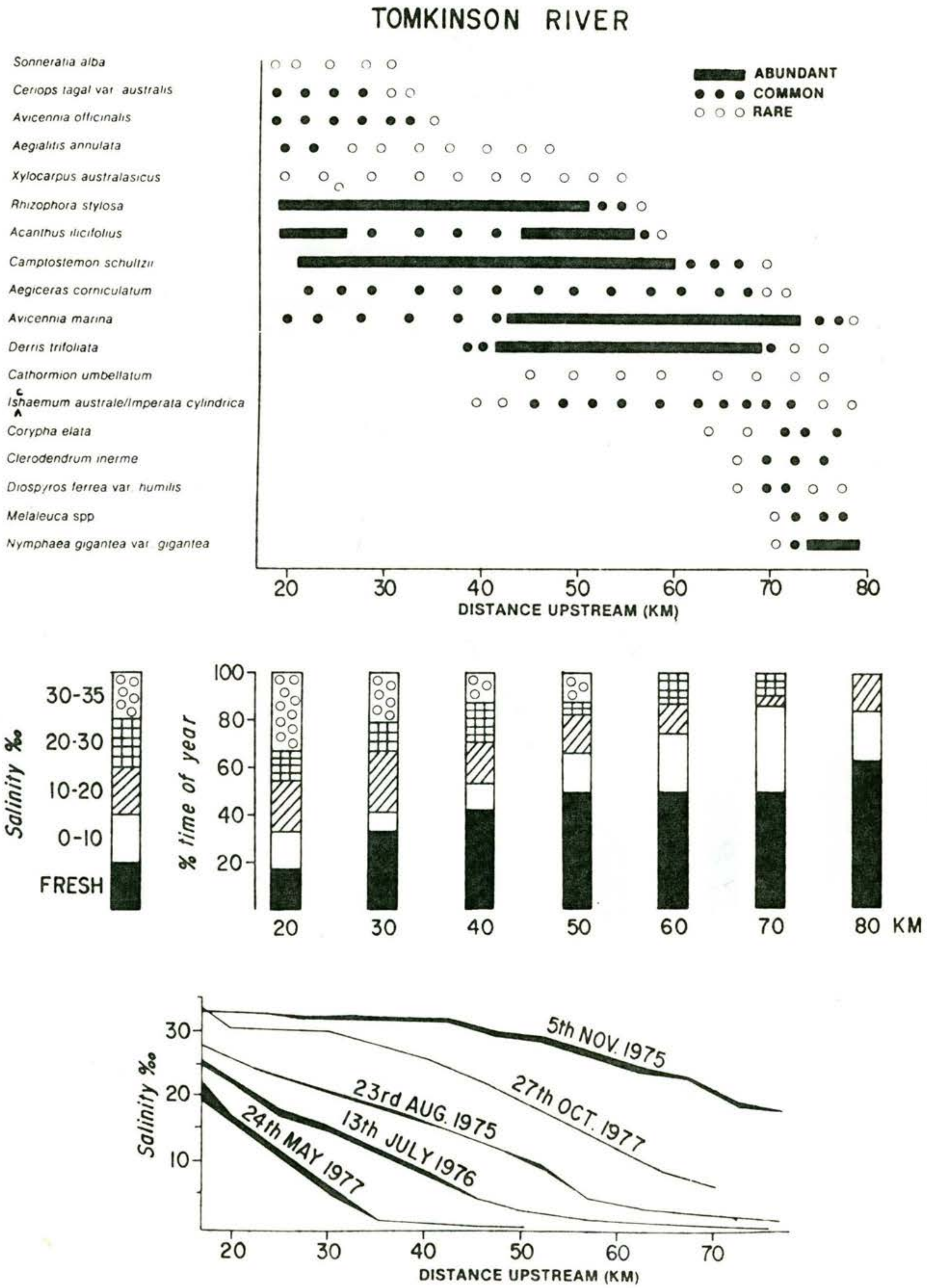


FIG. 3.3.10

Seasonal variations in high tide water salinities and the percentage time of year that such changes would affect plant species establishing as bankside vegetation along the Tomkinson River, N.T. (Type 1 waterway).

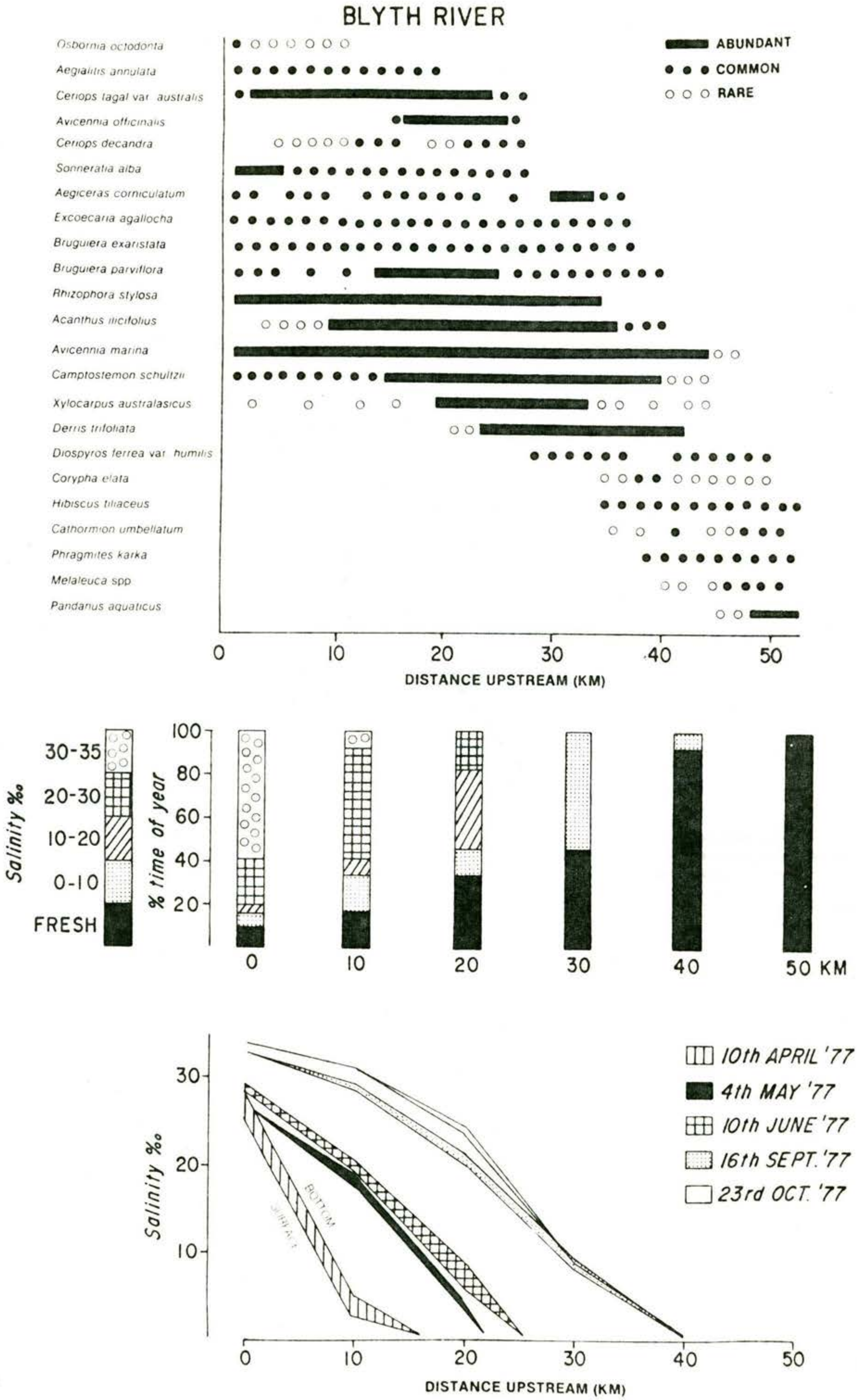


FIG. 3.3.11

Seasonal variations in high tide water salinities and the percentage time of year that such changes would affect plant species

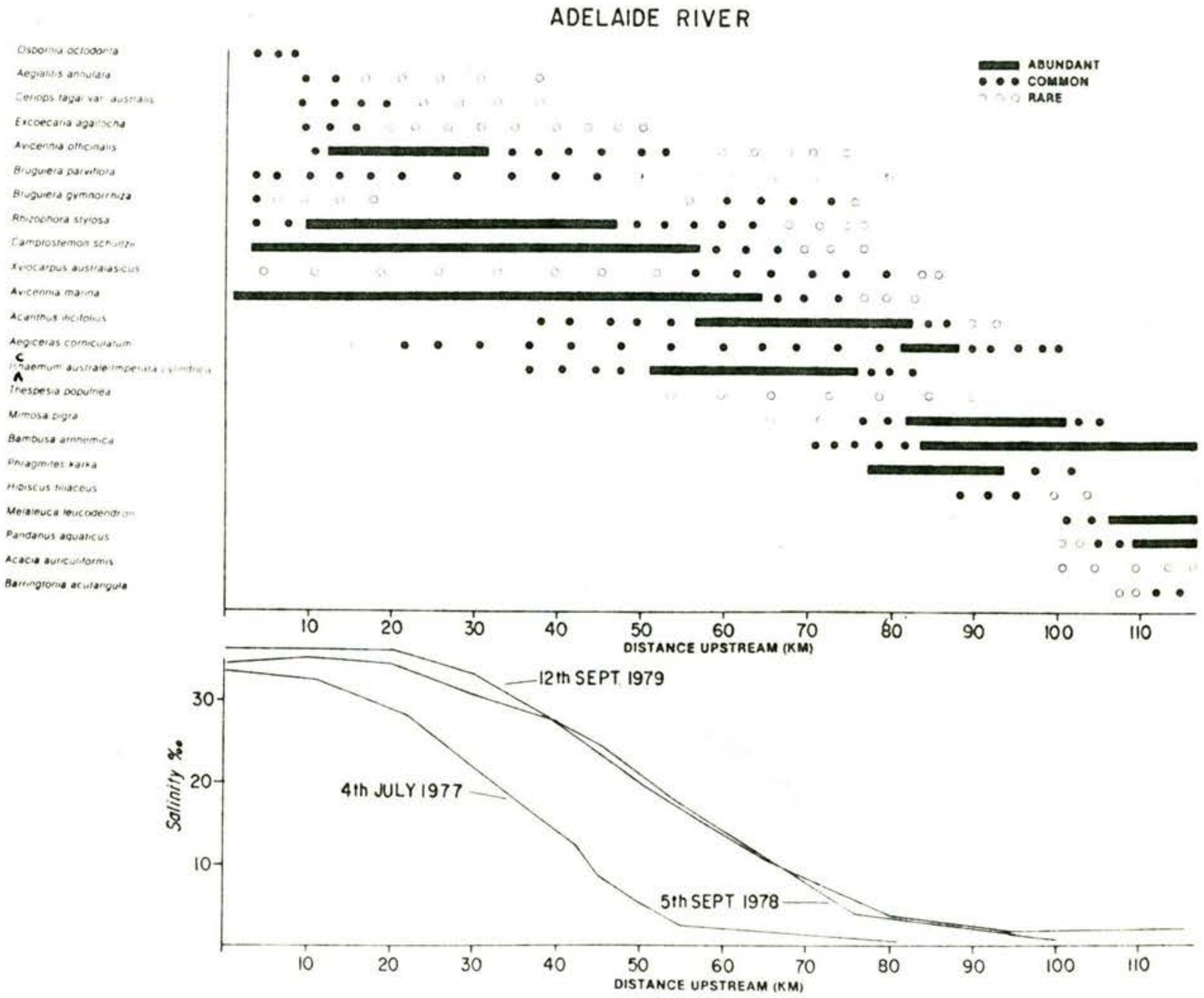


FIG. 3.3.12

Variations in high tide water salinities and distribution of bankside vegetation along the Adelaide River, N.T. (Type 1 waterway).

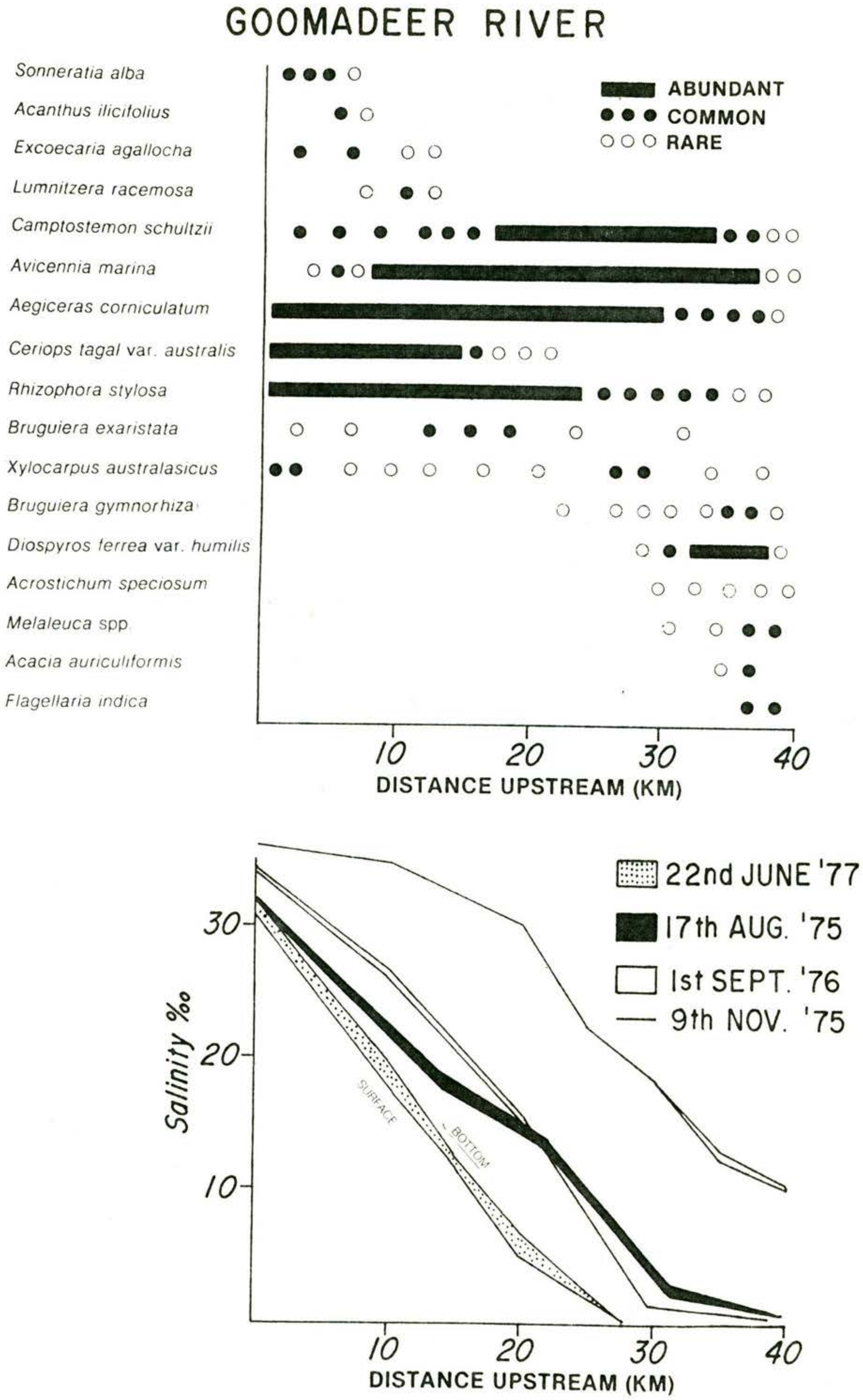


FIG. 3.3.13

Variations in high tide water salinities and distribution of bankside vegetation along the Goomadeer River, N.T. (Type 1 waterway).

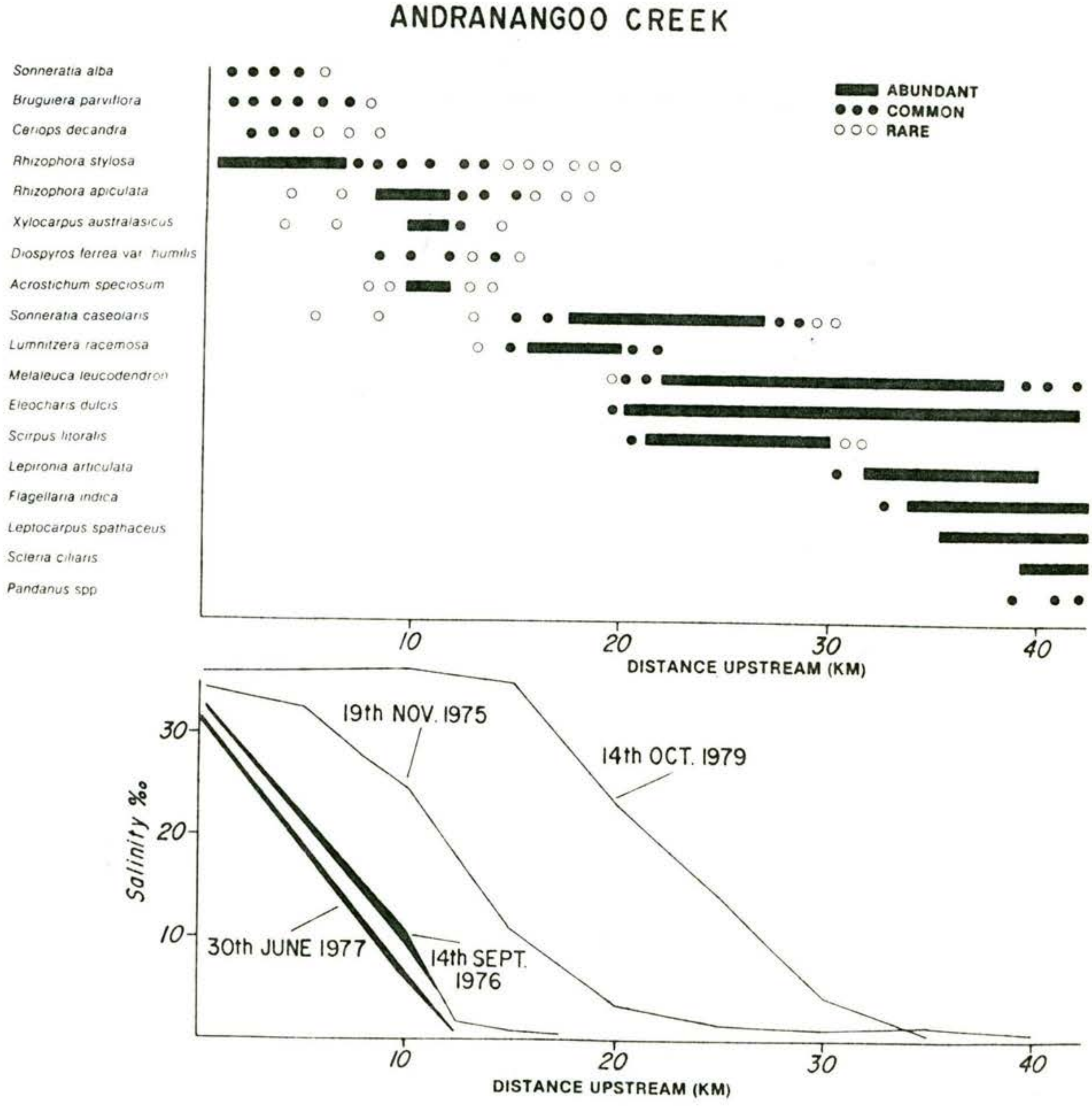


FIG. 3.3.14

Distribution of bankside vegetation and variations in high tide water salinities on Andranangoo Creek, N.T. (Type 1 waterway).

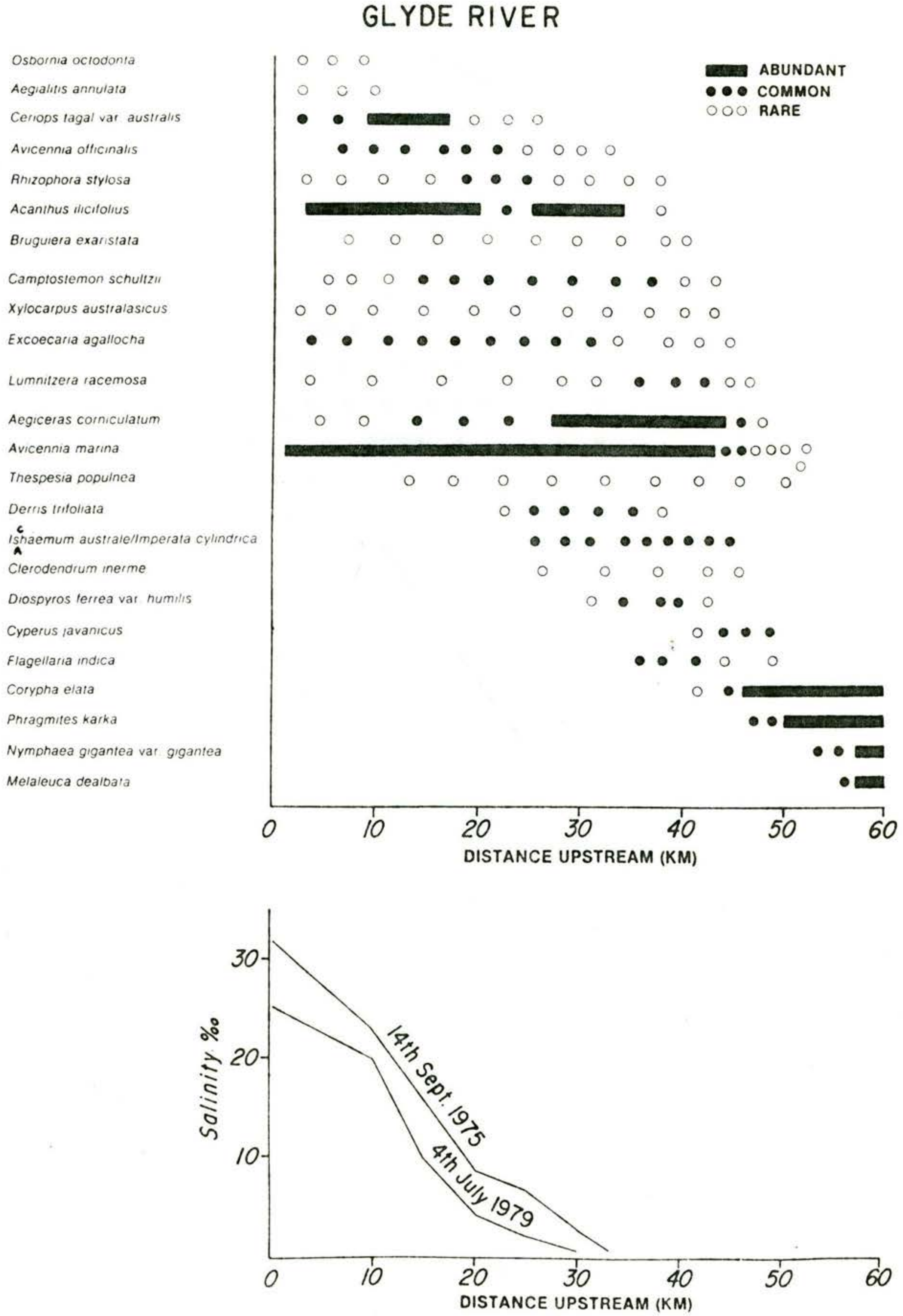


FIG. 3.3.15

Distribution of bankside vegetation and variations in high tide water salinities on the Glyde River, N.T. (Type 1 waterway).

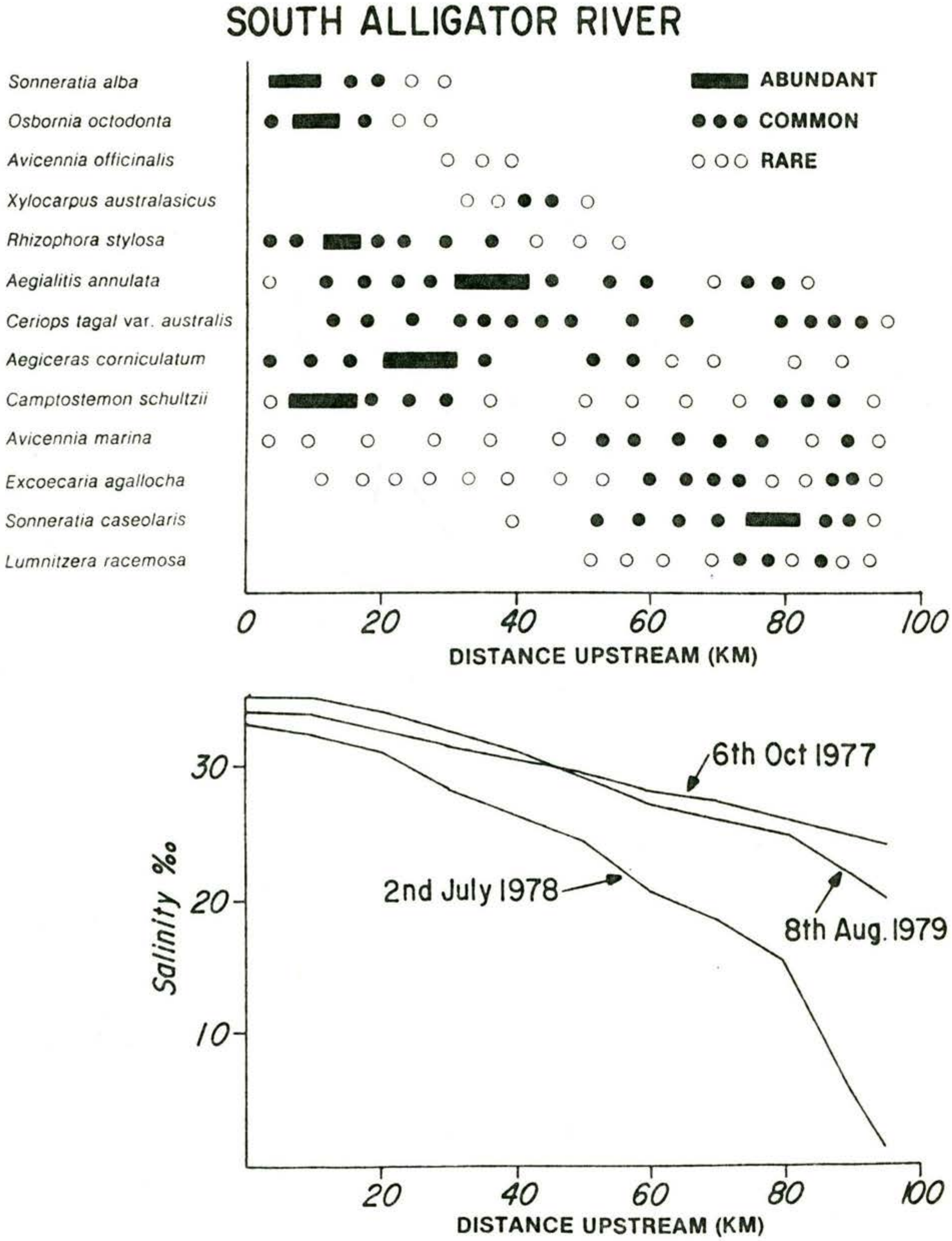


FIG. 3.3.16

Distribution of bankside vegetation and variations in high tide water salinities on the South Alligator River, N.T. (Type 2 waterway).

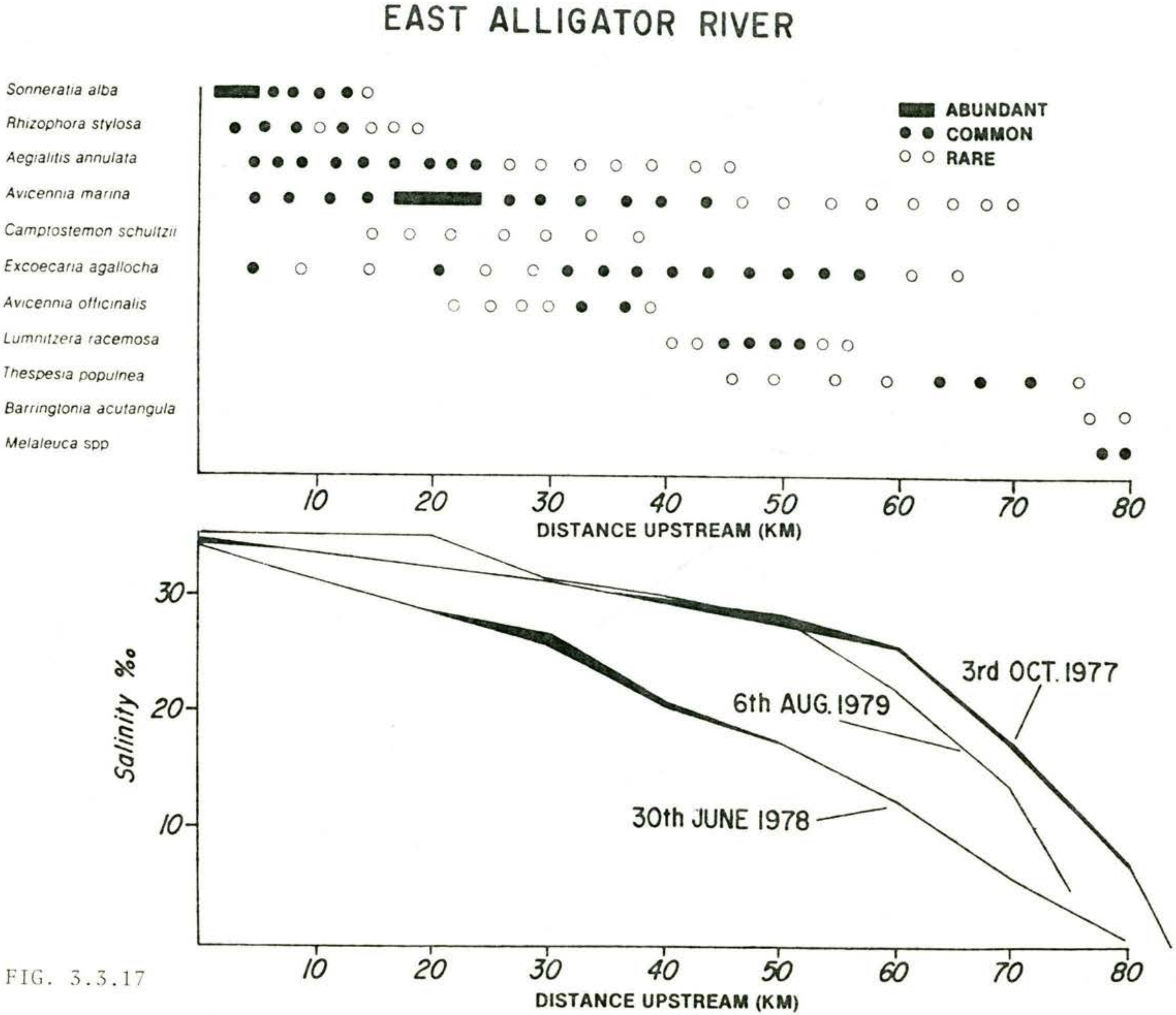


FIG. 3.3.17

Distribution of bankside vegetation and variations in high tide water salinities on the East Alligator River, N.T. (Type 1 waterway).

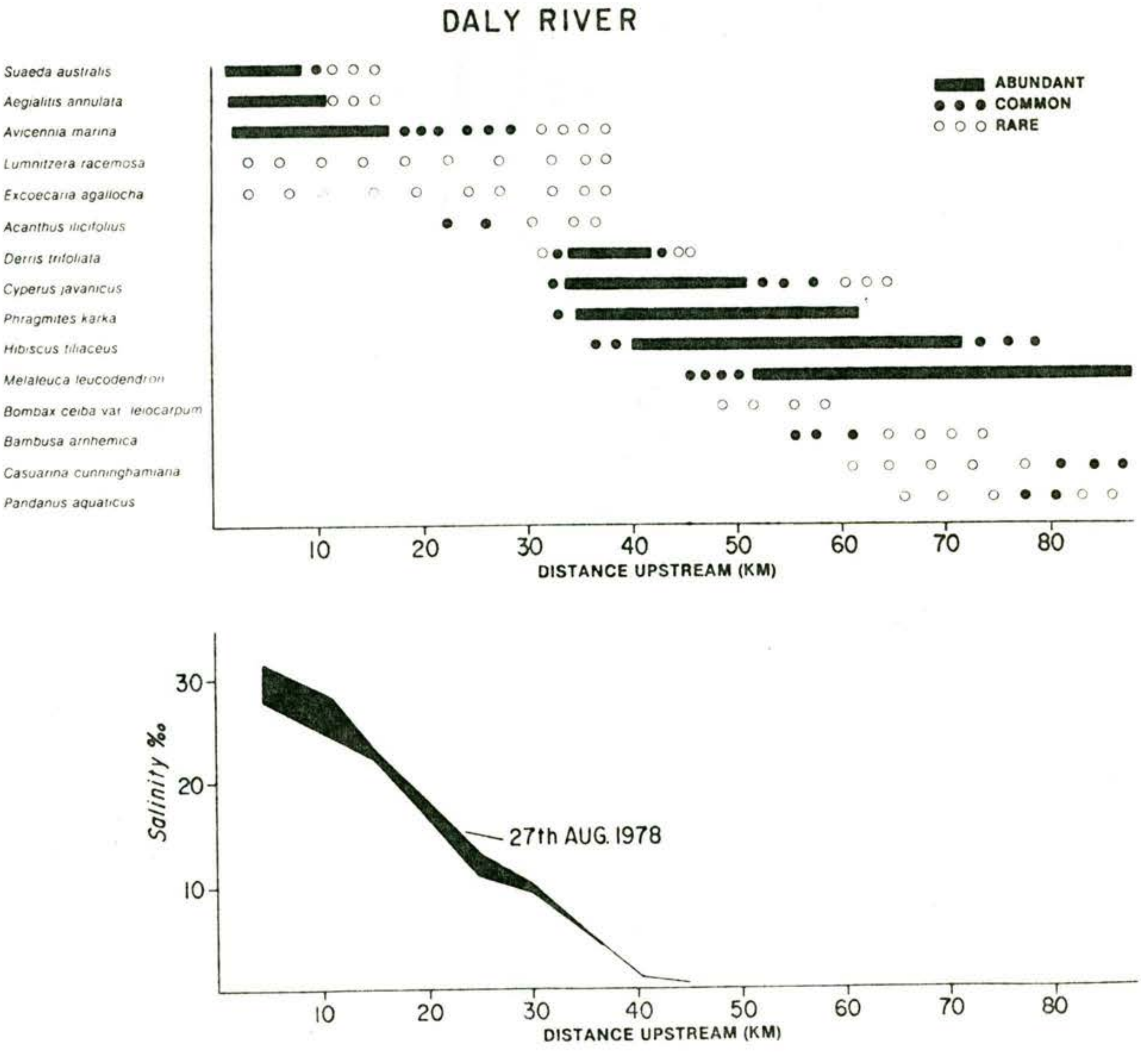


FIG. 3.3.18

Distribution of bankside vegetation and high tide water salinity on the Daly River, N.T. (Type 1 waterway).

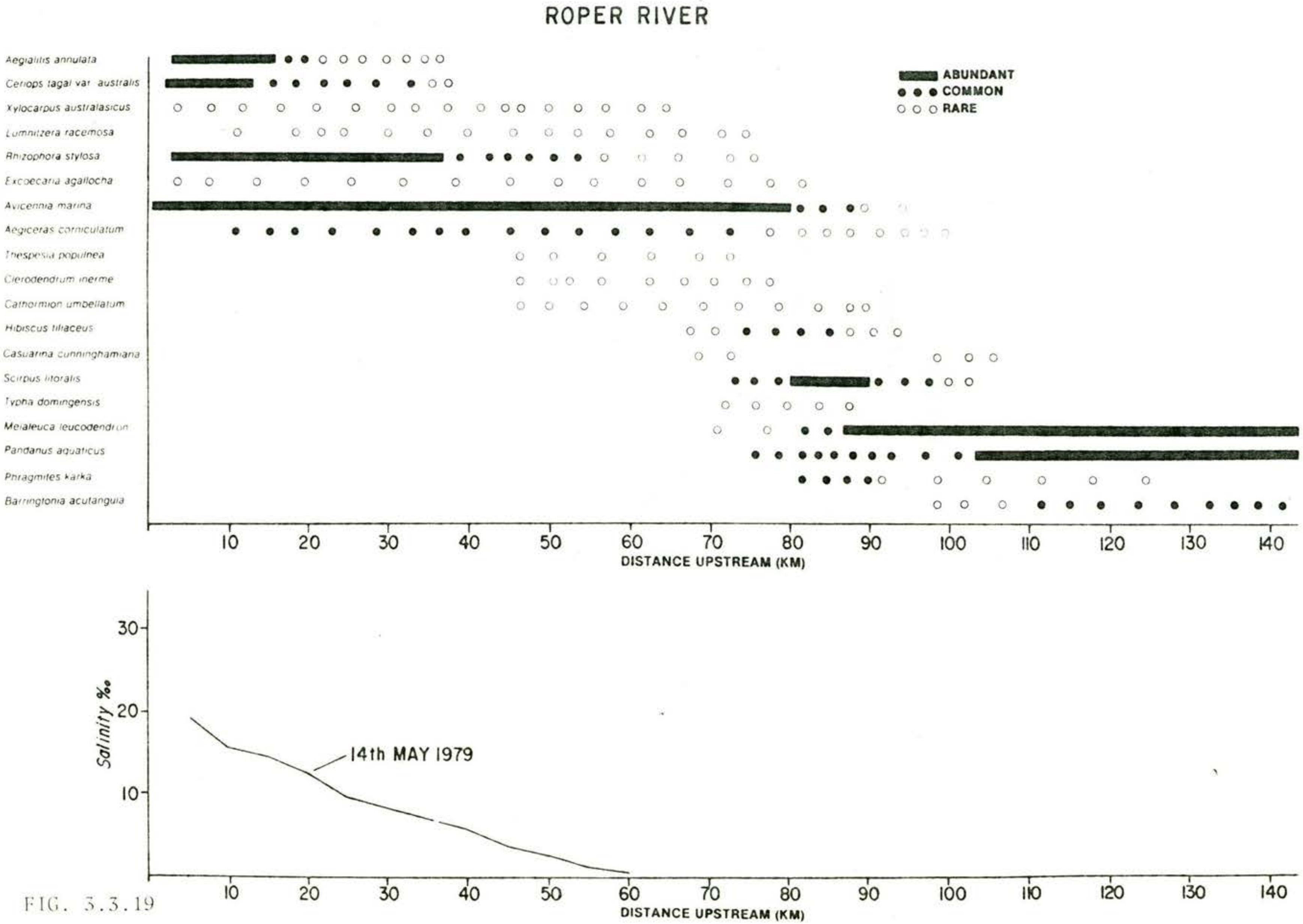


FIG. 3.3.19

Distribution of bankside vegetation and high tide water salinity on the Roper River, N.T. (Type 1 waterway).

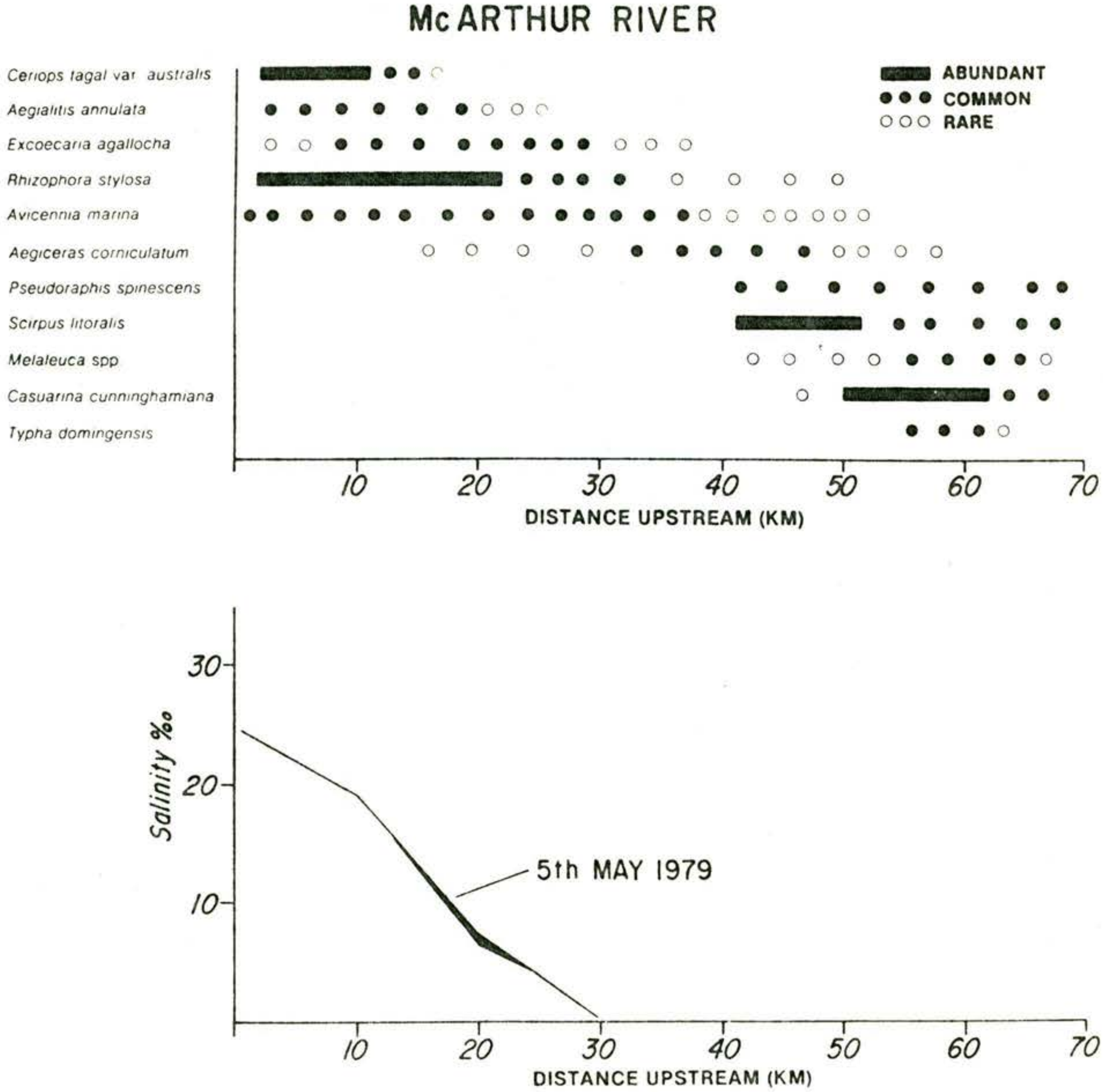


FIG. 3.3.20

Distribution of bankside vegetation and high tide water salinity on the McArthur River, N.T. (Type 1 waterway).

Annual and seasonal variations in high tide water salinity measurements during the period 1975-1979 are shown in Figs. 3.3.21, 22, 23 and 24 for the Blyth, Liverpool and Tomkinson Rivers and Mungardobolo Creek respectively. These figures exemplify the range of salinities experienced in the five types of waterways previously described. It is seen that for any month, the variation of salinity between the years of measurement do not, in most instances, exceed 6‰. In exceptionally dry years (1979), especially in Figs. 3.3.21 and 3.3.22, salinity measurements shown vary considerably from salinities experienced at any particular site in a 'normal' year.

For the Liverpool River it can be seen (at stations km20, 30, 40, 50 and 60) that the 1975 salinity value for October is considerably depressed. This depression of salinity was caused by rains from 'early' wet season storms falling upon the catchment area. The sudden influx of freshwaters into the upstream tidal portions of the Liverpool River flushed all saline waters downstream, and resulted in freshwater being recorded at km40 and sites at km20 and km30 and reduced salinities below those that would normally be expected at that time of year.

Variations in amplitude and periodicity of high tide water salinity along the Liverpool/Tomkinson River System and Mungardobolo Creek over the period 1976-1979 are shown in Figs. 3.3.25-3.3.27.

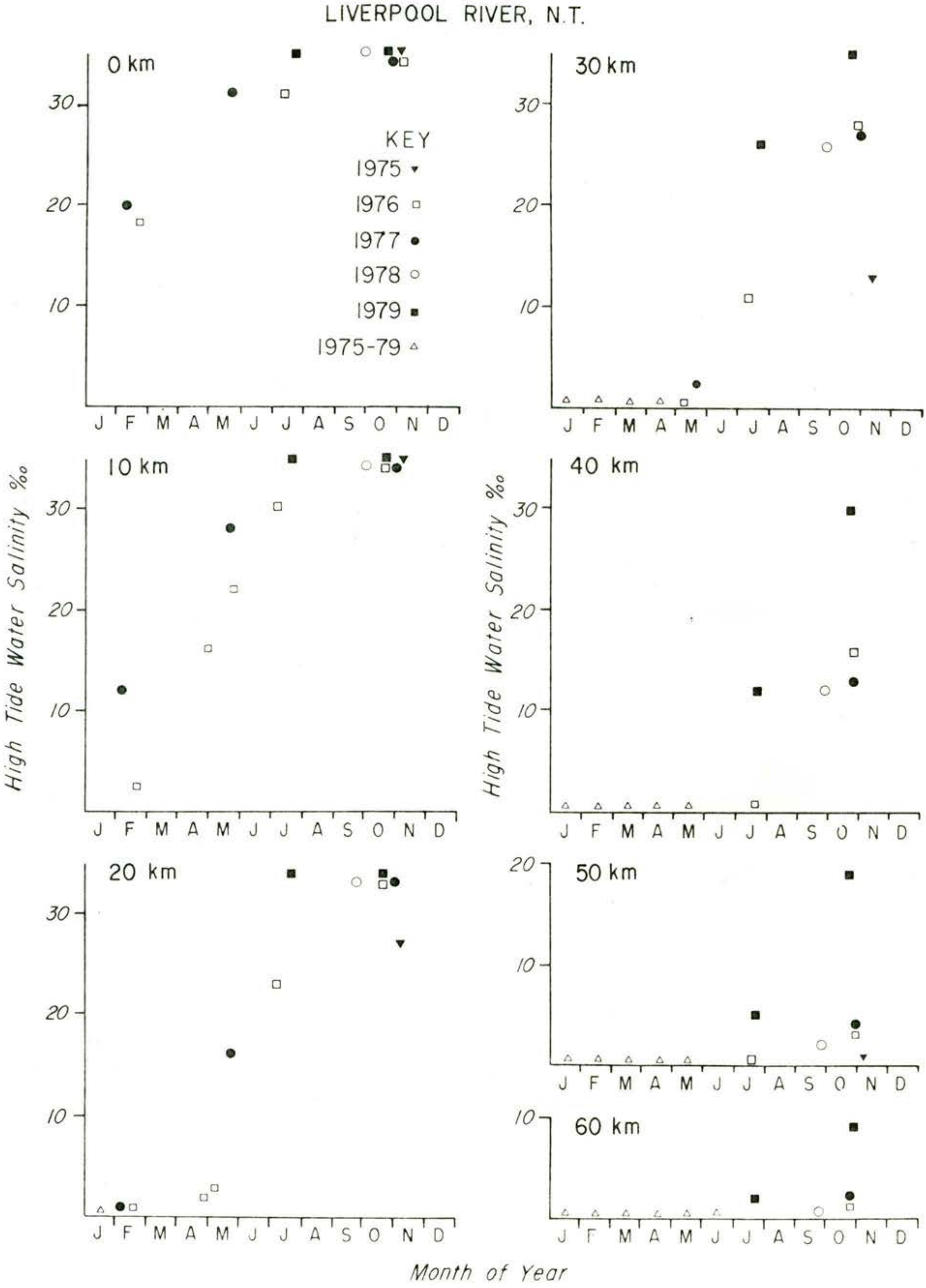


FIG. 3.3.21

Variations in high tide water salinities at stations on the Liverpool River, N.T. during the period 1975-1979. (Type 1 waterway).

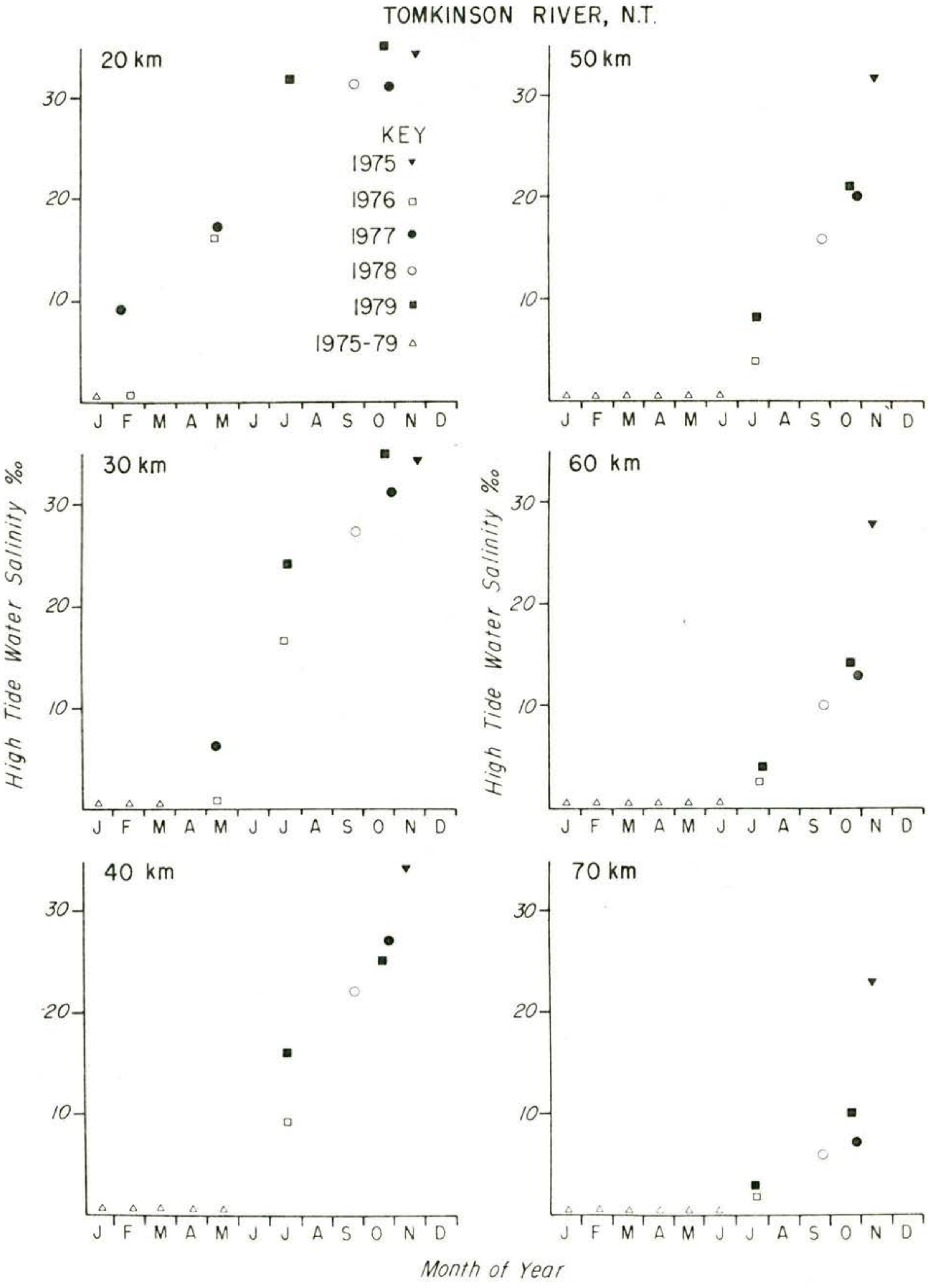


FIG. 3.3.22

Variations in high tide water salinities at stations on the Tomkinson River, N.T. during the period 1975-1979. (Type 1 waterway).

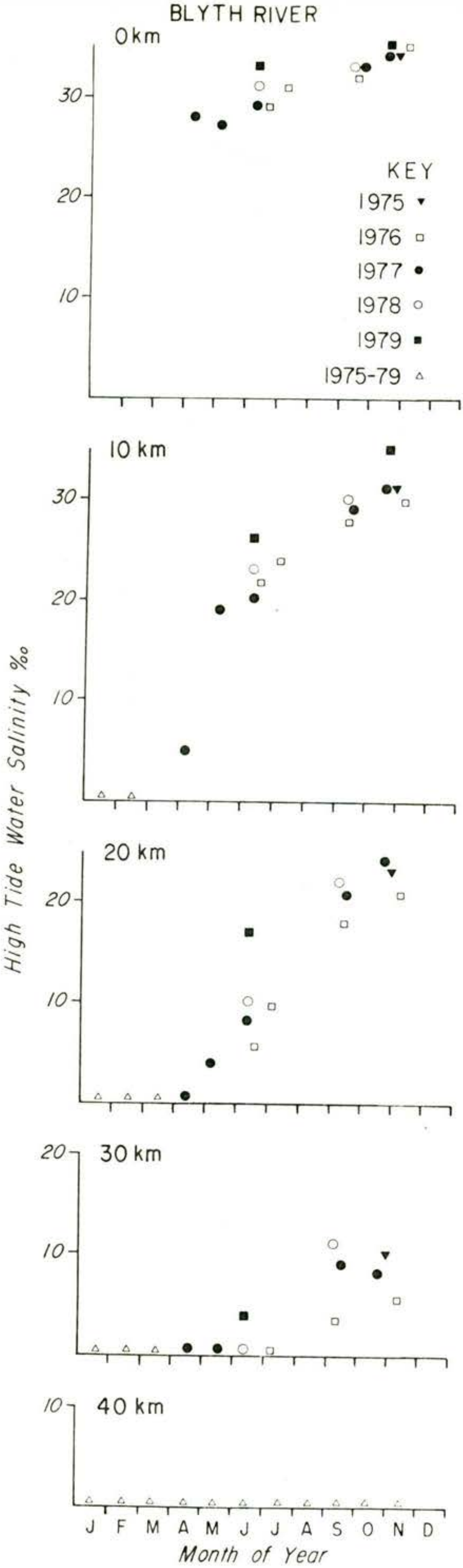


FIG. 3.3.23

Variations in high tide water salinity at stations on the Blyth River, N.T. during the period 1975-1979. (Type 1 waterway).

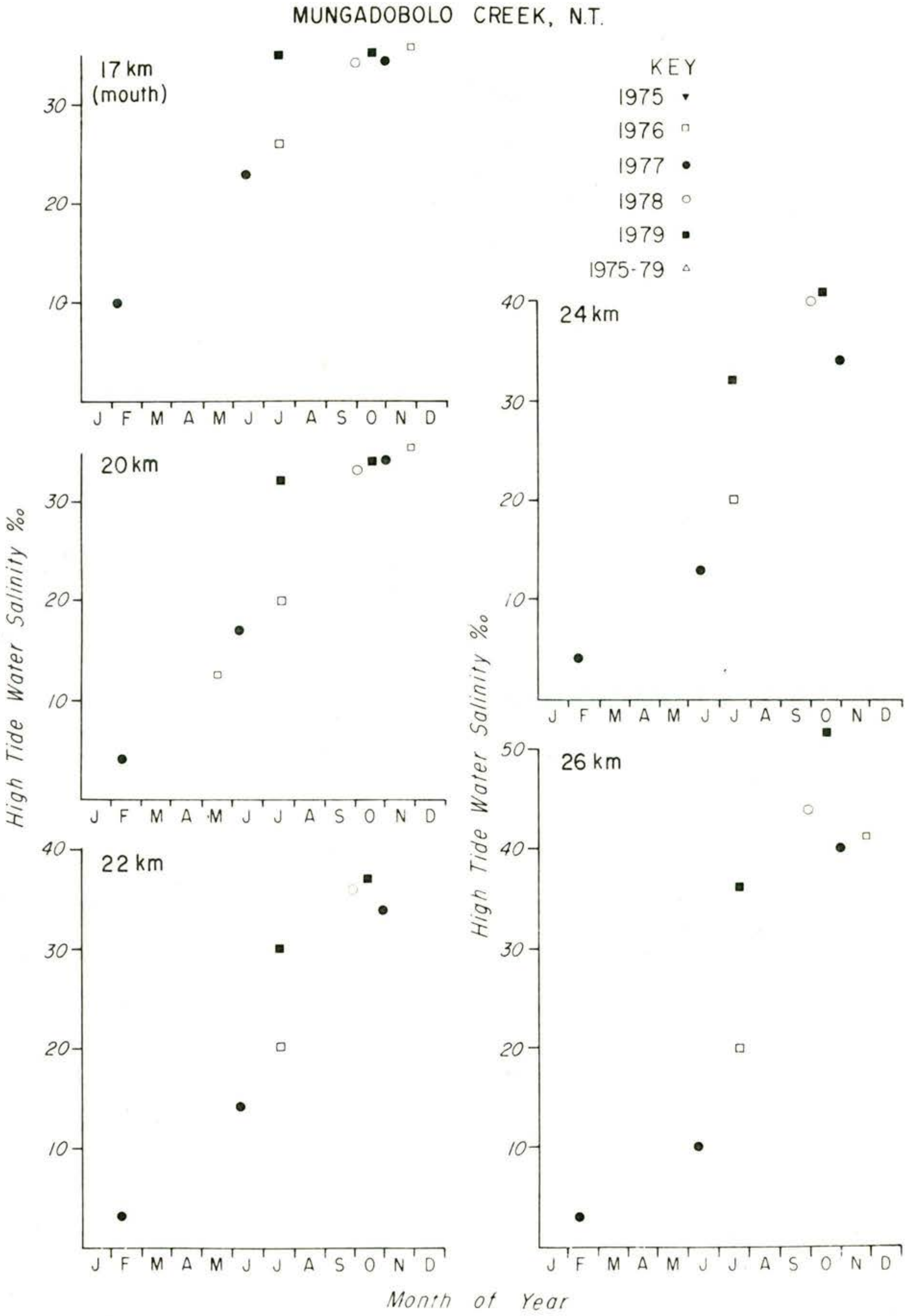


FIG. 3.3.24

Variations in high tide water salinity at stations on Mungardobolo Creek, N.T. during the period 1975-1979. (Type 5 waterway).

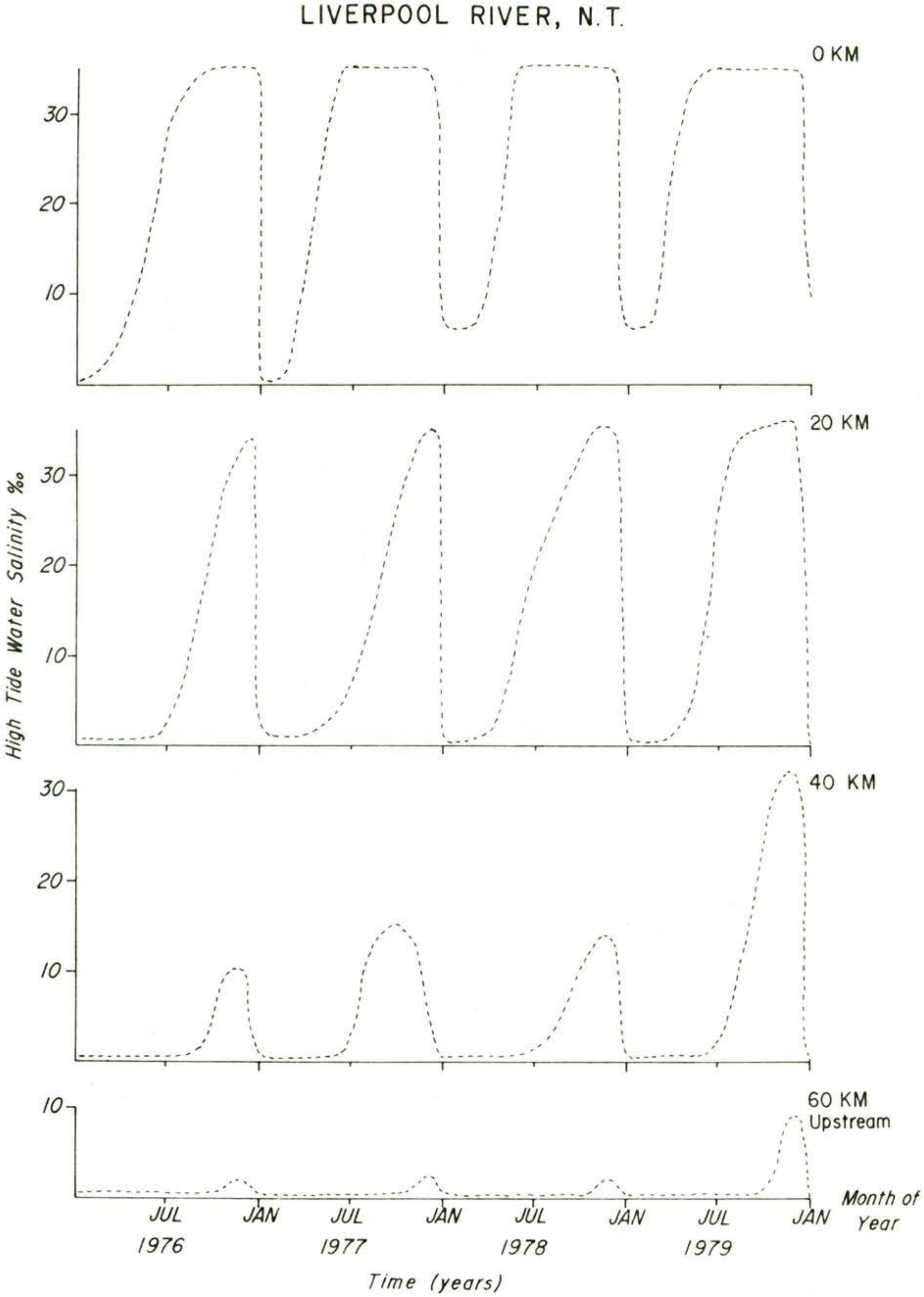


FIG. 3.3.25

Variations in amplitude and periodicity of saline waters at stations on the Liverpool River, N.T. during the period 1976-1979. (Type 1 waterway).

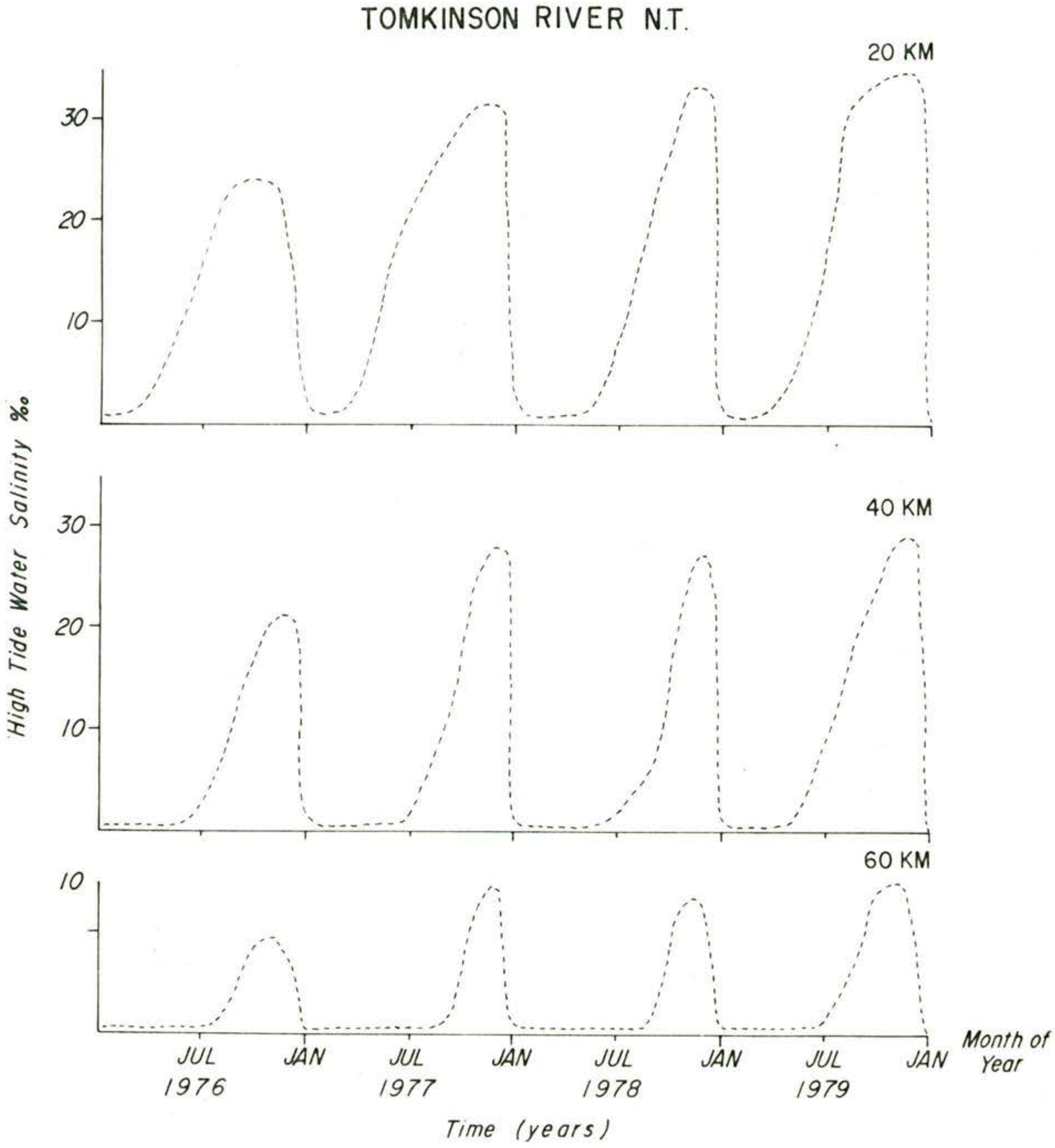


FIG. 3.3.26

Variations in amplitude and periodicity of saline waters at stations on the Tomkinson River, N.T. during the period 1976-1979. (Type 1 waterway).

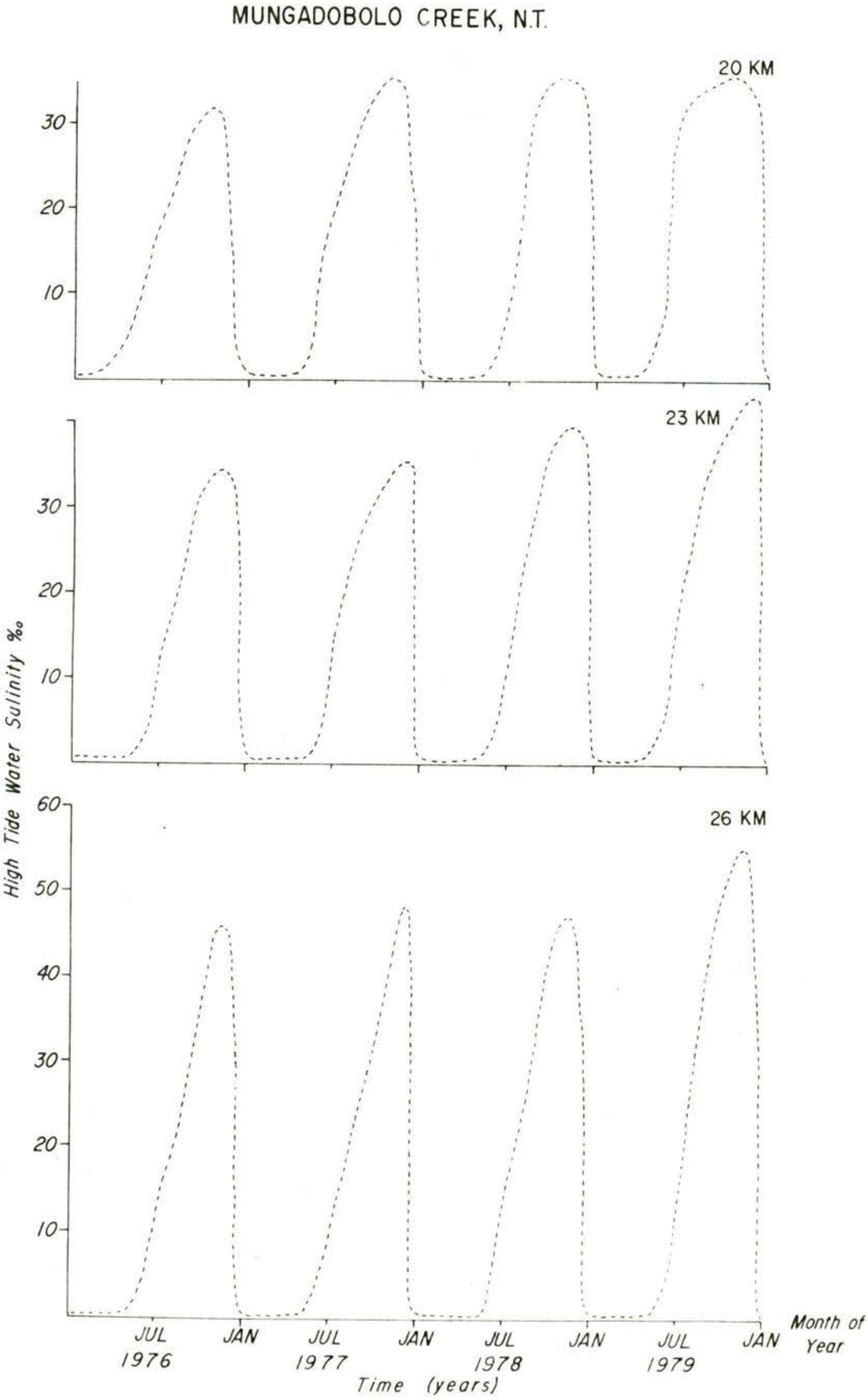


FIG. 3.3.27

Variations in amplitude and periodicity of saline waters at stations on Mungardobolo Creek, N.T. during the period 1976-1979. (Type 5 waterway).

On the Liverpool and Tomkinson Rivers ('Type 1' waterways) it is seen that salinity amplitudes decrease in a regular manner as distance upstream increases. It is evident from comparing Figs. 3.3.25 and 3.3.26 that waterways receiving greater amounts of freshwaters into their upstream reaches will show smaller amplitudes and this is the case for the Liverpool River. The reductions in amplitudes upstream on these two rivers not only reflect the quantity of water entering a catchment area in the previous 'wet' season, but are also a measure of the stability of waters at any particular point along a waterway over time. In Figs. 3.3.25 and 3.3.26 an amplitudinal decrease in 1976 at all stations relative to amplitudes in 1977-1979 is evident and shows that 1976 must have been wetter than 1977-1979. Similarly, an increase in amplitude and increases in the period of the salinity wave in 1979 at all sites on the Liverpool and Tomkinson Rivers indicates from the salinity signatures alone that 1979 must have been a considerably drier year than years 1976-1978. This conclusion is borne out by climatic records for the Maningrida meteorological station, which is located on the Liverpool/Tomkinson River System in central Arnhem Land.

Fig. 3.3.27 also shows Mungardobolo Creek (a 'Type 5' waterway) as having smaller amplitudes in 1976 at all sites upstream again indicating that 1976 was the wettest year and 1979 the driest year as seen through the salinity signatures. The increase in amplitudes as distance upstream increases is exactly the reverse situation to Figs. 3.3.25 and 3.3.26, but reflects salinity fluctuations in a waterway that has an extremely small catchment area and receives negligible freshwater input after commencement of the 'dry' season.

That variations in salinity amplitudes over time reflect annual climatic fluctuations is not unexpected but reinforces the view that tidal waterways in the survey area can be grouped into various types based upon seasonal variations in their water salinity signatures.

The different types of waterways provide then a wide range of habitats for the various mangrove species to colonize. However as shown in Figs. 3.3.9-3.3.20, many species have quite specific habitat requirements, and lack of these results in non-occurrence of the particular species. Other species are shown to be ubiquitous throughout the survey area and their occurrence at most sites is indicative of their wide tolerances to varied edaphic, physiologic and environmental conditions. Leading on from this approach which concentrated on variations in salinity and floristics within tidal waterways in different regions of the survey area, the following chapter focuses, with computational analyses, on the grouping of waterways using presence/absence of individual mangrove species as a further tool in attempting to understand present distributions of species.

CHAPTER 4:

GROUPING OF SITES WITHIN THE SURVEY AREA ON PRESENCE/ABSENCE OF MANGROVE SPECIES

4.1 INTRODUCTION

The use of a classificatory approach has a long tradition in many subjects. Classificatory methods suitable for examining plant/ environment relationships on a local and/or regional scale range from Braun-Blanquet's traditional phytosociological method to an ever expanding number of numerical taxonomic methods such as association analysis and other clustering techniques.

Classifications obtained by any of these methods are then evaluated in terms of the clarity of the hierarchical groups and the ease with which some rational hypotheses can be formulated concerning these groups and their environmental relationships. Of particular relevance to this study are the findings of Williams *et al.*, (1966), Williams, (1971), Frenkel and Harrison, (1974) and Clifford and Stephenson (1975) and Sandland and Young (1979).

Little information exists on grouping of tidal waterways and systems on the basis of occurrence/non-occurrence of particular mangrove species. Some species appear to be useful indicators of specific habitats and/or local environmental conditions. Schimper (1903) was amongst the earliest of workers to emphasize that many mangrove species are useful biological indicators within intertidal areas often reflecting changes in local microtopographic and edaphic as well as climatic conditions. Other workers, including Fosberg (1961, 1975), Macnae (1966, 1968), Chapman (1970, 1975, 1976), Zahran (1975) and Cintron *et al.* (1978), have stressed that increasing climatic aridity results in a reduction of floristic diversity of mangroves in both tropical and sub-tropical regions.

Within the survey area, 110 tidal waterways (Fig. 1.2.1), which are further grouped into 82 distinct tidal systems (Fig. 1.2.2), were floristically sampled during the years 1975-79. Twenty-four mangrove species (Table 1.2.1) of those recorded in this area which ranged over 5° of latitude between 11-16°S around the coastline of the Kimberley region of Western

Australia and the entire coastline of the Northern Territory are used in analyses. Variation in floristic diversity of mangrove species between sites represents the basis of this study. A similar study grouping tidal waterways down the east Queensland coast is being undertaken by the Inshore Productivity Group (Australian Institute of Marine Science) (Bunt and Williams, 1980; Bunt *et al.*, 1982; Duke, pers.comm.).

The major purpose of this chapter is to explore from an environmental viewpoint the floristic groups of tidal waterways and systems in the survey area. The site groupings obtained in this study are dependent on the present diversity of mangrove species in various regions of the survey area. Levels of species diversity do not appear to be due to any one factor but rather result from complex interactions of the biological, chemical and physical environments now and in the past.

In Chapter 1 it was shown that considerable variations in climate occurred throughout the survey area, whereas Chapter 2 examined, in particular, distributions of individual mangrove species and suggested that local climatic factors appeared to be largely responsible for much of the present variation in species diversity. Chapter 3 distinguished five types of waterways using seasonal variations in their water salinity signatures. Here it was shown that although species diversity is usually greater in 'Type 1" waterways within any band of latitude in the survey area - due to the presence of a wider range of habitats - prevailing local climatic conditions in many cases appeared to determine the number of species that could ultimately colonize any particular region of the survey area even though suitable edaphic conditions for other species to become established may exist.

4.2 METHODS

Within the survey area, lists of mangrove species were recorded for each site. These are provided in Appendix Al. Overall, 4,525 km of tidal waterways were surveyed using outboard-powered work boats. In most cases, sites were revisited and the likelihood of mangrove species actually occurring at a particular site not being recorded for that site is considered to be quite small.

Voucher specimens of the various mangrove species have been deposited with the Northern Territory Herbarium, Darwin.

Groupings of tidal waterways and systems were obtained using the Multbet non-combinatorial information statistic programme within the TAXON package (Dale *et al.*, 1980). Data reduction and analysis was made possible through the considerable help of W.T. Williams at the C.S.I.R.O. Davies Laboratory, Townsville, who provided access to the C.S.I.R.O. computer facility, Canberra. In this study, all species recorded in the survey area are included in analyses of the two matrices of 24 species X 110 and 82 sites, respectively. The "rarer" species, although often eliminated from consideration for reasons given elsewhere (Clifford and Stephenson, 1975), have been included as they are in most instances useful indicators of specific habitats.

4.3 RESULTS

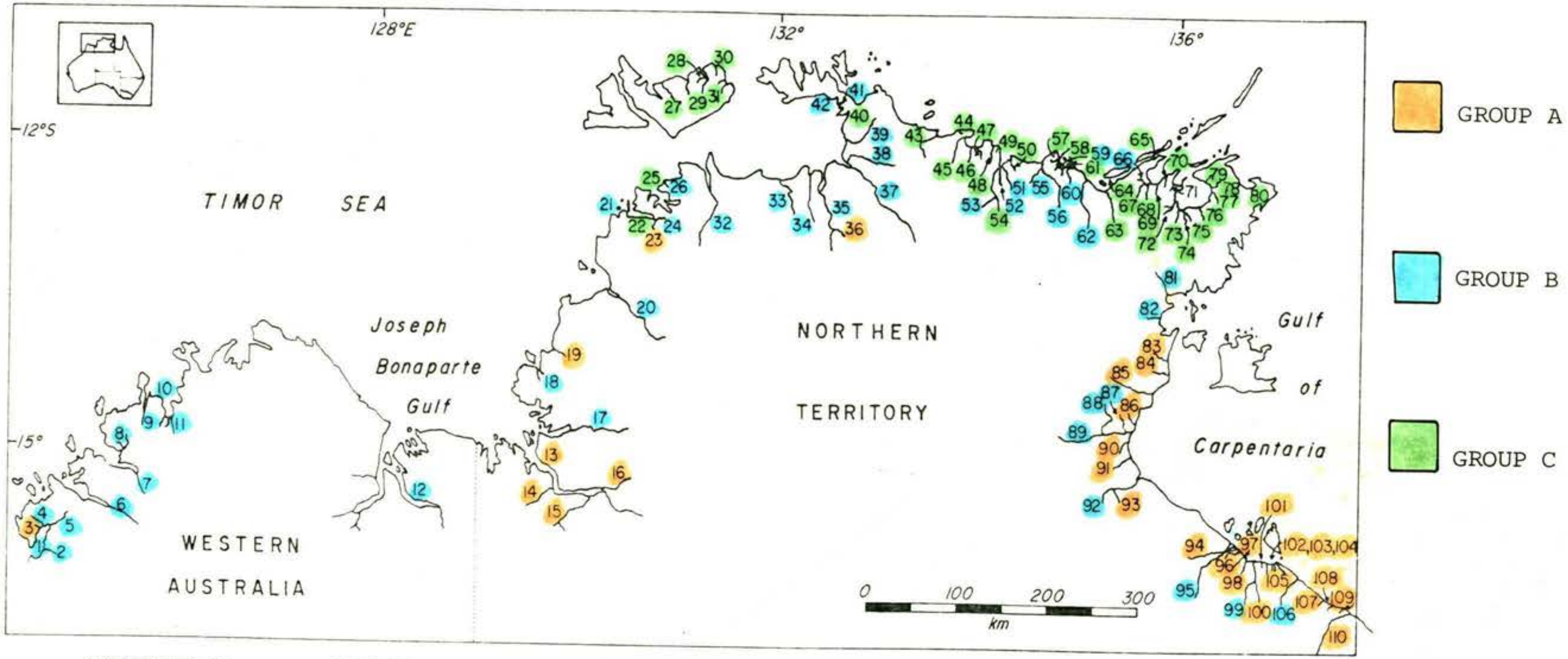
The classification of data according to the Multbet analyses is shown in Figs. 4.3.3 and 4.3.5. Here coherent groups of waterways and systems have been arbitrarily truncated at the 15 and 12 group levels, respectively. The twenty-four mangrove species fell into seven groups in both data analyses (Figs. 4.3.4; 4.3.6). All of these groupings are depicted in dendrogram form which are hierarchial arrangements of sites by their floristic similarities and dissimilarities.

Two-way tables showing the obtained groupings of both the tidal waterways and systems based upon the presence/absence of mangrove species are shown in Tables 4.3.1 and 4.3.2.

Pictorial displays of site groupings throughout the survey area are given in Figs. 4.3.1., 4.3.2 and 4.3.7. From the dendrograms of site groupings three major groups were initially accepted and labelled A, B, C in both Figs. 4.3.3 and 4.3.5. In Fig. 4.3.1 (for the 110 tidal waterways examined), sites in Group A contained between 3-10 mangrove species - a low level of floristic diversity - and these sites are seen to be largely concentrated throughout the Gulf of Carpentaria and Joseph Bonaparte Gulf in more seasonally arid portions of the survey area.

Group B includes sites throughout the survey area that possess between 9-14 species - a slightly higher level of floristic diversity than Group A sites. Included in Group C are sites possessing between 14-21 species and these are, within the survey area, floristically the most diverse. Group C sites are seen, however, only to occur across the northern coastline of the Northern Territory in the least arid portions of the survey area.

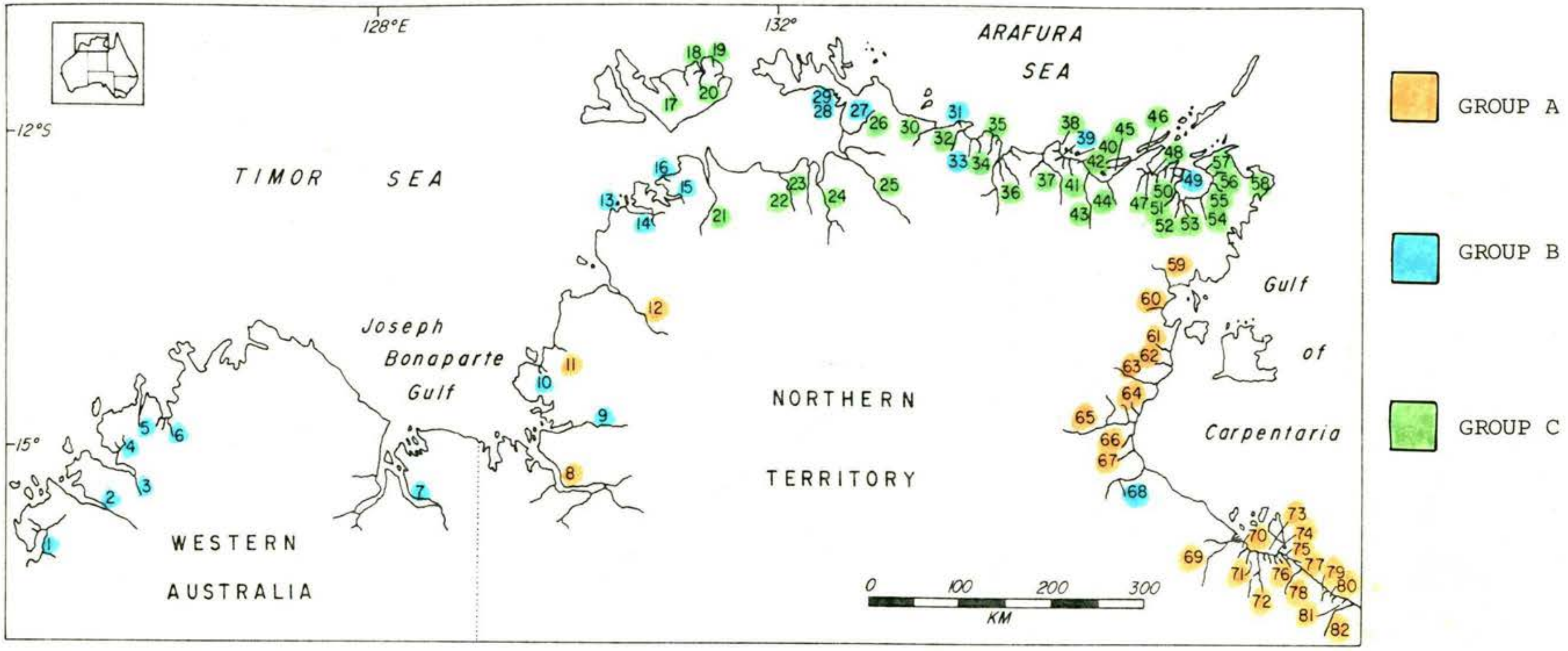
In Fig. 4.3.2, groupings of the 82 tidal systems are shown. The grouping of 'systems' as opposed to 'individual waterways' eliminates the 'between waterway' variations in species composition in any particular system. Here between 4-14 species occur in Group A systems which represent floristically the least diverse sites. Such sites are seen in this analysis to occur only in the Gulf of Carpentaria and Joseph Bonaparte Gulf, the more arid portions of the survey area. Systems intermediate in their level of floristic diversity (Group B with between 11-16 species) have in this analysis shrunk considerably from the previous representation of intermediate sites in Fig. 4.3.1. Groups A and C in Fig. 4.3.2 have effectively 'captured' many of the intermediate sites in Fig. 4.3.1. Group C systems with between 14-21 species again are seen to occur only in the least arid sites across the northern coastline of the Northern Territory at 11-12°S in latitude.



1 GEORGE WATER
2 SALE R.
3 BARLEE IMPEDIMENT
4 GAIRDNER R.
5 GLENELG R.
6 PRINCE REGENT R.
7 ROE R.
8 HUNTER R.
9 MITCHELL R.
10 PORT WARRENDER
11 LAWLEY R.
12 ORD R.
13 VICTORIA R.
14 BULLO R.
15 BAINES R.
16 ANGALARRI R.
17 FITZMAURICE R.
18 PORT KEATS
19 MOYLE R.
20 DALY R.
21 PORT PATERSON
22 BYNOE HARBOUR
23 ANNIE R.
24 CHARLOTTE R.
25 DARWIN HARBOUR
26 BUFFALO CK.
27 ANDRANANGOO CK.
28 BATH CK.
29 JOHNSTON R.
30 DONGAU CK.
31 TINGANOO CK.
32 ADELAIDE R.
33 WILDMAN R.
34 WEST ALLIGATOR R.
35 SOUTH ALLIGATOR R.
36 NOURLANGIE CK.
37 EAST ALLIGATOR R.
38 COOPERS CK.
39 MURGENELLA CK.
40 MINI MINI CK.
41 IWALG CK.
42 ILAMARYI R.
43 KING R.
44 ARRLA CK.
45 GOOMADEER R.
46 WURUGOIJ CK.
47 MAJARIE CK.
48 NUNGBALGARRIE CK.
49 TOMS CK.
50 GUDJERARMA CK
51 TOMKINSON R.
52 MUNGADOBOLO CK.
53 MARAGULIDBAN CK.
54 LIVERPOOL R.
55 CADELL R.
56 BLYTH R.
57 NGANDADAUDA CK.
58 DJABURA CK.
59 DJIGAGILA CK.
60 DARBITLA CK.
61 BENNETT CK.
62 GLYDE R.
63 WOOLEN R.
64 HUTCHINSON STRAIT
65 CADELL STRAIT
66 KALARWOI R. (CK. B)
67 KALARWOI R.
68 BUCKINGHAM R.
69 WARAWURUWOI R.
70 KURALA R.
71 SLIPPERY CK.
72 DARWARUNGA R.
73 HABGOOD R.
74 BARALMINAR R.
75 GOBALPA R.
76 GOROMURU R.
77 CATO R.
78 PETER JOHN R.
79 BURUNGBIRINUNG R.
80 MELVILLE BAY
81 KOOLATONG R.
82 WALKER R.
83 HART R.
84 MUNTAK CK.
85 ROSE R.
86 YIWAPA CK.
87 PAINNYILATYA CK.
88 PHELP R.
89 ROPER R.
90 NAYARNPI CK.
91 TOWNS R.
92 LIMMEN BIGHT R.
93 NATHAN R.
94 BATTEN CK.
95 McARTHUR R.
96 'JOHNSON' R.
97 'COULOMB' CK.
98 'FARADAY' CK.
99 WEARYAN R.
100 FOELSCHE R.
101 'BOHR' CK.
102 'PLANCK' CK.
103 'ARCHIMEDES' CK.
104 'GALILEO' CK.
105 FAT FELLOWS CK.
106 ROBINSON R.
107 'EINSTEIN' CK.
108 'NEWTON' CK.
109 'PAULI' CK.
110 CALVERT R.

FIG. 4.3.1

Classification of sites from the 110 tidal waterways in the survey area into three major groups based on variations in floristic diversity of mangrove species.



1 GEORGE WATER
2 PRINCE REGENT
3 ROE
4 HUNTER
5 MITCHELL
6 PORT WARRENDER
7 ORD
8 VICTORIA
9 FITZMAURICE
10 PORT KEATS
11 MOYLE
12 DALY
13 PORT PATERSON
14 BYNOE HARBOUR
15 DARWIN HARBOUR
16 BUFFALO
17 ANDRANANGOO
18 JOHNSTON/BATH
19 DONGAU
20 TINGANOO
21 ADELAIDE
22 WILDMAN
23 WEST ALLIGATOR
24 SOUTH ALLIGATOR
25 EAST ALLIGATOR
26 MURGENELLA
27 MINI MINI
28 IWALG
29 ILAMARYI
30 KING
31 ARRLA
32 GOOMADEER
33 WURUGOIJ
34 MAJARIE
35 NUNGBALGARRIE
36 LIVERPOOL/TOMKINSON
37 BLYTH/CADELL
38 NGANDADAUDA
39 DJABURA
40 DJIGAGILA
41 DARBITLA
42 BENNET
43 GLYDE
44 WOOLEN RIVER
45 HUTCHINSON STRAIT
46 CADELL STRAIT
47 BUCKINGHAM/KALARWOI
48 WARAWURUWOI
49 KURALA
50 SLIPPERY
51 DARWARUNGA
52 HABGOOD
53 BARALMINAR/GOBALPA
54 GOROMURU
55 CATO
56 PETER JOHN
57 BURUNGBIRINUNG
58 MELVILLE BAY
59 KOOLATONG
60 WALKER
61 HART
62 MUNTAK
63 ROSE
64 YIWAPA
65 ROPER
66 NAYARNPI
67 TOWNS
68 LIMMEN BIGHT
69 McARTHUR
70 'COULOMB'
71 'FARADAY'
72 WEARYAN
73 'BOHR'
74 'PLANCK'
75 'ARCHIMEDES'
76 'GALILEO'
77 FAT FELLOWS
78 ROBINSON
79 'EINSTEIN'
80 'NEWTON'
81 'PAULI'
82 CALVERT

FIG. 4.3.2

Classification of sites from the 82 tidal systems in the survey area into three major groups based on variations in floristic diversity of mangrove species.

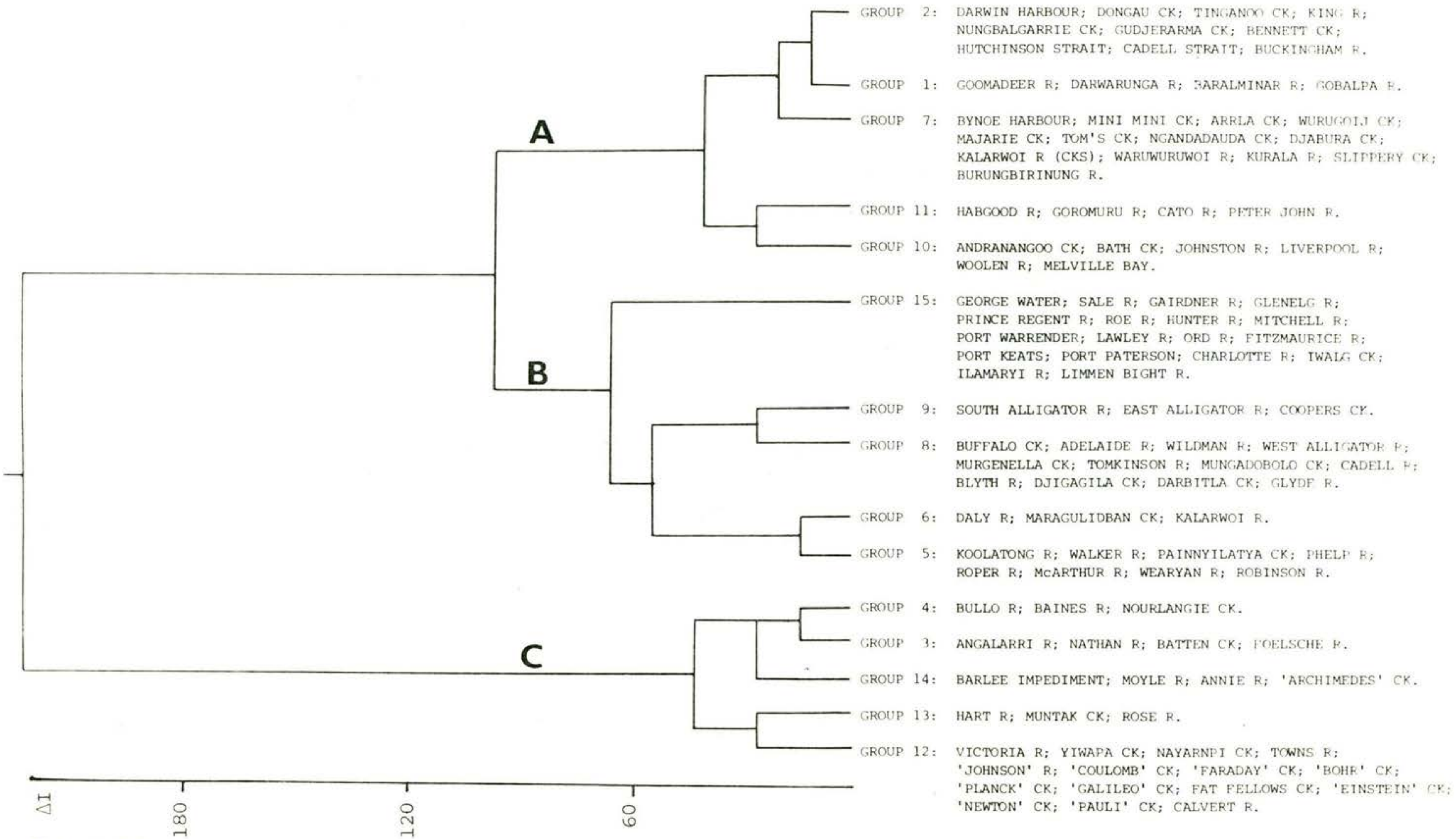


FIG. 4.3.3

Dendrogram of site groupings obtained by Multbet analysis of the 110 tidal waterways in the survey area. (ΔI is change in value of the information statistic of Dale *et al.*(1980))

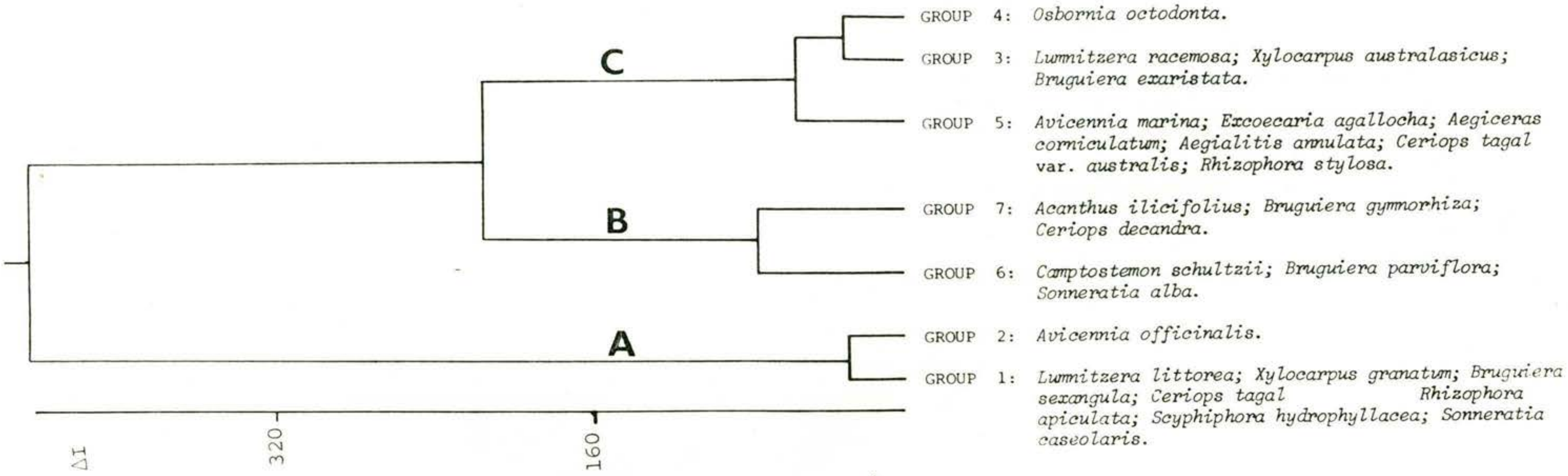


FIG. 4.3.4

Dendrogram of species groupings obtained through Multbet analysis of mangrove species on the 110 tidal waterways in the survey area. (ΔI is change in value of the information statistic of Dale *et al.*(1980)).

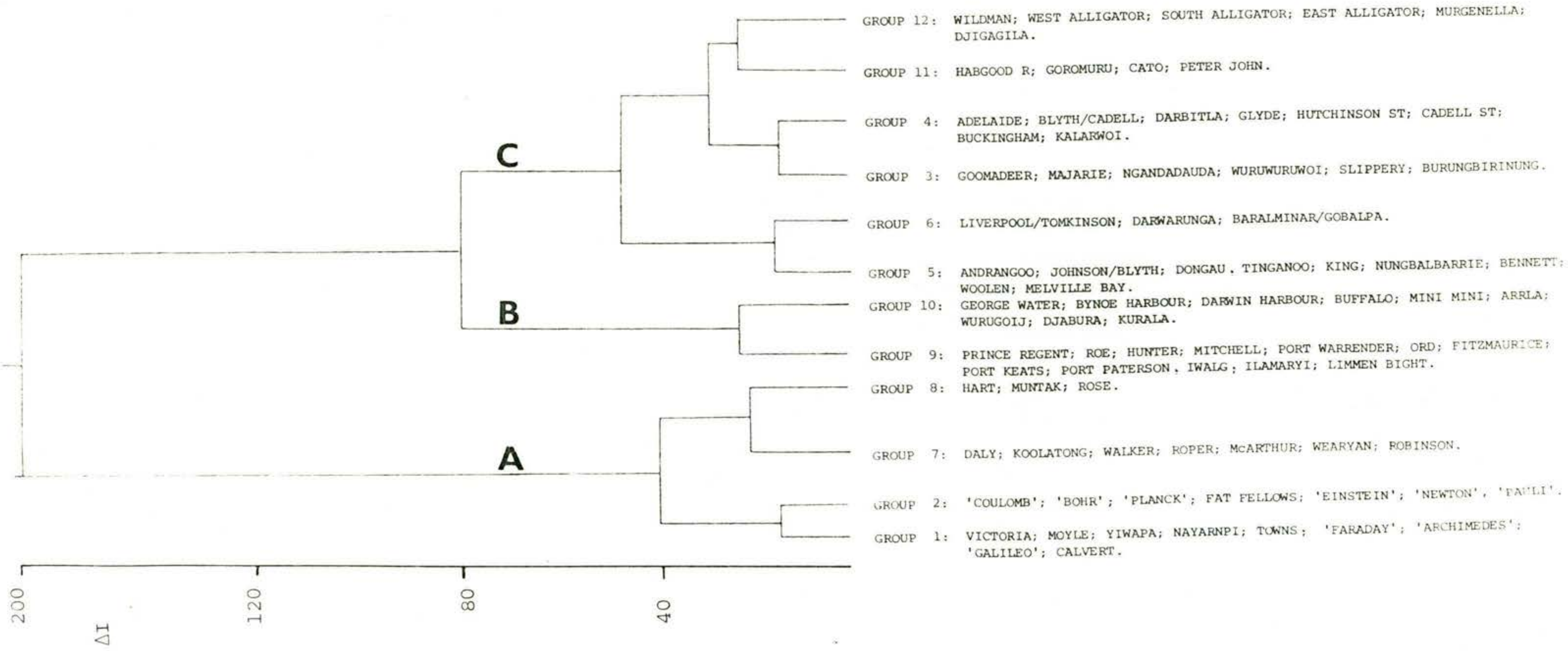


FIG. 4.3.5

Dendrogram of site groupings obtained through Multbet analysis of the 82 tidal systems in the survey area. (ΔI is change in value of the information statistic of Dale *et al.* (1980))

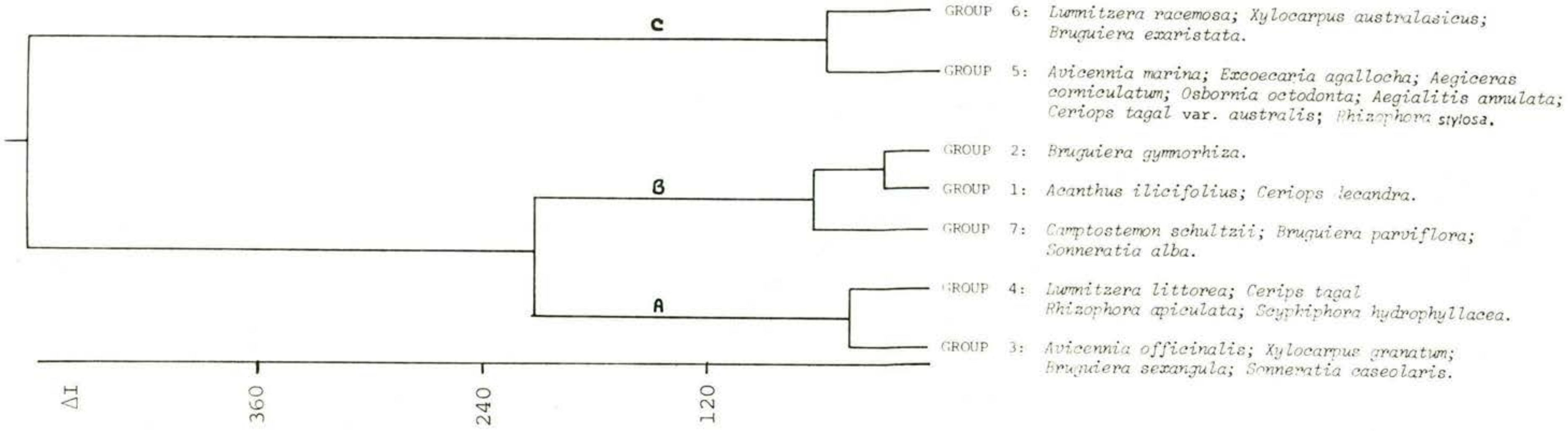


FIG. 4.3.6

Dendrogram of species groupings obtained through Multbet analysis of mangrove species recorded for the 82 tidal systems in the survey area. (ΔI is change in value of the information statistic of Dale *et al.*(1980))

From the dendrograms of mangrove species groupings (Figs. 4.3.4 and 4.3.6) three major groups can be accepted for both the 110 tidal waterways and the 82 tidal systems. These are labelled A, B, C in both figures.

The species composition of Group A includes :

Avicennia officinalis
Bruguiera sexangula
Ceriops tagal
Lumnitzera littorea
Rhizophora apiculata
Scyphiphora hydrophyllacea
Sonneratia caseolaris
Xylocarpus granatum

These species were recorded sporadically at certain sites within the survey area. They are largely absent from more arid portions of the survey area and occur in most cases infrequently at sites across the northern coastline of the Northern Territory.

Group B is also of identical species composition in both Figs. 4.3.4 and 4.3.6, although groupings 6 and 7 in Fig. 4.3.4 now branch into three groups 1, 2 and 7 in Fig. 4.3.6. Species occurring in Group B :

Acanthus ilicifolius
Bruguiera gymnorhiza
Bruguiera parviflora
Camptostemon schultzii
Ceriops decandra
Sonneratia alba

are also species that occur, in most instances, at sites throughout less arid portions of the survey area. These species are considerably more common in occurrence than species represented in Group A.

Group C represents mangrove species that are particularly ubiquitous at least in some portion of most sites in the survey area. They include:

Aegiceras corniculatum
Aegialitis annulata
Avicennia marina
Bruguiera exaristata
Ceriops tagal var. *australis*
Excoecaria agallocha
Lumnitzera racemosa
Osbornia octodonta
Rhizophora stylosa
Xylocarpus australasicus

Again, species composition of Group C is identical in Figs. 4.3.4 and 4.3.6, but in the analysis shown in Fig. 4.3.4 three groupings, 3, 4 and 5, occurred within Group C while only two groups, 5 and 6, occurred within it in the other analysis (Fig. 4.3.6).

In Table 4.3.1 it is seen that a ubiquitous group of species (Group 5), comprising *Avicennia marina, Excoecaria agallocha, Aegiceras corniculatum, Aegialitis annulata, Ceriops tagal* var. *australis* and *Rhizophora stylosa* occur at most sites. The grouping of tidal waterways on the basis of presence/absence of particular species or groups of species presents problems, not least of which is the increased importance of the 'rarer' species. Many species often emphasize specific habitats, assuming a disproportionate importance and are ultimately responsible for many of the groupings formed in the analyses. The ubiquitous species, however, often contribute little to most groupings. Considerable care is thus required in interpreting some groupings, particularly from the 110 tidal waterways' study.

In Table 4.3.1, for the 110 tidal waterways examined, Group 1 sites - comprising the Goomadeer, Darwarunga, Baralminar and Gobalpa Rivers - are differentiated from other waterways on their floristic similarity which includes sporadic occurrences of *Lumnitzera littorea, Ceriops tagal* and *Scyphiphora hydrophyllacea.*

In Tables 3.3.1 - 3.3.5, tidal waterways in the survey were divided into types based upon seasonal variations in water salinity and it was shown that the Goomadeer River is a 'Type 1' waterway entering Junction Bay. The Darwarunga, Baralminar and Gobalpa Rivers are, however, 'Type 4' waterways in their seasonal salinity signatures and although adjacent to each other in Arnhem Bay, appear to have grouped with the Goomadeer River through the occurrence of the rare species, *Ceriops tagal* at all sites.

Group 2 waterways possess an average of sixteen mangrove species - principally in species groups 3-7 (Table 4.3.1) and include waterways across the northern coastline of the Northern Territory. Darwin Harbour, Bennett Creek and Hutchinson and Cadell Straits have been shown to be 'Type 3' waterways, experiencing seawater salinities throughout most of the year and are closely allied with Tinganoo and Gudjerarma Creeks and the King River - 'Type 4' waterways which attain salinities slightly above seawater by the end of the dry season. Also included in this grouping are the Buckingham River and Nungbalgarrie Creek - 'Type 2' waterways that remain brackish for a considerable period of the year but attain seawater salinities by the end of the dry season. Group 2 then, in essence includes many waterways in the general area of 12^{O}S latitude that are inundated by seawater salinities often for considerable periods of the year. The grouping does not include any waterways occurring at any of the higher latitudes (i.e. 13-16^{O}S) in the survey area.

MANGROVE SPECIES — / TIDAL WATERWAY	Group 1							Group 2	Group 3			Group 4	Group 5						Group 6			Group 7		
	Lumnitzera littorea	*Xylocarpus granatum*	*Bruguiera sexangula*	*Ceriops tagal*	*Rhizophora apiculata*	*Scyphiphora hydrophyllacea*	*Sonneratia caseolaris*	*Avicennia officinalis*	*Lumnitzera racemosa*	*Xylocarpus australasicus*	*Bruguiera exaristata*	*Osbornia octodonta*	*Avicennia marina*	*Excoecaria agallocha*	*Aegiceras corniculatum*	*Aegialitis annulata*	*Ceriops tagal* var. *australis*	*Rhizophora stylosa*	*Camptostemon schultzii*	*Bruguiera parviflora*	*Sonneratia alba*	*Acanthus ilicifolius*	*Bruguiera gymnorrhiza*	*Ceriops decandra*
Group 1																								
45. GOOMADEER R.	○	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
72. DARWARUNGA R.	●	○	○	●	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
74. BARALMINAR R.	○	○	○	●	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
75. GOBALPA R.	●	○	○	●	○	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●
Group 2																								
25. DARWIN HARBOUR	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
30. DONGAU CK.	○	○	○	○	●	●	○	○	●	●	●	●	●	●	●	●	●	○	○	●	●	○	●	●
31. TINGANOO CK.	○	○	○	●	●	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	●	○	●	●
43. KING R.	○	○	○	○	●	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
48. NUNGBALGARRIE CK.	○	○	○	○	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
50. GUDJERARMA CK.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
61. BENNETT CK.	○	○	○	○	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●
64. HUTCHINSON STRAIT	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
65. CADELL STRAIT	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
68. BUCKINGHAM R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Group 3																								
16. ANGALARRI R.	○	○	○	○	○	○	○	○	○	○	○	○	●	●	●	○	○	○	○	○	○	○	○	○
93. NATHAN R.	○	○	○	○	○	○	○	○	●	●	○	○	●	●	●	○	○	●	○	○	○	○	○	○
94. BATTEN CK.	○	○	○	○	○	○	○	○	●	○	○	○	●	●	●	○	○	●	○	○	○	○	○	○
100. FOELSCKE R.	○	○	○	○	○	○	○	○	●	○	○	○	●	●	●	○	○	●	○	○	○	○	○	○
Group 4																								
14. BULLO R.	○	○	○	○	○	○	○	○	●	●	○	○	●	●	●	●	●	○	○	○	○	○	○	○
15. BAINES R.	○	○	○	○	○	○	○	○	●	●	○	○	●	●	●	●	●	○	○	○	○	○	○	○
36. NOURLANGIE CK.	○	○	○	○	○	○	●	○	●	●	○	○	●	●	●	●	●	○	○	○	○	○	○	○
Group 5																								
81. KOOLATONG R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○	●	●	○
82. WALKER R.	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○	●	●	○
87. PAINNYILATYA CK.	○	○	○	○	○	○	○	○	●	○	●	○	●	●	●	●	●	●	○	●	○	●	○	○
88. PHELP R.	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	○	○	○	●	●	○
89. ROPER R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○	●	●	○
95. McARTHUR R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	○	○	●	○	○
99. WEARYAN R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	○	○	○	○	○
106. ROBINSON R.	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	○	○	○	○	○	○
Group 6																								
20. DALY R.	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	○	○	●	○	○	●	○	○
53. MARAGULIDBAN CK.	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	●	●	○	●	●	●
67. KALARWOI R.	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	●	○	●	●	○	●
Group 7																								
22. BYNOE HARBOUR	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	●
40. MINI MINI CK.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	●
44. ARRLA CK.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	●
46. WURUGOIJ CK.	○	○	○	○	○	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	○	●
47. MAJARIE CK.	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●
49. TOMS CK.	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●
57. NGANDADAUDA CK.	○	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●
58. DJABURA CK.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	●
66. KALARWOI R.(CK.B)	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●
69. WARAWURUWOI R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●
70. KURALA R.	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●
71. SLIPPERY CK.	○	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●
79. BURUNGBIRINUNG R.	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	●	●	●	●	○	●
Group 8																								
26. BUFFALO CK.	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	○
32. ADELAIDE R.	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
33. WILDMAN R.	○	○	○	○	○	○	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	○	●
34. WEST ALLIGATOR R.	○	○	○	○	○	○	●	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●
39. MURGENELLA CK.	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●
51. TOMKINSON R.	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
52. MUNGADOBOLO CK.	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
55. CADELL R.	○	○	○	○	○	○	○	●	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●
56. BLYTH R.	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
59. DJAGAGILA CK.	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●
60. DARBITLA CK.	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
62. GLYDE R.	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●

TABLE 4.3.1

Two-way table of site/species groups for the 110 tidal waterways in the survey area. Group numbers refer to results of Multbet analysis, given for waterways in Fig. 4.3.3 and for spp. in Fig. 4.3.4.

MANGROVE SPECIES — TIDAL WATERWAY	Group 1							Group 2	Group 3			Group 4	Group 5						Group 6			Group 7		
	Lumnitzera littorea	*Xylocarpus granatum*	*Bruguiera sexangula*	*Ceriops tagal*	*Rhizophora apiculata*	*Scyphiphora hydrophyllacea*	*Sonneratia caseolaris*	*Avicennia officinalis*	*Lumnitzera racemosa*	*Xylocarpus australasicus*	*Bruguiera exaristata*	*Osbornia octodonta*	*Avicennia marina*	*Excoecaria agallocha*	*Aegiceras corniculatum*	*Aegialitis annulata*	*Ceriops tagal var. australis*	*Rhizophora stylosa*	*Camptostemon schultzii*	*Bruguiera parviflora*	*Sonneratia alba*	*Acanthus ilicifolius*	*Bruguiera gymnorhiza*	*Ceriops decandra*
Group 9																								
35. SOUTH ALLIGATOR R.	○	○	○	○	○	○	●	●	○	●	●	●	●	●	●	●	●	●	●	○	●	○	○	○
37. EAST ALLIGATOR R.	○	○	○	○	○	○	●	●	●	●	○	●	●	●	●	●	●	●	●	○	●	●	○	○
38. COOPERS CK.	○	○	○	○	○	○	●	●	●	●	●	○	●	●	●	●	●	●	●	○	○	●	○	○
Group 10																								
27. ANDRANANGOO CK.	○	●	○	○	●	●	●	○	●	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●
28. BATH CK.	●	○	○	○	●	●	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○	●	●	●
29. JOHNSTON R.	●	○	○	○	●	●	○	○	●	●	●	●	●	●	●	●	●	●	○	●	●	○	●	●
54. LIVERPOOL R.	●	○	○	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
63. WOOLEN R.	●	○	○	○	●	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
80. MELVILLE BAY	●	●	○	○	●	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Group 11																								
73. HABGOOD R.	○	○	○	●	●	○	●	○	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●
76. GOROMURU R.	○	○	○	●	○	○	●	○	●	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●
77. CATO R.	○	○	●	●	●	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
78. PETER JOHN R.	○	○	●	○	●	●	●	○	●	●	●	●	●	●	●	○	●	●	○	●	●	●	○	●
Group 12																								
13. VICTORIA R.	○	○	○	○	○	○	○	○	●	●	○	●	●	●	●	●	●	●	●	○	○	○	○	○
86. YIWAPA CK.	○	○	○	○	○	○	○	○	●	●	○	●	●	●	●	●	●	●	○	○	○	○	○	○
90. NAYARNPI CK.	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	○	○	○	○
91. TOWNS R.	○	○	○	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	○	○	○	○	○	○
96. 'JOHNSTON' R.	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	○	○	○	○	○	○
97. 'COULOMB' CK.	○	○	○	○	○	○	○	○	●	○	●	●	●	●	●	●	●	●	○	○	○	○	○	○
98. 'FARADAY' CK.	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	○	○	○	○
101. 'BOHR' CK.	○	○	○	○	○	○	○	○	●	○	●	●	●	●	●	●	●	●	○	○	○	○	○	○
102. 'PLANCK' CK.	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	○	○	○	○	○
104. 'GALILEO' CK.	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	○	○	○	○	○	○	○
105. FAT FELLOWS CK.	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	○	○	○	○	○
107. 'EINSTEIN' CK.	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	○	○	○	○	○
108. 'NEWTON' CK.	○	○	○	○	○	○	○	○	○	○	●	○	●	●	●	●	●	●	○	○	○	○	○	○
109. 'PAULI' CK.	○	○	○	○	○	○	○	○	●	○	●	●	●	●	○	●	●	●	○	○	○	○	○	○
110. CALVERT R.	○	○	○	○	○	○	○	○	○	●	○	●	●	●	●	●	●	●	○	○	○	○	○	○
Group 13																								
83. HART R.	○	○	○	○	○	●	○	○	●	●	●	●	●	●	○	●	●	●	○	○	○	○	○	○
84. MUNTAK CK.	○	○	○	○	○	●	○	○	●	●	●	●	●	●	○	●	●	●	○	○	○	○	●	○
85. ROSE R.	●	○	○	○	○	●	○	○	○	●	○	●	●	●	○	○	○	●	○	○	○	○	●	○
Group 14																								
3. BARLEE IMPEDIMENT	○	○	○	○	○	○	○	○	○	○	○	○	●	○	○	●	○	●	●	○	●	○	○	○
19. MOYLE R.	○	○	○	○	○	○	○	○	○	○	○	○	●	●	○	●	●	●	●	○	○	○	○	○
23. ANNIE R.	○	○	○	○	○	○	○	○	○	○	○	○	●	○	●	●	○	●	●	●	●	○	○	○
103. 'ARCHIMEDES' CK.	○	○	○	○	○	○	○	○	○	○	○	○	●	○	○	●	●	●	○	○	○	○	○	○
Group 15																								
1. GEORGE WATER	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○	○	○
2. SALE R.	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
4. GAIRDNER R.	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
5. GLENELG R.	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
6. PRINCE REGENT R.	○	●	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
7. ROE R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
8. HUNTER R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
9. MITCHELL R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
10. PORT WARRENDER	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
11. LAWLEY R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
12. ORD R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	●	○	○	○
17. FITZMAURICE R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	○	○	○	○
18. PORT KEATS	○	○	○	○	○	○	○	○	●	●	○	●	●	●	●	●	●	●	●	●	●	○	○	○
21. PORT PATERSON	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○
24. CHARLOTTE R.	○	○	○	○	○	●	○	○	○	●	○	●	●	●	●	●	●	●	●	●	●	○	○	○
41. IWALG CK.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	●	○	○	○
42. ILAMARYI R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	●	○	○	○
92. LIMMEN BIGHT R.	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	○	○	○

TABLE 4.3.1 (contd)

Two-way table of site/species groups for the 110 tidal waterways in the survey area.

Only four waterways - Angalarri, Foelsche and Nathan Rivers and Batten Creek are included in Group 3 (Fig. 4.3.3). Between three to six mangrove species are present, and this represents an extremely low level of floristic diversity compared to many other sites. This floristic impoverishment is due to a number of factors. All four waterways branch off major trunk rivers, often at considerable distances upstream (Fig. 4.3.1) and due to increasing gradients upstream, the number of mangrove species, from the general pool of species in the region, having the ability to colonize such sites is reduced. It is also apparent that this grouping included only waterways from seasonally arid portions of the survey area (refer Sections 1.3.3 - 1.3.5).

Group 4 waterways are closely related to Group 3 (Fig. 4.3.3) and again include waterways such as the Bullo and Baines Rivers and Nourlangie Creek, branching off major trunk rivers - the Victoria and South Alligator Rivers, respectively (Fig. 4.3.1). Seven mangrove species occur on the Bullo and Baines Rivers whereas eight species occurred on Nourlangie Creek.

The absence of *Rhizophora stylosa* from Group 4 is the only difference separating it from Group 3 waterways. In the case of the Bullo and Baines Rivers and Nourlangie Creek, the non-occurrence of *Rhizophora stylosa* is explained principally through the lack of suitable sites for colonization due to increasing gradients upstream. Seasonal variations in salinity are well within the range of this species at all these sites and is not considered a factor limiting establishment.

An admixture of waterways - all from within the Gulf of Carpentaria - have been included in Group 5 (Fig. 4.3.3). The Koolatong, Walker, Phelp, Roper and McArthur Rivers are 'Type 1' waterways, having considerable freshwater inputs throughout the year, whereas the Wearyan and Robinson Rivers ('Type 2' waterways) do not. Painnyilatya Creek is a 'Type 5' waterway with minimal tidal flushing characteristics that becomes hypersaline by the mid-dry season. 9-14 mangrove species, principally in species groups 3, 4, 5 and 7 (Table 4.3.1) occur at these sites and with the exception of *Scyphiphora hydrophyllacea* (Walker River), other less common mangrove species in species groups 1 and 2 are absent. The non-occurrence of *Camptostemon schultzii* at all sites is a most important characteristic of this grouping. Reasons that may satisfactorily explain the absence of this species are given in Chapter 2 (in the discussion in that chapter).

Group 6 comprises the Daly River (10 species) and Maragulidban Creek (14 species), both 'Type 1' waterways and the Kalarwoi River (13 species) - a 'Type 4' waterway. This group is closely allied to Group 5 (Fig. 4.3.3). Species groups 1, 2 and 4 are absent from all sites (Table 4.3.1) and this site grouping does not appear explainable from either latitudinal positions of the waterways (Fig. 4.3.1) or local climatic conditions of the respective regions. Group 6 differs principally from Group 5 on occurrences of *Camptostemon schultzii* and *Acanthus ilicifolius* at all sites. Neither of these species occurs on Group 5 waterways. The presence of *Osbornia octodonta* (Group 5) and absence of this species (in Group 6) are also considered of major influence in the splitting of these groups.

Group 7 waterways include the Kalarwoi River (Creek B) ('Type 2'), Bynoe Harbour ('Type 3'), Mini Mini and Tom's Creeks, Warawuruwoi, Kurala and Burungbirinung Rivers ('Type 4') and Arrla, Wurugoij, Majarie, Ngandadauda, Djabura and Slippery Creeks ('Type 5').

Most of these waterways shown in Chapter 3, are seawater-hypersaline waterways and all occur only across the northern coastline of the Northern Territory (Fig. 3.3.1). Between 14-16 mangrove species from species groups 1, 3, 4, 5, 6 and 7 (Table 4.3.1) show the floristic similarity of these waterways. *Bruguiera gymnorhiza* is absent from all these sites except on the Kurala River and the rarer species *Lumnitzera littorea, Xylocarpus granatum, Bruguiera sexangula, Rhizophora apiculata, Sonneratia caseolaris* and *Avicennia officinalis* also are not recorded at any of the sites in Group 7.

Group 8 includes 'Type 1' waterways - the Adelaide and Wildman Rivers and Murgenella Creek entering into Van Diemen Gulf and the Tomkinson, Blyth, Cadell and Glyde Rivers on the northern Arnhem Land coastline. Buffalo and Darbitla Creeks and the West Alligator

Rivers are considered 'Type 2' waterways whereas other creeks in this grouping - Djigagila and Mungardobolo - are hypersaline ('Type 5') waterways by the end of the dry season.

All these waterways occur across the northern coastline of the Northern Territory and from Table 4.3.1 it is seen that this grouping relies principally on the occurrence of *Avicennia officinalis* at all sites. Thus, although these waterways are of different types, they all possess considerable floristic similarity with between 15-17 mangrove species. This grouping actually represents the range of habitats that *Avicennia officinalis* colonizes across the northern coastline of the Northern Territory.

Group 9 comprises only the South and East Alligator Rivers and Coopers Creek (Table 4.3.1). The East Alligator River (14 species) is a 'Type 1' waterway whereas the South Alligator River (14 species) and Coopers Creek (13 species) have been shown to be 'Type 2' waterways from seasonal variations in their salinity signatures (Figs. 3.3.1 and 3.3.2). This grouping, which is floristically most similar to Group 8 (Table 4.3.1) has been formed by joint occurrences of *Avicennia officinalis* and *Sonneratia caseolaris* at all three sites.

Group 10 also includes waterways from only across the northern coastline of the Northern Territory (Table 4.3.1). Andramangoo Creek and the Liverpool River are considered 'Type 1' waterways whereas the Woolen River and Melville Bay follow 'Type 3' salinity signatures. The Johnson River ('Type 4') and Bath Creek ('Type 5'), show that most waterway types are represented in this grouping. Between 17-21 species occur on these waterways, the major distinguishing feature being the occurrence of all 'rarer' species in species Group 1 (Table 4.3.1), except *Bruguiera sexangula*. This is floristically (with Group 11) a most diverse grouping and reflects, in particular, suitable local climatic conditions for establishment of these rarer mangrove species.

Group 11 represents a small assemblage of waterways within Arnhem Bay (Table 4.3.]) - the Habgood, Goromuru, Cato and Peter John Rivers, all of which are 'Type 1' waterways that are floristically most similar with between 18-20 mangrove species. Although Group 11 is most closely allied to Group 10 (Fig. 4.3.3) and both groupings occur within areas receiving relatively high rainfall (Section 1.3.4), the occurrence of *Sonneratia caseolaris*, in particular, has resulted in the slight separation of these groupings.

Group 12 includes waterways from seasonally arid regions of the survey area (refer Chapter 1). Although floristically most similar to each other, mangrove species diversity is quite limited. Only between 7-10 species principally from species groups 3, 4 and 5 (Table 4.3.1) occur. The Victoria ('Type 1'), Towns and Calvert Rivers ('Type 2') and the numerous coastal creeks ('Types 3, 4 and 5') all occur between latitudes 14-16^{o}S on both sides of the survey area.

Group 13 includes a small assemblage of waterways occurring along the western shores of the Gulf of Carpentaria. The Rose River (8 species), a 'Type 1' waterways, the Hart River (10 species) and Muntak Creek (11 species), both 'Type 3' waterways, differentiate from Groups 12 and 14 (Table 4.3.1) principally on the presence of *Scyphiphora hydrophyllacea* and *Bruguiera gymnorhiza*.

Group 14 is floristically most closely related to Groups 3 and 4 but also has close affinities with Groups 12 and 13. Included here are the Moyle River ('Type 1'), Barlee Impediment ('Type 3'), Annie River ('Type 4') and 'Archimedes' Creek ('Type 5'). Species diversity is relatively low with only between 4-7 species of mangroves in species groups 5 and 6 (Table 4.3.1). This grouping is considered to reflect both local site conditions and general seasonal aridity acting against species establishment.

In Group 15 are included most waterways of the Kimberley region in Western Australia - Glenelg, Roe and Prince Regent Rivers ('Type 1'); Gairdner, Mitchell, Lawley and Sale Rivers ('Type 2') and the George Water and Port Warrender ('Type 3') waterways. The Ord ('Type 1'), Fitzmaurice ('Type 2'), Port Keats and Port Paterson ('Type 3'), Charlotte and Ilamaryi Rivers and Iwalg Creek ('Type 4'), all occur around the north-western portion of the survey area (Fig. 4.3.1), whereas the remaining waterway in this grouping, the Limmen Bight River ('Type 1') occurs in the south-western portion of the Gulf of Carpentaria.

Between 11 and 14 mangrove species, principally from species groups 3, 4, 5 and 6 (Table 4.3.1) were recorded for these sites with the isolated occurrences of *Xylocarpus granatum* on the Prince Regent River and *Scyphiphora hydrophyllacea* on the Charlotte River, representing the westward limits of distribution of these species. The considerable seasonal aridity is considered to be a major factor limiting species diversity in the Kimberleys, Joseph Bonaparte Gulf region and on the Limmen Bight River. However, the decreased level of floristic diversity at Port Paterson, Charlotte and Ilamaryi Rivers and Iwalg Creek, all sites predominantly inundated by seawater, is considered to be principally the result of a lack of suitable sites for colonization by many of the other mangrove species that occur within this more northern latitudinal band (12-13^{o}S).

The analysis of the 82 systems has been truncated arbitrarily at the 12 group level (Fig. 4.3.5). Seven species groups were identified (Fig. 4.3.6), although some species groupings differ slightly from the seven species groups in the study of the 110 tidal waterways (Fig. 4.3.4). The ubiquitous group of species (Group 5) has remained relatively unchanged although here *Osbornia octodonta* has now been included. Species groups 3 (Table 4.3.1) and 6 (Table 4.3.2) are equivalent in both analyses although the more uncommon species now occur in groups 1-4 (Table 4.3.2) whereas in the analysis of the 110 tidal waterways these same species occurred in Groups 1-3 (Table 4.3.1).

Several of the site groupings are equivalent in both studies, however the study of the 82 tidal systems presents a tighter picture of floristic similarity and variation between latitudes and different climatic environments throughout the survey area. In grouping together all tidal waterways entering into a particular trunk stream, floristic variation between sites in a particular area are eliminated. Thus, the Victoria River System (Fig. 4.3.2) is taken to comprise the Victoria, Bullo, Baines and Angalarri Rivers, and the species used in this analysis are the pool of species common to this entire system.

MANGROVE SPECIES / TIDAL SYSTEM	Group I		Group 2	Group 3				Group 4				Group 5							Group 6			Group 7		
	Acanthus ilicifolius	*Ceriops decandra*	*Bruguiera gymnorhiza*	*Avicennia officinalis*	*Xylocarpus granatum*	*Bruguiera sexangula*	*Sonneratia caseolaris*	*Lumnitzera littorea*	*Ceriops tagal*	*Rhizophora apiculata*	*Scyphiphora hydrophyllacea*	*Avicennia marina*	*Excoecaria agallocha*	*Aegiceras corniculatum*	*Osbornia octodonta*	*Aegialitis annulata*	*Ceriops tagal var. australis*	*Rhizophora stylosa*	*Lumnitzera racemosa*	*Xylocarpus australasicus*	*Bruguiera exaristata*	*Camptostemon schultzii*	*Bruguiera parviflora*	*Sonneratia alba*
Group I																								
8. VICTORIA	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	○	●	○	○
11. MOYLE	○	○	○	○	○	○	○	○	○	○	○	●	●	○	○	●	●	●	○	○	○	●	○	○
64. YIWAPA	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	○	○	○	○
66. NAYARNPI	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	○	○	○	○
67. TOWNS	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	○	○	○	○
71. 'FARADAY'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	○	○	○	○
75. 'ARCHIMEDES'	○	○	○	○	○	○	○	○	○	○	○	●	○	○	○	●	●	●	○	○	○	○	○	○
76. 'GALILEO'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	○	○	○	○
82. CALVERT	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	●	○	○	○	○
Group 2																								
70. 'COULOMB'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	●	○	○	○
73. 'BOHR'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	●	○	○	○
74. 'PLANCK'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	●	○	○	○
77. FAT FELLOWS	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	●	○	○	○
79. 'EINSTEIN'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	○	●	○	○	○
80. 'NEWTON'	○	○	○	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	○	○	●	○	○	○
81. 'PAULI'	○	○	○	○	○	○	○	○	○	○	○	●	●	○	●	●	●	●	●	○	●	○	○	○
Group 3																								
32. GOOMADEER	●	●	●	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
34. MAJARIE	●	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	●	●	●	●	●
38. NGANDADAUDA	●	●	○	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
48. WARAWURUWOI	●	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
50. SLIPPERY	●	●	○	○	○	○	○	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
57. BURUNGBIRINUNG	●	●	○	○	○	○	○	○	○	○	●	●	●	●	○	●	●	●	●	●	●	●	●	●
Group 4																								
21. ADELAIDE	●	●	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
37. BLYTH/CADELL	●	●	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
41. DARBITLA	●	●	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
43. GLYDE	●	●	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
45. HUTCHINSON STRAIT	●	●	●	○	○	○	○	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
46. CADELL STRAIT	●	●	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
47. BUCKINGHAM/KALARWOI	●	●	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
Group 5																								
17. ANDRANANGOO	●	●	●	○	●	○	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●
18. JOHNSTON/BATH	●	●	●	○	○	○	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●
19. DONGAU	○	●	●	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○	●	●
20. TINANGOO	○	●	●	○	○	○	○	○	●	●	○	●	●	●	●	●	●	●	●	●	●	○	●	●
30. KING	●	●	●	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
35. NUNGBALGARRIE	●	●	●	○	○	○	○	○	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●
42. BENNET	○	●	●	○	○	○	○	○	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●
44. WOOLEN RIVER	●	●	●	○	○	○	○	●	○	●	●	●	●	●	●	●	●	●	○	●	●	●	●	●
58. MELVILLE BAY	●	●	●	○	●	○	○	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Group 6																								
36. LIVERPOOL/TOMKINSON	●	●	●	●	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
51. DARWARUNGA	●	●	●	○	○	○	○	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●
53. BARALMINAR/GOBALPA	●	●	●	○	○	○	○	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●

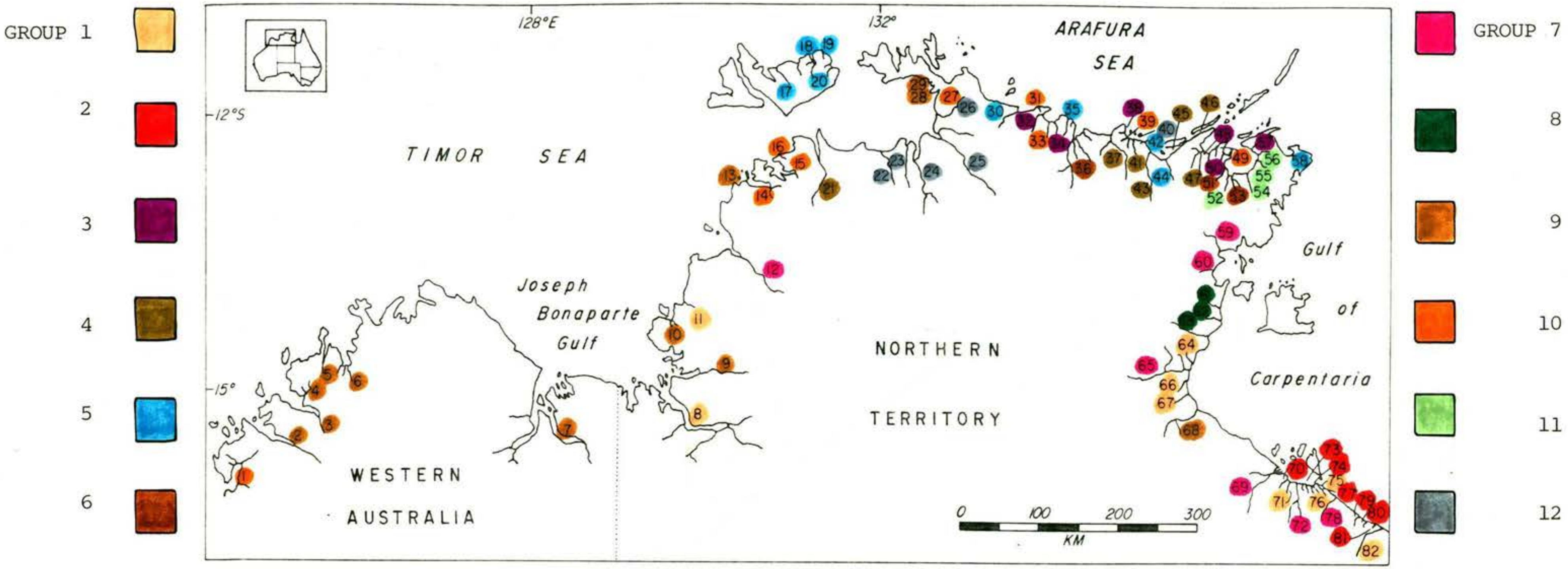
TABLE 4.3.2

Two-way table of site/species groups for the 82 tidal systems in the survey area. Group numbers refer to results of Multbet analysis, given for waterways in Fig. 4.3.5 and for spp. in Fig. 4.3.6.

TIDAL SYSTEM \ MANGROVE SPECIES	Group 1		Group 2	Group 3				Group 4				Group 5							Group 6			Group 7		
	Acanthus ilicifolius	*Ceriops decandra*	*Bruguiera gymnorrhiza*	*Avicennia officinalis*	*Xylocarpus granatum*	*Bruguiera sexangula*	*Sonneratia caseolaris*	*Lumnitzera littorea*	*Ceriops tagal*	*Rhizophora apiculata*	*Scyphiphora hydrophyllacea*	*Avicennia marina*	*Excoecaria agallocha*	*Aegiceras corniculatum*	*Osbornia octodonta*	*Aegialitis annulata*	*Ceriops tagal var. australis*	*Rhizophora stylosa*	*Lumnitzera racemosa*	*Xylocarpus australasicus*	*Bruguiera exaristata*	*Camptostemon schultzii*	*Bruguiera parviflora*	*Sonneratia alba*
Group 7																								
12. DALY	●	○	○	○	○	○	○	○	○	○	○	●	●	●	○	●	○	●	●	●	●	●	○	○
59. KOOLATONG	●	○	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○
60. WALKER	●	○	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	●	○
65. ROPER	●	○	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○
69. McARTHUR	●	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	○
72. WEARYAN	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	○	○
78. ROBINSON	○	○	○	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	○	○	○
Group 8																								
61. HART	○	○	○	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	●	○	○	○
62. MUNTAK	○	○	●	○	○	○	○	○	○	○	●	●	●	○	●	●	●	●	●	●	●	○	○	○
63. ROSE	○	○	●	○	○	○	○	●	○	○	●	●	●	○	●	○	○	●	○	●	○	○	○	○
Group 9																								
2. PRINCE REGENT	○	○	○	○	●	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
3. ROE	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
4. HUNTER	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
5. MITCHELL	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
6. PORT WARRENDER	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
7. ORD	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	●
9. FITZMAURICE	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	○
10. PORT KEATS	○	○	○	○	○	○	○	○	○	○	○	●	○	●	●	●	●	●	●	●	○	●	●	●
13. PORT PATERSON	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
28. IWALG	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	●
29. ILAMARYI	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	○	●	●
68. LIMMEN BIGHT	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	○
Group 10																								
1. GEORGE WATER	○	○	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	●	●	●	●	●
14. BYNOE HARBOUR	○	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●
15. DARWIN HARBOUR	○	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●
16. BUFFALO	○	○	●	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
27. MINI MINI	○	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
31. ARRLA	○	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
33. WURUGOIJ	○	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	●	●	●	●	●
39. DJABURA	○	●	○	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
49. KURALA	○	●	●	○	○	○	○	○	○	○	○	●	●	●	●	●	●	●	○	●	●	●	●	●
Group 11																								
52. HABGOOD	●	●	●	○	○	○	●	○	●	●	○	●	●	●	○	●	●	●	●	●	●	●	●	●
54. GOROMUPU	●	●	●	○	○	○	●	○	●	○	○	●	●	●	○	●	●	●	●	●	●	●	●	●
55. CATO	●	●	●	○	○	●	●	○	●	●	○	●	●	●	●	●	●	●	●	●	●	●	●	●
56. PETER JOHN	●	○	○	○	○	●	●	○	○	●	●	●	●	●	●	○	●	●	●	●	●	●	●	●
Group 12																								
22. WILDMAN	●	●	○	●	○	○	●	○	○	○	○	●	●	●	○	●	●	●	●	●	●	●	●	●
23. WEST ALLIGATOR	●	●	●	●	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	●
24. SOUTH ALLIGATOR	○	○	○	●	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	○	●
25. EAST ALLIGATOR	●	○	○	●	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
26. MURGENELLA	●	●	○	●	○	○	●	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●
40. DJIGAGILA	●	●	○	●	○	○	○	○	○	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●

TABLE 4.3.2 (contd)

Two-way table of site/species groups for the 82 tidal systems in the survey area.



1 GEORGE WATER
2 PRINCE REGENT
3 ROE
4 HUNTER
5 MITCHELL
6 PORT WARRENDER
7 ORD
8 VICTORIA
9 FITZMAURICE
10 PORT KEATS
11 MOYLE
12 DALY
13 PORT PATERSON
14 BYNOE HARBOUR
15 DARWIN HARBOUR
16 BUFFALO
17 ANDRANANGOO
18 JOHNSTON/BATH
19 DONGAU
20 TINGANOO
21 ADELAIDE
22 WILDMAN
23 WEST ALLIGATOR
24 SOUTH ALLIGATOR
25 EAST ALLIGATOR
26 MURGENELLA
27 MINI MINI
28 IWALG
29 ILAMARYI
30 KING
31 ARRLA
32 GOOMADEER
33 WURUGOIJ
34 MAJARIE
35 NUNGBALGARRIE
36 LIVERPOOL/TOMKINSON
37 BLYTH/CADELL
38 NGANDADAUDA
39 DJABURA
40 DJIGAGILA
41 DARBITLA
42 BENNET
43 GLYDE
44 WOOLEN RIVER
45 HUTCHINSON STRAIT
46 CADELL STRAIT
47 BUCKINGHAM/KALARWOI
48 WARAWURUWOI
49 KURALA
50 SLIPPERY
51 DARWARUNGA
52 HABGOOD
53 BARALMINAR/GOBALPA
54 GOROMURU
55 CATO
56 PETER JOHN
57 BURUNGBIRINUNG
58 MELVILLE BAY
59 KOOLATONG
60 WALKER
61 HART
62 MUNTAK
63 ROSE
64 YIWAPA
65 ROPER
66 NAYARNPI
67 TOWNS
68 LIMMEN BIGHT
69 McARTHUR
70 'COULOMB'
71 'FARADAY'
72 WEARYAN
73 'BOHR'
74 'PLANCK'
75 'ARCHIMEDES'
76 'GALILEO'
77 FAT FELLOWS
78 ROBINSON
79 'EINSTEIN'
80 'NEWTON'
81 'PAULI'
82 CALVERT

FIG. 4.3.7

Distribution of site groups from the Multbet analysis for the 82 tidal systems in the survey area based on variations in floristic diversity of mangrove species.

Group 1 (Fig. 4.3.7) includes the Victoria, Moyle, Towns and Calvert systems, as well as several short coastal systems along the south-western shores of the Gulf of Carpentaria. All of these systems lie within seasonally extremely arid regions of the survey area (Chapter 1) and this shows in a marked reduction in species diversity.

Group 2 includes several more coastal systems along the south-western shores of the Gulf of Carpentaria (Fig. 4.3.7). From an inspection of Table 4.3.2, it is seen that this group is floristically most similar to Group 1. As these systems also lie in seasonally arid regions of the survey area, there is considerable merit in fusing Groups 1 and 2 as systems of low species diversity occurring along quite seasonally arid coastlines.

Groups 3, 4, 5 and 6 are themselves floristically most similar to each other (Fig. 4.3.5, Table 4.3.2), and includes systems occurring across the northern coastline of the Northern Territory (Fig. 4.3.7). Sites within these groupings possess between 15-21 species, although it is apparent that irregular occurrences of less commonly recorded species (in species groups 2, 3 and 4 of Table 4.3.2) do not in any way distract from the overall pattern and groupings. Floristically, site groups 3, 4, 5 and 6 have on average at least twice the number of mangrove species as Groups 1 and 2.

Groups 7 and 8 (Fig. 4.3.5) are also closely related floristically to groups 1 and 2, and although considerably less diverse in species than Groups 3, 4, 5 and 6 (Table 4.3.2) have separated principally on irregular occurrences of *Acanthus ilicifolius*, *Bruguiera gymnorhiza*, *Camptostemon schultzii*, *Bruguiera parviflora*, *Lumnitzera littorea* and *Scyphiphora hydrophyllacea*. Increasing levels of seasonal aridity in these regions of the survey area are considered to be largely responsible for irregular occurrences of the latter mentioned species.

Groups 9 and 10, also quite similar, separate from each other principally on occurrences of *Ceriops decandra*, *Bruguiera gymnorhiza* and *Scyphiphora hydrophyllacea* - present only in Group 10 (Table 4.3.2). These groupings include all systems from the Kimberleys, in Western Australia, and some sites from Joseph Bonaparte Gulf and the northern coastline of the Northern Territory (Fig. 4.3.7).

Groups 11 and 12 represent systems, with the exception of Djigagila, which occur either within Arnhem Bay or Van Diemen Gulf on the northern coastline of the Northern Territory (Fig. 4.3.7) where the regionality of these two groups is dramatically shown. Floristically these systems are most similar to each other and have recorded between 14-20 mangrove species. The Groupings shown in Fig. 4.3.5 and Table 4.3.2 have been made principally on sporadic occurrences of many of the less frequently observed mangrove species in the survey area. The occurrence of *Sonneratia caseolaris* is considered as a major distinguishing species for both these groups from other groupings in this analysis and the additional presence of *Avicennia officinalis* at all sites in Group 12 only, has resulted in the splitting of Group 11 from Group 12.

4.4 DISCUSSION

As discussed in Chapter 2, there is a gradual loss of mangrove species as higher latitudes are attained down both the east and west coasts of Australia. At sites across the northern coastline of the Northern Territory (latitudes 11-13°S), although 27 mangrove species have been recorded (Section 1.2.2), the mangrove fern *Acrostichum speciosum*, the Ebony mangrove *Diospyros ferrea* var. *humilis* and the vine *Derris trifoliata* have not been included in the analyses. However only between 10-14 mangrove species are recorded at sites in the survey area between latitudes 13-16°S. This considerable loss in species diversity within only a few degrees of latitude is unusual and is not actually considered to result from latitudinal sifting, as on the east Australian coastline within an identical latitudinal range there is no real loss in species diversity (cf. Dowling and McDonald, 1982).

It has been shown (Chapter 2) that many mangrove species recorded in the survey area are disadvantaged in their ability to colonize all regions of this area due to the presence of unfavourable currents (Fig. 1.3.6) during the 'wet' season, this being the period when most fruiting occurs (Fig. 5.1, Table 5.1). However, during cyclonic storms, surface current directions are often reversed for considerable periods (Aust. Pilot Vol.5, p.13). It is considered that floating fruits and hypocotyls of those mangrove species with restricted discontinuous distributions across the northern coastline of the Northern Territory could theoretically reach all regions of the survey area. That all species recorded in this study do not occur at all sites is of considerable interest and in conjunction with reasons advanced in Chapter 2, this chapter attempts site-by-site and regional analyses of variations in mangrove species diversity throughout the survey area.

The acceptance of three major site groupings (A,B,C) in Figs. 4.3.1 and 4.3.3 for the 110 tidal waterways and in Figs. 4.3.2 and 4.3.5 for the 82 tidal systems provides in a broad sense many groupings that appear to reflect local climatic variations within the survey area. By grouping all mangrove species recorded in a series of waterways that merge into a common trunk stream (i.e. a system), a much tighter picture of the level of floristic diversity for particular regions is provided. A discussion of the results from Figs. 4.3.2 and 4.3.5 and Table 4.3.2 in particular, is then considered most appropriate as much "between system" variation appears largely explicable by climatic variations in the survey area.

Sites occurring in Group A (Fig. 4.3.2) show the lowest level of floristic diversity. They occur only within the Gulf of Carpentaria and Joseph Bonaparte Gulf regions and are indicative of sites subjected to considerable seasonal aridity. Although the degree of seasonal aridity has been shown (Chapter 1) to be greater within these portions of the survey area, such aridity is not the only factor responsible for much of the low floristic diversity of mangrove species in this area. The Daly River drains a large catchment area (51,800km^2) and remains fresh above km40 throughout most years (Messel *et al.* 1979) and the lack of suitable brackish water sites for species establishment has resulted in only 10 species being recorded on this system. In fact, the Daly River System, although occurring in what has been shown (Fig. 1.3.4) as nearly the wettest region, has amongst the lowest diversity of mangrove species for any site in the survey area. *Rhizophora stylosa*, a species which is fairly ubiquitous at most other sites, is only represented here by an occasional shrub, while absence of *Ceriops tagal* var. *australis* is most likely related to the nearly perennial freshwater inundation of sites. As Macnae (1966), in particular, has pointed out, *Ceriops tagal* var. *australis* is often absent or infrequently observed on what are considered "continually wet" portions of coastlines.

Sites occurring in Group B are distributed almost entirely adjacent to the Arafura and Timor Seas and are intermediate in floristic diversity between Groups A and C. The low diversity for sites within the Kimberley region of Western Australia (up to 14 species) and from the Joseph Bonaparte Gulf (up to 12 species) appears to be largely a response to considerable seasonal aridity experienced in these regions. However, a lack of suitable sites for colonization by many mangrove species due to rapidly rising land gradients and macro-tidal fluctuations (up to 11 metres) in many tidal waterways in the Kimberleys and unfavourable surface sea currents during fruiting periods are also considered as contributing factors influencing species establishment here.

Other sites in Group B, such as Port Paterson, Bynoe and Darwin Harbours, Buffalo, Mini Mini, Iwalg, Arrla, Wurugoij and Djabura Creeks; Ilamaryi and Kurala Rivers, although occurring across the northern coastline of the Northern Territory - a less seasonally arid area - are also quite poor in mangrove species. In Chapter 3 it was shown that all of the above mentioned sites experienced seawater salinities for most of the year and in some cases even became quite hypersaline by the end of the 'dry' season. It is considered that these saline conditions have limited the number of mangrove species able to establish at such sites due to an absence of quite specific habitats required for colonization of a number of mangrove species and their physiological inability to withstand prolonged periods of hypersaline or seawater inundation. Differentiation of Group B is due to an occurrence of *Camptostemon schultzii* - a species that has not otherwise been recorded from any system within the survey area in the Gulf of Carpentaria. Only the occasional shrub of this species occurs on the Limmen Bight system and the grouping away from other sites in the Gulf of Carpentaria on the basis of what may be a chance occurrence should be viewed with some caution. Reasons for absence of *Camptostemon schultzii* at other sites in the Gulf of Carpentaria are unknown although it is considered that its absence here and the extreme rarity of the species at sites around Joseph Bonaparte Gulf may be related to a slightly higher level of seasonal aridity and greater occurrences of desiccating south-east trade winds during the dry season. *Camptostemon schultzii* is, however, extremely abundant in mangrove swamps throughout the Kimberley region of Western Australia, which although experiencing considerable seasonal aridity, is largely protected from the south-east trade winds (blowing across from the interior of the Australian continent) by the high cliffs (~300 metres) abutting mangrove swamps here.

Group C sites are floristically most diverse with between 14-21 species. Such sites occur only across the northern coastline of the Northern Territory (11-12°S latitude). These sites are in regions receiving considerable annual precipitation and most also receive at least a minimal amount of precipitation throughout the 'dry' season months(Fig. 1.3.3). For Group C sites mean annual relative humidities are generally higher (Fig. 1.3.1) and mean annual evaporation losses much lower than for sites occurring throughout the Gulf of Carpentaria, Joseph Bonaparte Gulf and Kimberley regions.

Although the species/site groupings in Table 4.3.1 show many interesting patterns, it is important to appreciate, for the 110 tidal waterways, that much floristic variation between sites and subsequent grouping of these sites is largely dependent on geographical locality and 'type' of a waterway within any particular tidal system.

It is considered that species/site groupings given in Table 4.3.2, in particular, are greatly influenced by climatic variations within the survey area. Many other factors have been noted, particularly in Chapters 2 and 3, as influencing floristic diversity of mangrove species at certain sites, however local climatic conditions and their effects on tidal waterways appear to be largely responsible for present variations in species diversity throughout the survey area at regional levels.

An understanding of how climatic and other factors influence floristic diversity of mangroves at certain sites involves knowledge of environmental controls operating on the dispersal, survival, growth and reproduction in individual mangrove species. The following three chapters attempt to provide more information about environmental controls for some species and are concerned with flowering and fruiting (Chapter 5), size of surviving plants and population structure in relation to site characteristics (Chapter 6) and daily and seasonal variation of the xylem pressure potentials of individual mangrove species (Chapter 7).

The extent to which this leads to a better understanding of variation in species composition regionally and between sites is discussed particularly in the concluding chapter (Chapter 8).

CHAPTER 5

Flowering and fruiting periods of mangrove species across the northern coastline of the Northern Territory.

5.1 Introduction
5.2 Methods
5.3 Results
5.4 Discussion

5.1 INTRODUCTION

Limited information is available on flowering and fruiting periods of mangrove species in Australia. Studies in particular by Jones (1971a), Graham *et al*. (1975), Byrnes *et al* (1977), Specht *et al* (1977), Tomlinson *et al*. (1978, 1979), Duke and Bunt (1979), and Saenger (1982) record some information for species along the Queensland coastline (often at specific localities) and Semeniuk *et al* (1978) provides information on species occurring along the west Australian coast. For the north Australian coastline (this study), negligible information on flowering/fruiting periods has hitherto existed, except for occasional notes on some specimens lodged with the Northern Territory Herbarium (Darwin).

Many species of mangroves occurring throughout a wide latitudinal range and in different biogeographic areas down both the east and west coasts of the continent, show considerable variation in flowering/fruiting periods. Reasons for such variation, especially in flowering periods, are unknown although stimuli known to trigger flowering such as photoperiod and temperature shock as reviewed by Leopold (1964), Salisbury and Ross (1969) and Whitmore (1975) among others, may provide explanations. For each species variations in flowering/fruiting periods may well be a response to different climates experienced throughout its latitudinal range enabling a species to take advantage of periods of the year most favourable to growth.

The present study is concerned primarily with delineating the flowering and fruiting periods of twenty-four mangrove species occurring across the northern coastline of the Northern Territory. In addition, similarities and differences between these periods and flowering/fruting periods of some species that also occur in other regions around the Australian continent are discussed.

5.2 METHODS

Throughout the years 1975 - 1979 flowering and fruiting periods of the twenty-four mangrove species were determined by direct observation on tidal waterways (nos. 27 - 80) that lie within the survey area. These waterways are shown in Fig. 1.2.1.

Numerous mangrove specimens from sites throughout this area have been lodged with the Northern Territory Herbarium, Darwin.

Flowering periods refer to times when the various mangrove species were observed flowering.

Fruiting periods refer to the actual times when mature fruits, seeds or propagules were observed falling from the various species. Lists of insects, birds, and mammals that pollinate the various mangrove species are also based upon direct observation both during the day and night.

Flowering/fruiting percentages given in this chapter should be considered with some caution as only minimum estimates are provided for some species due to lack of observations in certain months. The percentages are considered as providing general indications only.

5.3 RESULTS

Flowering and fruiting periods of mangrove species in the survey area are shown in Table 5.1. Calculations of the number of spp. and percentage of the mangrove flora flowering and fruiting over each month are shown in Fig. 5.1 and Tables 5.2 and 5.3.

Table 5.4 shows variations in flowering and fruiting periods of *Avicennia marina* and *Aegiceras corniculatum* at selected regions around the Australian continent and the north island of New Zealand.

Both within- and between-site variations occur in flowering/fruiting periods in the study area. This is particularly so in species such as *Avicennia officinalis* that possess very restricted flowering and fruiting periods. In *A. officinalis*, flowering has been observed to commence on the Adelaide River up to three weeks earlier than on the Liverpool/Tomkinson River System (Fig. 1.2.1). (Both systems lie at equivalent latitude.) Reasons for such variation are unknown, although they may be specific to a certain population of a species in a particular area. Wium-Anderson (1981) also reports regional periodicity - but for falling propagules of *Rhizophora mucronata* in southern Thailand over a distance of only 60 km. *Avicennia marina*, on the other hand, commences flowering throughout the study area in mid October (Table 5.1) and detailed observations on the Liverpool/Tomkinson Rivers System show that flowering is initiated simultaneously in trees of this species growing over a wide range of salinities (i.e., in sites inundated by freshwater, brackish water, seawater or hypersaline water). Alwin (1964) has described this phenomenon for tropical trees as "gregarious flowering". Furthermore, according to Koriba (1958), intraspecific seasonality must be expected due to differences in monsoon regimes which for this survey area are discussed in section 1.3.4.

Most mangrove species in the study area (71%) are pollinated in some circumstances by insects, and these include:

Acanthus ilicifolius
Avicennia marina
Avicennia officinalis
Camptostemon schultzii
Lumnitzera racemosa
Xylocarpus australsicus
Xylocarpus granatum
Aegiceras corniculatum
Osbornia octondonta
Aegialitis annulata
Bruguiera parviflora
Ceriops decandra
Ceriops tagal var. *australis*
Ceriops tagal
Rhizophora apiculata
Rhizophora stylosa
Scyphiphora hydrophyllacea

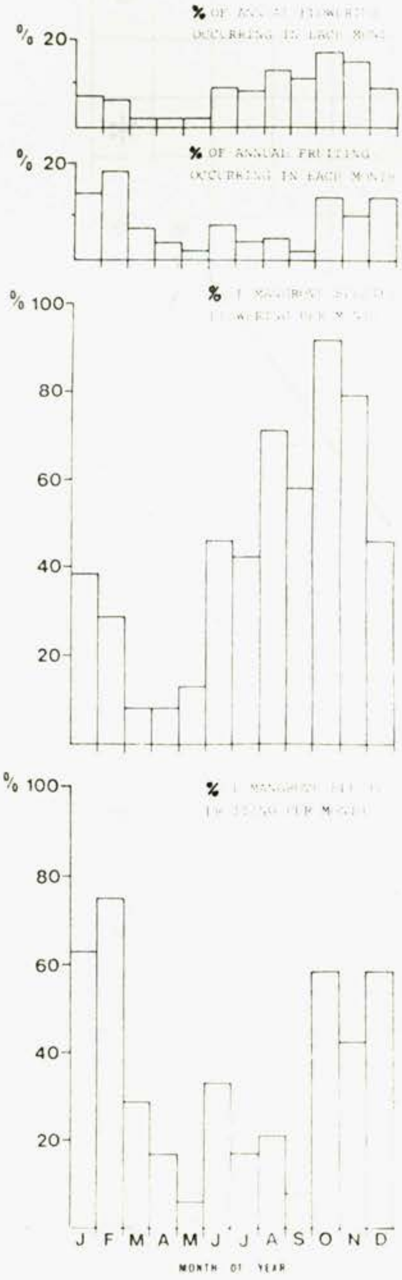


FIG. 5.1

Monthly occurrence of flowering/fruiting percentages of mangrove species occurring across the northern coastline of the Northern Territory during the period 1975-1979.

● FLOWERING ○ FRUITING

Mangrove Species	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Acanthus ilicifolius	● ○	● ○				●		●	●	● ○	● ○	● ○
Avicennia marina	● ○	○	○							●	●	●
Avicennia officinalis	○	● ○						●	●	●	●	
Camptostemon schultzii	● ○	○				●	●	●		●	●	● ○
Lumnitzera littorea	*	*	*	*	*			●	●	● ○		*
Lumnitzera racemosa	○	○				○				●	●	●
Excoecaria agallocha	● ○	○								●	●	●
Xylocarpus australasicus	○	○	○			● ○	●	● ○	●	●		○
Xylocarpus granatum	*	○				○		● ○		○	○	*
Aegiceras corniculatum	○	○	○	○			○	●	●	●	●	○
Osbornia octodonta	● ○	● ○	○	○							●	● ○
Aegialitis annulata	○	○							●	●	●	● ○
Bruguiera exaristata	● ○	● ○	● ○	● ○	● ○	●	●	● ○	●	●	● ○	● ○
Bruguiera gymnorhiza	○	○	○	○		●	●	●	●	● ○	○	○
Bruguiera parviflora	○	○				● ○	●	●	●	● ○	●	○
Bruguiera sexangula	*	*	*	*	*	●	*	*	*	● ○	○	○
Ceriops decandra	○	○	○			○	○	● ○	● ○	● ○	● ○	*
Ceriops tagal var. *australis*	● ○	● ○						●	●	● ○	●	● ○
Ceriops tagal	*	*	*	*	*	*	○	●	● ○	● ○	●	
Rhizophora apiculata	*	*	*			●	●			● ○	● ○	*
Rhizophora stylosa	● ○	● ○	●	●	● ○	● ○	● ○	● ○	●	● ○	● ○	● ○
Scyphiphora hydrophyllacea							●	●		● ○	● ○	○
Sonneratia alba	● ○	● ○			●	● ○	●	●	●	● ○	●	● ○
Sonneratia caseolaris	*	*	*	*	*	● ○	●	●	*	● ○	● ○	*

MONTH OF YEAR

TABLE 5.1

Monthly occurrence of flowering/fruiting of mangrove species across the northern coastline of the Northern Territory as observed during the period 1975-1979 (* indicates no observation).

Lumnitzera littorea is pollinated by various species of honeyeaters as well as insects (bees and wasps) whereas *Bruguiera exaristata* is pollinated principally by the red-headed honeyeater (*Myzomela erythrocephala*). *Bruguiera gymnorhiza* is pollinated by insects and the bee-eater (*Megalops ornatus*) and *Bruguiera sexangula* by insects and possibly by birds, although this has not been observed.

Excoecaria agallocha is dioecious - bearing extremely small flowers in catkins - and is presumed by Clifford and Specht (1979) to be wind-pollinated. Tomlinson *et al.* (1979), also consider the various *Rhizophora* sp. to be largely wind-pollinated. *Sonneratia alba* and *Sonneratia caseolaris* both possess large showy flowers with numerous long stamens (≃ 200 per flower) and produce copious amounts of slightly sticky pollen, which is released at dusk when the flower opens (Muller, 1969). This pollen is dispersed by small nectar-feeding bats - *Macroglossus* sp. - in the study area (Faegri and van der Pijl, 1971; pers. obs.), which alight upon flowers usually for an extremely short time (2-3 seconds).

Along the northern coastline of the Northern Territory, flowering of the twenty-four mangrove species present is most pronounced during the mid to late 'dry' season (August - November). During this period 56% of all flowering occurs (Table 5.2.). *Bruguiera exaristata* and *Rhizophora stylosa* were the only species observed flowering on an all year round basis (100%), although *Sonneratia alba* (83%), *Acanthus ilicifolius* (67%), *Camptostemon schultzii* and *Ceriops tagal* var. *australis* (58%) each have quite extended flowering periods. All remaining species flower for less than 50% of the year (Tables 5.1, 5.3), with the shortest flowering period (25%) being recorded for *Lumnitzera racemosa*.

Fruiting is most pronounced during the late 'dry' season and throughout the greater period of the 'wet' season (October - February) when 71% of all fruiting occurs (Table 5.2). No species were observed fruiting over an entire year, although *Rhizophora apiculata* and *Rhizophora stylosa* frequently possess hypocotyls at different stages of development

FLOWERING

N = 24 species	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Number of mangrove species flowering	9	7	2	3	3	11	10	17	14	22	19	11
Percentage of spp. in flower	38	29	8	8	13	46	42	71	58	92	79	46
Percentage of spp. in flower in the month/ Total for 12 months of no. of spp. in flower each month	7	6	2	2	3	9	8	13	11	17	15	9

FRUITING

N = 24 species	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Number of mangrove species fruiting	15	18	7	4	2	8	4	5	2	14	10	14
Percentage of spp. in fruit	63	75	29	17	8	33	17	21	8	58	42	58
Percentage of spp. in fruit in the month/ Total for 12 months of no. of spp. in fruit each month	15	18	7	4	2	8	4	5	2	14	10	14

Table 5.2 Calculations of the number of spp., percentage of the mangrove flora flowering and fruiting in each month and percentages of annual flowering occurring in each month along the northern coastline of the Northern Territory (data from Table 5.1).

Mangrove Species	FLOWERING % of year	FRUITING
Acanthus ilicifolius	67	42
Avicennia marina	33	25
Avicennia officinalis	42	17
Camptostemon schultzii	58	25
*Lumnitzera littorea**	25	8
Lumnitzera racemosa	25	25
Excoecaria agallocha	33	17
Xylocarpus australasicus	42	50
*Xylocarpus granatum**	8	42
Aegiceras corniculatum	33	50
Osbornia octodonta	33	42
Aegialitis annulata	33	25
Bruguiera exaristata	100	67
Bruguiera gymnorhiza	42	58
Bruguiera parviflora	50	42
*Bruguiera sexangula**	17	25
Ceriops decandra	33	75
Ceriops tagal var. *australis*	58	33
Ceriops tagal	33	25
*Rhizophora apiculata**	33	17
Rhizophora stylosa	100	75
Scyphiphora hydrophyllacea	33	25
Sonneratia alba	83	42
*Sonneratia caseolaris**	42	25

Table 5.3. Flowering and fruiting periods as percentage of year for mangrove species on the northern coastline of the Northern Territory (data from Table 5.1). Species marked * are minimum estimates due to limited observation periods.

hanging from fruits. *Rhizophora stylosa* and *Ceriops decandra* were observed fruiting for 75% of the year, the only other species fruiting for periods greater than 50% of the year being *Bruguiera exaristata* (67 %) and *Bruguiera gymnorhiza* (58%) (Tables 5.1, 5.3). The shortest fruiting periods were *Avicennia officinalis* and *Excoecaria agallocha*, which were recorded fruiting for only 17% of the year.

Flowering and fruiting periods for *Lumnitzera littorea*, *Xylocarpus granatum*, *Bruguiera sexangula*, *Ceriops tagal* and *Sonneratia caseolaris* are minimum estimates as, due to their restricted distributions, it was not possible to observe these species over all months of the year.

From Fig. 5.1 and Table 5.3, it is evident that a flowering period between 31 - 40% of the year is most common with 37.5% of species flowering for this length of time. In Fig. 5.1 and Table 5.3, however, the most favoured fruiting period is between 21 - 30% of the year and 33.3% of species fruit for this time. No clear trends are apparent from Table 5.3, although distinctions between the more or less regular periodic flowering periods of most species and the continuous flowering periods of *Bruguiera exaristata* and *Rhizophora stylosa* can be made.

Considerable variation in flowering/fruiting periods for particular species occurs around the Australian coastline. In the most dramatic example, *Avicennia marina*, flowering is recorded from November - January in the north-west Kimberley region of Western Australia (Semeniuk *et al.*, 1978); October - January throughout the Northern Territory (this study) and also October - January for the Port Curtis district, Queensland (Saenger, 1982). In Sydney, NSW, flowering occurs much later, during March to mid May (with a flowering peak in March) (Goulter 1977; Goulter and Allaway, pers. comm.), and at Bunbury, Western Australia during March to May (Semeniuk *et al.*, 1978). In

	West Australia Kimberley region (15°S) (Semeniuk *et al.*, 1978)		West Australia Bunbury (33°S) (Semeniuk *et al.*, 1978)		Northern Territory Northern Coastline (12°S) (this study)		Queensland Port Curtis (23°S) (Saenger, 1982)		New South Wales Sydney (33°S) (Clarke & Hannon, 1969) (Goulter & Allaway, pers. comm.)		New Zealand Auckland (37°S) (Chapman, pers. comm.)	
	FLOWERING	FRUITING	FLOWERING	FRUITING	FLOWERING	FRUITING	FLOWERING	FRUITING	FLOWERING	FRUITING	FLOWERING	FRUITING
Avicennia marina	Nov-Jan	Jan-Mar	May-Mar	Dec	Oct-Jan	Jan-Mar	Oct-Jan	Jan-Mar	Mar-mid May	Nov-mid Jan	Mar-June	Dec-Jan
Aegiceras corniculatum	May-Dec				Aug-Sep	Dec-July	July-Feb	Nov-Mar	Jan-Feb	May		
First flowering to first fruiting (*Avicennia marina*)	2 months		9 months		3 months		3 months		8 months		9 months	
Last flowering to last fruiting (*Avicennia marina*)	3 months		7 months		3 months		3 months		8 months		7 months	
Flowering period (*Avicennia marina*)	3 months		3 months		4 months		4 months		2½ months		4 months	
Fruiting period (*Avicennia marina*)	3 months		1 month		3 months		3 months		2½ months		2 months	

Table 5.4 Flowering and fruiting periods of *Avicennia marina* and *Aegiceras corniculatum* at selected localities in Australia and New Zealand.

Westernport Bay, Victoria, flowering occurs only in some years, and is then during August-September (Attiwill, pers. comm.). The species thus shows the general trend of later flowering in its occurrence at higher latitudes down both the east and west coasts of the continent. Chapman's observations in New Zealand (pers. comm.) also conform to this picture.

Table 5.4 provides some data on flowering and fruiting periods of *Avicennia marina*, and it should be noted that whereas across the northern portion of the continent, a flowering period extends for an average of c.17 weeks in the Sydney district this period only averages c.10 weeks In fruiting, *Avicennia marina* fruits on average for c.13 weeks across the northern portion of the continent but for only c.10 weeks in the Sydney district. The time from first flowering to first fruiting averages c.17 weeks across the north, however c.35 weeks elapse for this same process in the Sydney district. Also, from last flowering to last fruiting takes c.8 weeks in the north but c.35 weeks are required for this process to be achieved in Sydney. Such variations in flowering/ fruiting strategies for *Avicennia marina*, in particular the doubling of the time required between first flowering and first fruiting and last flowering and last fruiting between populations of this species inhabiting the northern portions of the continent and those occurring at higher latitudes (e.g., Sydney, NSW; Bunbury, W.A.) perhaps indicates greater environmental and physiological stresses in this species affecting reproduction toward the edges of its range in southern Australia. In Westernport Bay, Victoria - at the near southern extremity of its range - shrubs of *Avicennia marina* only flower every two or three years (Clough, pers. comm.).

5.4 DISCUSSION

Evidence of seasonal variations in flowering and fruiting of plant species within tropical climates is reviewed by Whitmore (1975) and is based on numerous studies carried out in west Malaysia, Sarawak and Singapore. For many lowland rainforest tree species, it was shown that marked seasonal cycles in flowering and fruiting could be correlated with changes in water supply. Of particular interest was the finding that flowering was often promoted by water stress.

For the mangrove environment, little is known although besides photoperiod, other factors such as water stress, tidal cycles and salinity regimes may influence flowering and fruiting periods of populations of a particular species in a certain region. Clarke and Hannon (1969) found - for the Sydney, NSW, district - that dispersal of *Aegiceras* fruits coincided with unusually high tides at a certain period of the year, whereas fruit fall of *Avicennia marina* coincided with low tides at another time of year.

It has often been argued that it is advantageous for a species to have individuals blossom together. In this way, cross-pollination between indivuals of a particular species will maintain high variability and this appears to occur in most species of long-lived trees (Stebbins, 1950). Of particular interst, then, are the various methods of pollination discussed in Section 5.3. In the study area, flowering periods of most mangrove species occur towards the end of the "dry" season (Fig. 5.1). Such flowering periods are perplexing, as it is during this period of the year that insect activity is minimal (when compared to the incessant insect activity during the "wet" season). Tomlinson *et al.*, (1979) however consider that the mangrove environment is edaphically suited to winter flowering, since trees are not limited by soil moisture. Most fruiting, however, of the various species occurs during the "wet" season when tidal inundation is more pronounced (refer to Section 1.3.8), and a greater range of sites are available for colonization. As Bunt (1982) shows for the mangrove species on the east Queensland coastline, this is also the period of the year that appears most favourable for growth.

Although it would seem disadvantageous for most mangrove species to flower during the 'dry' season, this possible handicap is outweighed by the advantages of fruiting periods during the 'wet' season. If the timing of fruiting and thus dispersal of seedlings is paramount, it would suggest that establishment and early growth of seedlings may be particularly critical for survival of many mangrove species in the study area. It has also been suggested by numerous workers - in particular Whitmore (1975) - that continuous flowering and fruiting, as occurs amongst many rainforest trees, may confer some ecological advantages to a species. Whitmore states that this condition occurs especially amongst many pioneer rainforest species in south-east Asia. For mangroves it is seen from Tables 5.1 and 5.3, that *Rhizophora stylosa* and *Sonneratia alba* have lengthy flowering and fruiting periods. Both these species are also often pioneers colonizing newly accreting mudbanks in the study area and perhaps some advantages do accrue to these lengthy flowering and fruiting periods in the study area. However, *Avicennia marina* *Avicennia officinalis*, *Acanthus ilicifolius* and *Aegiceras corniculatum* also may occur as pioneering species, although these latter species have much shorter flowering and fruiting periods. The year-round flowering of *Bruguiera exaristata* is also unusual as this species has never been observed to form a pioneer zone.

Likewise in fruiting periods, *Ceriops decandra*, which fruits for 75% of the year, has never been observed as a pioneering species. Overall it does not appear that any of the mangrove species in the study area gain any real advantage over each other by having either short or long periods of flowering and fruiting. Advantages in fruiting during the 'wet' season do seem to exist for some species - particularly the Rhizophoraceae - as seedling establishment at this time of year appears to result in considerably less predation from sesarmid crabs in particular.

The predation of hypocotyls and small seedlings by sesarmid crabs appears greatest during the 'dry' season when saline waters occur throughout most portions of tidal waterways. During the 'wet' season, saline waters are largely flushed from the waterways by freshwaters entering the systems from areas of upstream drainage, and sesarmid crabs either die or migrate downstream with the saline waters. Thus, along portions of waterways that remain fresh for considerable periods of the year, seedling establishment (from the Rhizophoraceae) tends to proceed relatively unhindered by predators. During the next 'dry' season sesarmid crabs gradually recolonize areas as saline waters again penetrate upstream and have often been observed eating even established seedlings from the base of the upright hypocotyl.

Although some mangrove species appear to benefit by fruiting during the 'wet' season, other species - *Avicennia* spp. - *marina* and *officinalis*; *Xylocarpus* spp. - *australasicus* and *granatum* and *Sonneratia* spp. *alba* and *caseolaris* - seem prone to considerably greater insect attack during the 'wet' than during the 'dry' season.

Seedlings of these species also establish quite readily along waterways during this period of the year but boring insects destroy large numbers of fruits, seeds and seedlings. The fruits of *Lumnitzera racemosa* have been found in considerable quantity (at certain times of the year) amongst stomach contents pumped from juvenile saltwater crocodiles (*Crocodylus porosus*) (Taylor, 1977), although this animal may ingest such fruits inadvertently due to its shallow water feeding habit.

In some species of mangroves variations in flowering/fruiting periods are difficult to explain. In *Camptostemon schultzii*, flowering periods differ even between populations occurring along the northern coastline of the Northern Territory (this study) and around the northern portion of Cape York Peninsula (Queensland) and the Gulf of Papua (New Guinea). In the Northern Territory, flowering is initiated in June, usually peaking around August (Table 5.1). On Cape York, flowering has not been observed commencing before November (pers. obs.), whereas in the Gulf of Papua, New Guinea, the species does not flower until December (Floyd, 1977).

Fruiting occurs during December - February in the Northern Territory (Table 5.1), but not until April in the Gulf of Papua (Floyd, 1977). Reasons for such variation between regions within nearly the same latitude are unknown, but different populations of the species may be responding to the most favourable periods for growth in their respective regions.

In *Aegiceras corniculatum* (Table 5.4), flowering is observed during May - December in Western Australia (Semeniuk *et al.*, 1978); August - November in the Northern Territory (this study); July to February at Port Curtis, Queensland (Saenger, 1982) and January - February in Sydney (Goulter, pers. comm.) - although some flowering still occurs there till June (per. obs). Fruiting periods occur throughout the 'wet' season in northern Australia (November - March), but not until May (autumn) in the Sydney district (Clarke & Hannon, 1969).

Why *Aegiceras corniculatum* fruits during May in Sydney is unknown. In northern Australia, the species fruits during the 'wet' season, when water temperatures are highest (30 - 32°C), but its fruiting period in Sydney corresponds to water temperatures of 18°C. It would seem reasonable to relate this simply to latitudinal differences, however *Avicennia marina* fruits in Sydney during December when water temperatures are considerably higher (22°C), although not nearly as high as the 30 - 32°C water temperatures experienced during its fruiting period in northern Australia. Clarke and Hannon (1969) show that dispersal of *Aegiceras* seedlings corresponded with unusually high tides during autumn in the Sydney area, and differed from dispersal in *Avicennia marina* which occurred in December. Though December in Sydney is a favourable period of the year for growth, it has a low frequency of high spring tides possibly limiting the landward spread of *A. marina*.

Dispersal of *Aegiceras corniculatum* fruits in the Sydney district during periods of unusually high tides should be an advantage to the species, allowing it to colonize considerably more sites than *Avicennia marina*. However, this is not the case and *Aegiceras corniculatum* has less success in establishing itself in the Sydney district. Perhaps plants of *Aegiceras* are close to the limits of the physiological tolerance in the prevailing environmental conditions of Sydney, which is close to the southern edge of the geographical range of the species, and can only survive in a very restricted range of sites.

Innumerable other problems exist in seeking adaptive explanations of variations in flowering/fruiting periods of mangrove species throughout the range of each species. It is also worthwhile noting that although some workers have provided information on the time taken for a mature propagule to develop from flower in certain species (cf. Christensen and Wium-Anderson, 1977) - 3 years in *Rhizophora apiculata;* 1 year in *Aegiceras corniculatum* (Carey & Frazer, 1932) and *Rhizophora mangle* (Gill & Tomlinson, 1969), such times will change depending on the particular location of a given population within the geographical range of a species. Overall, it appears that shortening of flowering/fruiting periods, coupled with an extension of the time required to change from flower to fruit, will occur in populations of a particular species nearing the edges of its latitudinal range - probably in both hemispheres. In populations of a species occurring in the most environmentally suitable portions of its range, a lengthening of flowering/fruiting periods and a reduction in the developmental time required between flower and fruit set can be expected.

CHAPTER 6

Variations in girth, basal area and density in three mangrove species along seasonal salinity gradients in the Liverpool-Tomkinson Rivers System, Northern Territory.

- 6.1 INTRODUCTION
  - 6.1.1 Study Setting
  - 6.1.2 Study Area Selection
  - 6.1.3 The Ideal Study Area
  - 6.1.4 The Study Area
  - 6.1.5 Vegetation Considerations
  - 6.1.6 Probable Age of Mangrove Stands in the Study Area
- 6.2 METHODS
  - 6.2.1 Selection of Stations and Quadrats
  - 6.2.2 Measurement of Stems
  - 6.2.3 Measurement of Tree Heights
  - 6.2.4 Measurement of Quadrats
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  - 6.2.6 Determination of Tree Densities
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  - 6.2.8 Measurement of Water and Soil Salinities
  - 6.2.9 Safety Precautions
  - 6.2.10 Access to Study Area
  - 6.2.11 Data Availability
- 6.3 RESULTS
  - 6.3.1 Girth
  - 6.3.2 Basal Area
  - 6.3.3 Density
  - 6.3.4 Canopy Height
- 6.4 DISCUSSION

6.1 INTRODUCTION

Throughout the published literature on mangrove swamps there is an overall awareness of a plant community which becomes established within a harsh coastal saline environment. Most researchers, in particular Schimper (1903), Davis (1940), Mogg (1963), Macnae (1966, 1968), Chapman (1975), Fosberg (1975), Cintron *et al.* (1978) and Pool *et al.* (1977) comment on mangrove growth in relation to salinity.

In this study, tree size, basal area and density of stands of three mangrove species that are widely distributed as fringing bankside vegetation are examined over wide ranges of salinity in the Liverpool-Tomkinson Rivers System, Northern Territory. Casual observations between 1974-76 indicated that these three characteristics might vary with edaphic environment. The species chosen for measurement were *Avicennia marina,* a "salt excreter" and two largely "salt-excluding" species, *Camptostemon schultzii* and *Rhizophora stylosa.* Stands were sampled randomly at sites in different portions of the tidal waterways.

Avicennia marina was the most widely distributed species occurring further upstream in all tidal waterways of the Liverpool-Tomkinson system irrespective of whether those upstream portions were seasonally dominated by hypersaline or fresh-brackish waters. *Camptostemon schultzii* in its distribution appeared less tolerant of inundation by excessively hypersaline or fresh water. Of the three species, *Rhizophora stylosa* appeared to be the least tolerant of inundation either by excessively hypersaline or admixtures of fresh-brackish waters.

6.1.1 STUDY SETTING

The Crocodile Research Programme of the University of Sydney surveyed tidal waterways across northern Australia between 1974-83. During these surveys it was observed that tree girths and heights in many mangrove species, which occur over a wide range of saline conditions, appeared to be greatest in localities that remained slightly brackish for most of the year and least in localities where waters became seasonally hypersaline.

6.1.2 STUDY AREA SELECTION

Initial surveys of most of the tidal waterways across northern Australia showed that, due to the inherent geomorphic variation of each waterway, it might be difficult to study structural characteristics of certain mangrove species over wide salinity gradients in the field. It became apparent that the area required for such a study should be homogeneous in substrate and dynamically stable in the geomorphic sense. Such an investigation should include replicates of waterways possessing the entire range of saline regimes, from fresh-brackish - seawater - hypersaline conditions, in which the three chosen mangrove species grew. In addition patterns of high tide inundation at the different "stations" chosen along the waterways should be as nearly identical as possible. This requirement necessitated choosing for study waterways with low banks and low stream gradients over considerable distances upstream. It was also imperative that mangrove species in the area chosen be in a pristine state.

Many of these conditions were fulfilled in certain tidal waterways - the Adelaide, Blyth-Cadell, Glyde, Goomadeer and Liverpool-Tomkinson systems - all of which occur across the northern coastline of the Northern Territory (Fig. 1.2.1). They were investigated as possible study sites and all received further studies on seasonal variations in water salinity and the distribution of the three chosen mangrove species. The Adelaide and Goomadeer systems were later excluded from consideration because of the considerable damage evident in the mangrove swamps from the browsing and trampling of introduced water buffaloes over the previous one hundred years and the additional knowledge that trees on the Adelaide River had been logged for firewood for steamers during the last century (Searcy, 1905). The Glyde River system draining seawards from the Arafura Swamp was considered ideal for sampling trees in the fresh-brackish saline regimes but possessed no hypersaline waterways. This tidal system was also logistically inaccessible to repeated surveys. Of the remaining two systems - both occurring in central Arnhem Land - the Liverpool-Tomkinson system was much better known from historical and present day surveys and was thus chosen as the study area.

In fact, the historical observation of Captain P.P. King in H.M.C. Mermaid on August 6th, 1819 on the growth of *Avicennia* in the upstream reaches of the Liverpool River could be considered as a major factor in the selection of the area of study.

August 6th, 1819: Liverpool River

> ... "At one place where the bank was about fifteen feet high and formed of red clay (Red Cliffs; km48), Mr. Cunningham landed and collected a variety of interesting plants. The open banks of the river were covered with salicornae and other common chenopodeae and in the midst of the usual assemblage of Rhizophoreae, the avicennia tomentosa, Linn. was observed of remarkable growth, being in many parts from fifty to sixty feet high, three feet in diameter at the base, and of a straight tapering poplar shape."

P.P. King p.259-260

(In Narrative of a survey of the intertropical and western coasts of Australia performed between the years 1818 and 1822, Vol. 1). Cunningham himself in his manuscript journal (1819-1822) does not, however, provide any reference to the growth of *Avicennia* on the Liverpool River.

In addition the meticulous Royal Naval hydrographic survey of the Liverpool system carried out in 1861 by Lieuts. Howard and Guy (1866) and more recent surveys undertaken by Rushworth (1975) and the observations of Commdrs. R.S. Schofield and C.H. Little - former Hydrographers to the Australian Navy (pers. comm) show that there has been negligible change in depths, channel widths/positions and meander courses over the last 120 years. Thus for the purposes of this study the Liverpool-Tomkinson Rivers System may best be described as currently stable.

6.1.3 THE IDEAL STUDY AREA

It is known from other studies, particularly those of Watson (1928), Macnae (1966, 1968), Clarke and Hannon (1967, 1969, 1970), Lugo and Snedaker (1974), Thom *et al.* (1975) and Ball (1980), that many factors act upon the mangrove environment. It is also generally considered that patterns of distribution and zonation of the various species in this vegetation formation are primarily influenced by physiographic relief, substrate type, degrees of tidal inundation and waterlogging and subsequent fluctuations in soil and water salinity that occur due to tidal flushing characteristics and seasonal climates.

Salinity as a major determinant of structural form has been emphasized by Mogg (1963), Chapman (1975) and Pool *et al.* (1977), among others. Studies by Beard (1967) and Zahran (1975) show that one species, *Avicennia marina*, survives and reproduces in saline areas that are not tidally inundated. Conversely, in northern Australia, no mangrove species occurs in the upstream portions of waterways that remain totally fresh but are subjected to tidal fluctuations. Their absence may be related to a total lack of any saline condition. However even this observation requires further explanation as Steenis (1963) has recorded planted specimens of *Bruguiera gymnorhiza* and *Sonneratia caseolaris* (two species possessing an extremely high tolerance of freshwater inundation) growing and reproducing at an altitude of 175 metres in Indonesia while Chapman (1975) reports *Rhizophora mangle* growing amongst water lilies in Jamaica.

A satisfactory test of the existence in the field of relationships between salinity regimes and tree growth requires that a study area be chosen such that as many as possible of the other factors acting in the mangrove environment be kept constant.

Ideally a series of tidal waterways should be chosen that

a) occur on a relatively homogeneous floodplain to minimize substrate fluctuations,

b) encompass the entire range of saline conditions under which the species examined are known to grow,

c) possess pristine vegetation that has not been exposed to any recent natural calamity or man-induced interference,

d) are of low stream gradients so that equivalent patterns of inundation occur in fringing bankside mangrove vegetation throughout the length of the waterway,

e) comprise at least two replicates of each type of waterway to allow tests to be performed against river effect, i.e., at least two each of brackish/freshwater, seawater and hypersaline waterways within a homogeneous floodplain,

f) possess fringing vegetation that is not markedly affected by changes in physiographic relief back from the bank.

Obviously such a system of tidal waterways is well-nigh impossible to locate.

The Liverpool-Tomkinson System ultimately chosen for this study is considered to encompass many of these ideal conditions. It does not, however, possess two hypersaline waterways. Also it was necessary to minimize problems associated with changes in physiographic relief back from the bank and the concurrent changes in zonation patterns by stipulating that all quadrats randomly chosen within the various stations throughout the waterways would not extend more than 20 metres back into the vegetation (refer to methods section).

6.1.4 THE STUDY AREA

The Liverpool-Tomkinson Rivers system lies at latitutde 12°00'S, longitude 134°15'E in central Arnhem Land, Northern Territory. It discharges into the Arafura Sea and with Entrance Island possesses a fairly protected estuary. The system, shown in Fig. 6.2.1, comprises two long tidal waterways, the Liverpool and Tomkinson Rivers, which meander extensively across floodplains, and several smaller waterways including Gudjerama, Morngarrie and Mungardobolo Creeks which enter the mainstream of the Liverpool River.

Although the Liverpool and Tomkinson Rivers and Mungardobolo Creek possess a common junction to the estuary, all three waterways drain separate catchment areas. The Liverpool River, as discussed by Rushworth (1975), drains a largely Pre-Cambrian sandstone escarpment area, whereas the Tomkinson River drains extensive lowland plains. Mungardobolo Creek drains a very restricted lowland area that lies between the drainage basins of the Liverpool and Tomkinson Rivers.

During the "wet" season, discussed in section 1.3.4, rain falls intermittently over the entire Liverpool-Tomkinson system. Flooding patterns as shown in Magnusson (1978) vary from year to year depending mainly on the proximity of rain depressions emanating from tropical cyclones.

In some years during periods of extensive flooding (which may last several weeks) saline waters are flushed from all tidal waterways in the system (Chapter 3) and a freshwater wedge may occur out to sea in the vicinity of Entrance Island. During such times all tidal effects are negated by the effect of the considerable quantities of freshwater entering the previously tidal portions of the waterways from upstream catchment areas. Mangrove forests along the upstrem reaches of the Liverpool and Tomkinson Rivers may then be continuously inundated by freshwaters above their root systems for between 1-3 months.

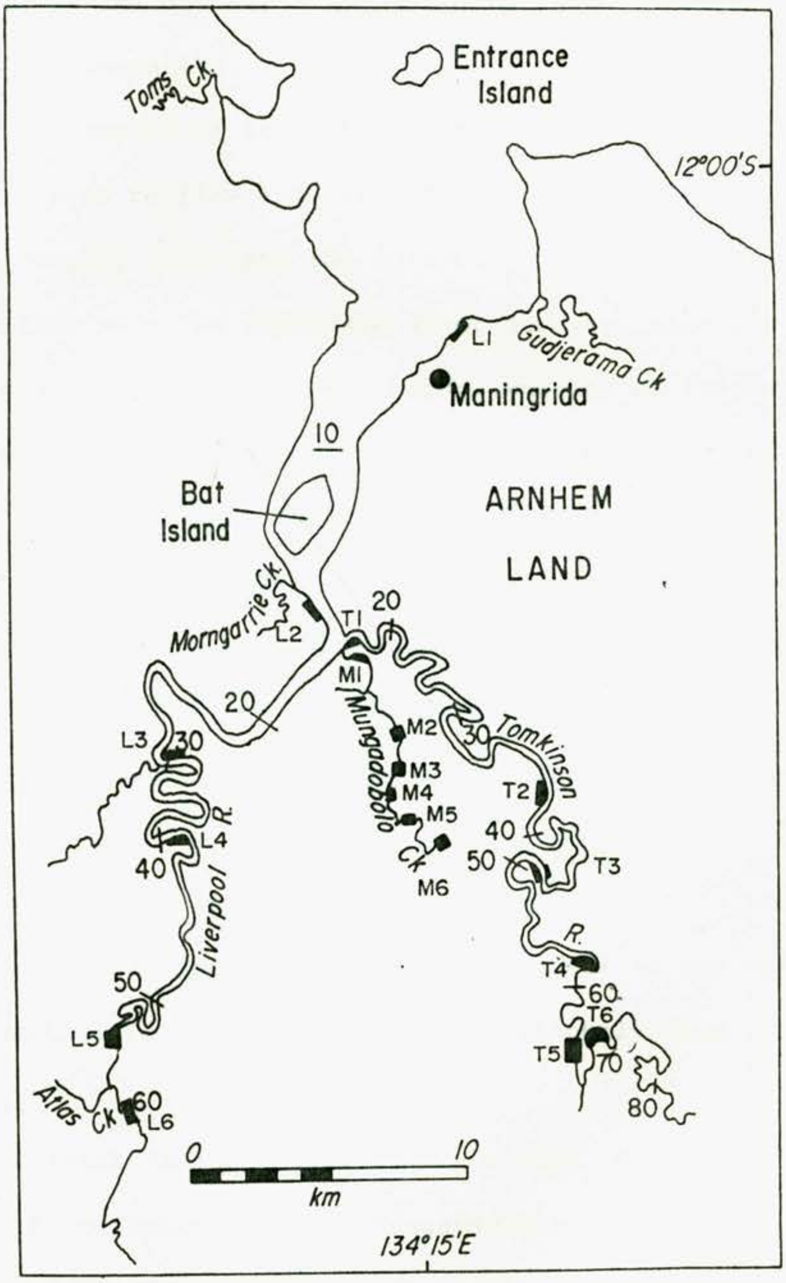

Figure 6.2.1

Location of stations used for girth, basal area and density studies of three mangrove species on the Liverpool-Tomkinson Rivers System, Northern Territory.

During other years no flooding may occur and although "wet" season precipitation may lower surface water salinity, all saline waters are not entirely flushed from the system. In fact, as Messel *et al.* (1979) have shown, saline wedges commonly develop in the truly estuarine portion of the system due to differences in densities of fresh, brackish and seawaters.

As a consequence of its larger drainage basin, large amounts of freshwater continue to flow into upstream tidal portions of the Liverpool River usually well into the following "dry" season. Freshwater ceases to flow into the Tomkinson River however, within a month or two after cessation of "wet" season rains, whereas no freshwater enters the tidal portions of Mungardobolo Creek after the rains cease.

With the onset of the "dry" season, tidal effects are again seen to occur up to km 68.5 on the Liverpool River; km80 on the Tomkinson River and km27 on Mungardobolo Creek. Saline waters penetrate upstream on the three tidal waterways at different rates dependent on the inflow and remaining bodies of freshwater in upstream reaches.

As discussed in Chapter 3 and in Messel *et al.* (1979), it is seen that seasonal variations in water salinity occur in the waterways giving rise to certain patterns that fluctuate slightly from year to year.

After initial flushing from the waterways, during the "wet" season, of most of the saline waters, Mungardobolo Creek re-establishes saline conditions rapidly after the onset of the following "dry" season (see Chapter 3 and Messel *et al*, 1979). By the end of the "dry" season the upstream reaches of the Liverpool (km60) and Tomkinson Rivers (km68) are brackish (9‰ and 15‰ respectively, 1979 readings) whereas the upstream reaches of Mungardobolo Creek (km26) now consist of hypersaline waters (50-60‰; 1979 readings). It is also evident (as discussed in Chapter 3) that over the "dry" season as distance upstream increases in the Liverpool and Tomkinson Rivers the water salinities decrease, with high tide salinity readings always being greater than low tide measurements at any point along the waterways. This is a direct effect of saline waters being "pushed" upstream by high tides, and freshwaters from upstream river portions being "dragged" downstream by ebbing tides.

Additionally, for Mungardobolo Creek it is seen that after the creek attains seawater salinities, (usually in the "mid-dry" season, June-July; Messel *et al*, 1979), salinities at low tides in any month are always greater than those at corresponding high tides. This reversal of the usual condition occurs as high tides flood the surrounding saltpans and deposit salt which crystallizes during daytime low tides. Successive high tides deposit more saline waters for crystallization but also flush back into the mainstream ever increasingly saline waters. Thus a seasonal hypersaline condition exists until rains in the "wet" season again flush all saline waters from the creek. Recent studies by Wolanski and Gardiner (1981) on a tidal creek in north Queensland also show that saline interstitial soil waters are also seasonally flushed from tidal waterways.

The dynamic nature of saline fluctuations in these tidal waterways are shown in Figs. 3.3.9 - 3.3.17 and 6.3.13.

6.1.5 VEGETATION CONSIDERATIONS

Firstly it was necessary that regimes of disturbance of mangrove swamps on the Liverpool-Tomkinson Rivers system should be known in as much detail as possible. Such regimes of disturbance were then subdivided into natural and "man-induced" changes.

1. Natural Regimes of Disturbance

Cyclonic Storms

Although occurring in the northern cyclonic belt, this river system is not known to have received the full force of cyclonic winds that would have resulted in tree windthrow.

This conclusion results from discussions with Aboriginal elders of the Gunavidgi tribe (who can still relate back to the arrival of the Macassan fishermen from the Indonesian Archipelago in the 17th-18th centuries) and from records in journals written during naval and land-based explorations of the area in the 19th and 20th centuries (cf. King 1827, Cadell 1867; Searcy 1905; Kyle-Little 1959). Cyclonic damage to mangrove swamps is well known to this writer and has been documented for the Darwin region (N.T.) by Stocker (1976). From personal examination of the mangrove forests in the Liverpool-Tomkinson system no cyclonic damage is evident today.

Fire

Damage to mangrove associations is usually restricted to shrubs of *Avicennia marina, Lumnitzera racemosa, Excoecaria agallocha* and *Aegialitis annulata* that establish at landward locations around seasonally burnt grassplains.

Floods

Any flooding that occurs is seasonal. Damage to mangrove vegetation from floating logs is minimal although considerable debris is often observed amongst the branches of mangrove trees in the upstream portions of the Liverpool and Tomkinson Rivers. After floods, bank slump commonly occurs around the concave portions of meanders (areas not sampled in this study).

River Morphology

As previously stated (section 6.1.2) the waterways have remained remarkedly stable over the past 120 years in depths, channel widths and meander courses.

Tree Fall

Tree fall occurs quite frequently throughout the mangrove forests.

Lightning Strikes

Lightning strikes occur relatively frequently throughout these forests during the build-up of monsoon clouds (October-November). As described for New Guinea mangrove forests (Paijmans, 1976), they create small usually circular areas (c. 20 metres diameter) that remain relatively free of mangrove vegetation for a number of years.

Die-Back

In exceptionally dry years, water and soil salinities rise to high levels. Mangrove species establishing in peripheral locations (i.e., around saltpans) may die. Likewise, for fringing mangrove vegetation distributional limits of each species although fluctuating slightly on a year-to-year basis due to possibly "atypical" conditions for seedling establishment remain static over longer periods.

Trunk Rot

Trunk rot in the low estuarine portions of the waterways is principally caused by teredo worms. Tissue death in trunks of *Avicennia marina* of large girth is often observed.

2. "Man-Induced" Regimes of Disturbance

Located in central Arnhem Land, an Aboriginal Reserve, the Liverpool-Tomkinson Rivers system has not been subjected to any agricultural or pastoral activities. The mangrove forests likewise have not been subjected to any indigenous or commercial logging pressures.

From tree scars on *Avicennia* of large girth, and discussions with Aboriginal elders it is known that formerly sections of the trunks of the species were prised off with stone axes for shields and food carrying dishes. No mangrove species are used by Aboriginals for dugout or bark canoes in this area.

Some forked trunks and upper branches of *Avicennia marina* have been split open with axes by Aborigines searching for native bee's honey.

Deadwood from the mangrove forests is often gathered for firewood by Aborigines.

Beche-de-mer (trepang) fishermen visiting the area from Makassar (Sulawesi) (Macknight, 1976) are known to have collected firewood from mangrove forests of the Liverpool River in the 18th and 19th centuries. Aboriginal elders have shown this writer the areas from where the wood was procured - Entrance Island and Gudjerama Creek, which lie outside the areas of the studies described in this chapter.

Captain Francis Cadell R.N. whilst surveying, collected firewood for his steamer in 1867 and from his journal the wood getting area was determined by this writer to occur in a eucalypt-dominated forest. From discussions with former officers of the Northern Territory Forestry Department it is known that the foresters logging cypress pine in the 1960's noticed several unexplained sawn tree stumps around the Maningrida settlement (J. Hauser, pers.comm.) which provides supportive evidence of the location of the original area logged.

6.1.6 PROBABLE AGE OF MANGROVE STANDS IN THE STUDY AREA

The age structure of the stands of the various mangrove species in "stations" chosen throughout the waterways is obviously important in this study. Unfortunately, age structure cannot be estimated by dendrochronology in species like *Avicennia marina* whose wood cannot be dated by analysis of rings in it (cf. Zamski, 1981).

However, ontogeny in the three mangrove species studied falls into several periods and age states as discussed by Gatsuk *et al.* (1980).

Species	Ontogenetic Period	Age State
	Latent	Seed
Camptostemon schultzii	Pre-reproductive	Seedling
Avicennia marina		(Juvenile, immature plants)
Rhizophora stylosa		
	Reproductive	Young, mature old
	Post-reproductive*	Subsenile, senile.

* It is not known whether post-reproductive periods occur for these species.

In this study preliminary observations suggested that trees of each species grew at different rates and into different structural forms at various sites along gradients of salinity in the waterways. If this were so, then it would not be possible to determine maturity of trees from height estimates and girth measurements. For example, the small stunted shrubs of *Avicennia marina* (2-3 metres in height) that occur along portions of waterways which become seasonally hypersaline could be just as old as the trees of large girth that grow to 25-30 metres in height along portions of tidal waterways which remain brackish for most of the year. Additionally, the ability of trees of the three species studied to flower and set fruit from an early age (4-6 years) does not permit use to be made of reproductive characteristics for determination of age states.

However Captains King's and Alan Cunningham's previously discussed observations of *Avicennia marina* in the upstream portions of the Liverpool River in 1819 may provide some insight into age states.

In 1819 they recorded that *Avicennia marina* attained great girth and height around km48 on the Liverpool River. Given that some 165 years have elapsed (till 1984) and the knowledge that the course of the waterway has remained relatively stable, it would be reasonable to assume that all trees of any of the three species studied would have had ample time to attain considerable girth and height increments in all portions of the study area.

It is tentatively suggested that the trees of large girth occurring in portions of waterways dominated by admixtures of fresh/brackish waters may not be any older than the short trees of small girth that are established along seasonally hypersaline waterways. From Captain King's historical observation and present day knowledge of changing gradients of salinity in the Liverpool-Tomkinson Rivers System (Messel *et al.*, 1979) the hypothesis is advanced that variations in salinity may be responsible for the differences in girth and height observed along the waterways in trees of various mangrove species.

6.2 METHODS

6.2.1 SELECTION OF STATIONS AND QUADRATS

Six "stations" were chosen on each of the Liverpool and Tomkinson Rivers and Mungardobolo Creek (Fig. 6.2.1) to examine tree girths in the three mangrove species studied along gradients of salinity. The sites were chosen on the basis of profiles of salinity obtained by Messel *et al.* (1979) at high tide in the peak of the dry season. On both the Liverpool and Tomkinson Rivers the set of six "stations" encompassed localities that were inundated by waters varying from seawater to slightly brackish saline waters whereas on Mungardobolo Creek the six "stations" included sites inundated, in the dry season, by seawater to increasingly hypersaline waters.

Water salinity was measured using an Autolab salinity-temperature bridge (Model 602). Interstitial soil salinities were measured using a temperature-compensated hand refractometer made by American Optics (Model 10419). Three Foxboro tide gauges positioned at different localities in the survey area showed how tidal amplitudes, delays and periods changed with increasing distances upstream. The low stream gradients of the three waterways used in the study ensured approximately equivalent inundation of the mangrove vegetation fringing the convex portions of their meanders and their straight reaches by high spring tides during the dry season.

Upstream, tidal amplitudes are dampened and it was observed that the substrate in the fringing mangrove forests was inundated to different depths. However, the only requirement of the study was that the substrate at each site be inundated, and this was met. At each "station", sampling of vegetation was confined to a strip 20 metres wide along the bank. This was to guard against traversing possible zonation of species related to changing physiography back from the bank.

A balanced experimental design was achieved with the six stations on each waterway. However, the waterways differ in length, and it was arbitrarily decided to set the length of each station in which trees were to be measured to 1 km in the Liverpool and Tomkinson Rivers and 0.5 km in Mungardobolo Creek. Five non-overlapping quadrats were then chosen in each station using random numbers (ranging from 0-100) to determine for each quadrat the starting point in metres from the datum point in the station with a 10x multiplication for the Liverpool and Tomkinson Rivers and a 5x multiplication for Mungardobolo Creek. These data are provided in Appendix 2.

In each quadrat the occurrence of all plant species was noted and the girths of all trees greater than 2.5 cm D.B.H. (diameter at breast height) of *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* were obtained. These girths were then marked according to whether they came from trees that reached the "canopy height" at any station or from trees (at "all inclusive heights") irrespective of whether or not they attained the overall canopy height of the forest at that station.

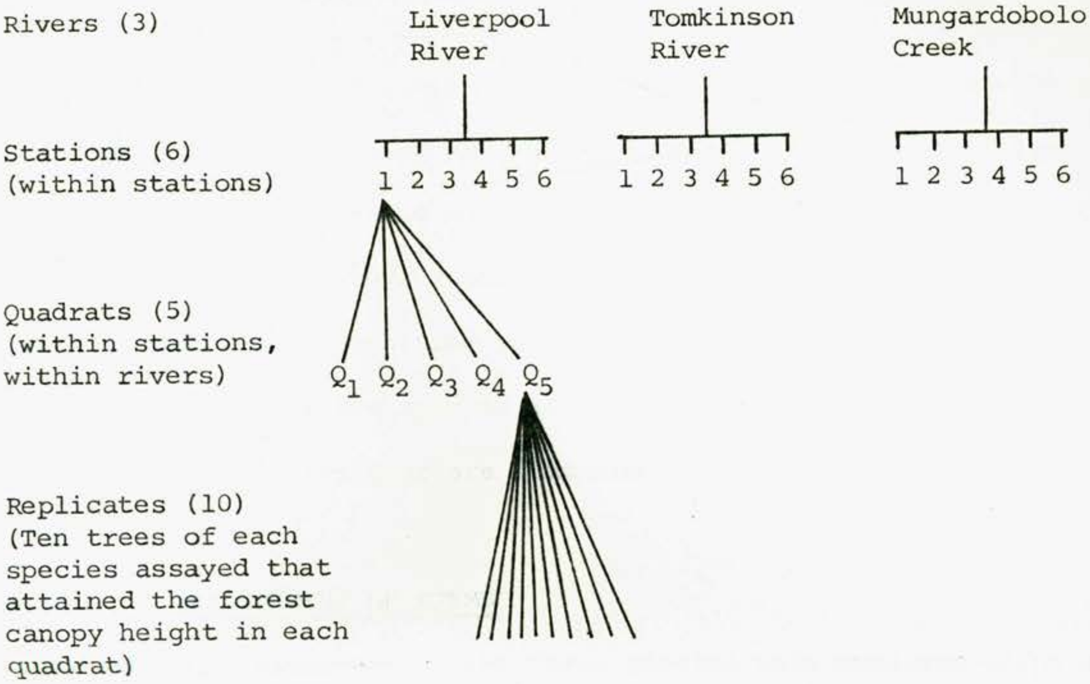

Fig. 6.2.2

Hierarchical (or nested) experimental design layout for study.

As indicated earlier, the width of each quadrat in which girths of trees were measured was 20 metres from the edge of the bank. The length of each quadrat was specified by the distance upstream from the starting point at which the tenth tree of canopy height of any of the three mangrove species under study had been obtained. The point at which the tenth tree stood then fixed the length of a given quadrat for each of the species at that station. Details of the design of the observations are summarized in Fig. 6.2.2.

6.2.2 MEASUREMENT OF STEMS

Bole diameters of the three species were measured using a spring-loaded steel diameter tape at breast height (D.B.H. c.1.3 metres). Following the convention of Carron (1968), if the bole of a tree forked between ground and breast height it was regarded as two trunks, and the two diameters obtained were then averaged to provide a single girth. Trunk forking above breast height was regarded as one stem. Although trees of both *Avicennia marina* and *Camptostemon schultzii* have well developed trunks for D.B.H. measurement, *Rhizophora stylosa* does not possess a trunk that reaches to ground level. This species is supported by numerous stilt roots that arch away from the trunk with the original base of the single trunk being destroyed by teredo and insect attack. For D.B.H. measurements of *Rhizophora stylosa*, diameters were obtained on the trunk proper, immediately above the stilt roots. As stilt roots may occur near ground level or up to five metres above ground, no precise height above ground level for such measurements is possible. All D.B.H. data are provided in Appendix 7 and refer to "over bark" measurements.

6.2.3 MEASUREMENT OF TREE HEIGHTS

During measurements of tree girths, visual estimates were made of tree heights. Due to qualitative errors inherent in such estimates, no calculations involving changes in tree height of the different species in different stations throughout the tidal waterways are attempted. However, during later construction of traps for salt-water crocodiles, trees of *Camptostemon schultzii* were felled and accurate measurements of heights for many quadrats were obtained. These measurements did not differ markedly from those given for tree heights in Appendix 7. Additionally, in any locality the canopy of a mangrove forest is markedly uniform in height and all three species studied show considerable uniformity in their respective canopy heights at most stations.

6.2.4 MEASUREMENT OF QUADRATS

Surveyors' measuring tapes (P.V.C. coated glass fibre) on reels ("Elson" 30 metre; "Z-lon" 200 metre) were utilized, and were appropriate in the muddy conditions of the swamps. Distances measured by tape in the various quadrats sometimes differed slightly from the midstream distances provided by Messel *et al.* (1982) due to bank curvatures. All quadrats commence on the upstream side of their randomly chosen starting point. The abbreviations "R.H.B." and "L.H.B." refer to the right hand and left hand banks respectively as one progresses upstream on any waterway.

6.2.5 MEASUREMENT OF BOLE BASAL AREA

Following usual convention, the sectional area at breast height is given the name basal area (Carron, 1968). In this study basal areas for trees of *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa* were derived from measurements of diameters obtained from trees at selected stations within the Liverpool-Tomkinson Rivers system. Basal areas for each tree were obtained from diameter measurements through the formula

$$\frac{\pi d^2}{4} \quad \text{(expressed in square cm)}$$

To obtain the bole basal area of trees of each species studied (that attained forest canopy height) per hectare of riverine forest involved summation of basal areas of fifty trees at each station. This summed basal area was then divided by the area in which the trees grew. In this study bole basal area of each species is given in m^2/hectare.

The formula used for obtaining the bole basal area of each tree assumes a circular section. Most stems in this study, as in others, are however irregular in outline and not absolutely circular. For practical convenience the area of the section was calculated as if the section were circular. Bole area measurements given refer to area of trunk inclusive of bark. Data on bole basal areas are provided in Appendix 4.

6.2.6 DETERMINATION OF TREE DENSITIES

In each of the three species studied at each quadrat an overall density was obtained for all trees and shrubs of the species taller than one metre and also a density for trees that attained the canopy height of the forest. Densities obtained in each of the quadrats were then summed to provide densities for each species at a particular station. Densities are given in trees/hectare though none of the quadrats actually sampled was as much as a hectare of riverine forest. Data on densities are provided in Appendix 3.

6.2.7 LOCATION OF STATIONS AND QUADRATS

Detailed locality diagrams are provided in Appendix 2. For the stations, distances upstream were determined using the river work maps published in Monograph 15 of Messel *et al.* (1982). These maps show midstream distances and fringing mangrove swamps throughout all tidal waterways in the survey area.

6.2.8 MEASUREMENTS OF WATER AND SOIL SALINITIES

Water salinities were measured at high and low tides at 5 km intervals throughout tidal waterways in the study area at different periods over the years 1975-79. These studies of salinity form part of the Crocodile Research Programme and are given in Messel *et al.* (1979) for the study area. Additional high tide water salinity measurements were obtained by this writer for the various stations reported on in this study throughout 1977-79 as these tides inundated the fringing mangrove forests.

Interstitial soil salinities were obtained in each of the quadrats within each station at the end of the 1979 dry season. Small pits (50 cm deep) were dug into the mud substrate as it is above this depth that most nutritive and cable roots of the mangrove species examined occur. Interstitial water permeated into the holes and was left until these waters became clearer. Drops of this water were then placed under the lens of a hand-held refractometer (American Optics, Model 10419) and soil salinities (in parts per thousand ‰) were obtained.

The five interstitial soil salinities from quadrats within each station were then averaged giving a soil salinity for each station. In the analyses following, the 1979-peak-dry-season water and soil salinities are utilized as they represent the most saline conditions encountered in the study area over the period 1975-79.

6.2.9 SAFETY PRECAUTIONS

As most girth measurements were obtained during the 1976-77 "wet" season, suitable protective clothing, footwear and Australian Army mosquito head nets were utilized. During tree measurements in the upstream flooded portions of the Tomkinson River a tomahawk was always carried due to prevalence of saltwater crocodiles. Whilst this writer waded through flooded swamps a sharp lookout for crocodiles was also undertaken by at least two other armed observers in a nearby boat.

6.2.10 ACCESS TO STUDY AREA

Through the considerable logistic and financial support provided by Professor H. Messel, use was made of the University of Sydney's Cessna 206 aircraft for transport to and from the Arnhem Land study area (ex Sydney). In addition, the University's 21-metre research vessel was utilized as a base on the Liverpool-Tomkinson Rivers system. One 5.5-metre radio-equipped workboat was used for transport to the various stations with breakdown safety backup services provided by the ship's Chief Engineer.

6.2.11 DATA AVAILABILITY

Detailed appendices of much of the data used in this study are provided in Volume 2. All computations for girth, basal area and densities, regressions, are also available upon request.

6.3 RESULTS

6.3.1 GIRTH

In each of the three species studied the frequency distribution of girths at the eighteen stations (Fig. 6.3.1 - 6.3.12) shows a tendency for the range of girths in the randomly chosen quadrats to vary between stations, increasing particularly noticeably in the upstream portions of the Liverpool and Tomkinson Rivers. This trend can be related to the relative periods of the year the stations experience waters of particular ranges of salinity (Fig. 6.3.13). However both the trend and its possible relation to water salinity require examining in the light of rigorous statistical analyses of the data. The data do not lend themselves readily to such analyses. There is non-homogeneity of variances at the various stations for each mangrove species studied on each waterway. This was investigated in the search for a possible transformation of the data to allow their use in parametric statistical analyses.

Linear relationships are found between standard deviations and means (of girth measurements) in all three species (Fig. 6.3.14) on the Liverpool and Tomkinson Rivers and to a lesser degree in *Camptostemon schultzii* and *Rhizophora stylosa* on Mungardobolo Creek. In these cases the constant coefficient of variation indicates a logarithmic transformation as most appropriate allowing subsequent parametric statistical analyses to be attempted. A series of Cochran's tests confirmed homogeneity of the variances of most of the transformed ($\log_e$) girth data for each of the three mangrove species on tidal waterways of the Liverpool-Tomkinson Rivers system (Table 6.3.1).

It can be seen that hypotheses of equal variances are accepted at the 95% level of significance in *Avicennia marina* on the Tomkinson River, in *Camptostemon schultzii* on all three waterways and *Rhizophora stylosa* on the Tomkinson River and Mungardobolo Creek. It is also apparent that acceptance is only possible at the 99% level for *Avicennia marina* on the Liverpool River and that hypotheses of equal variance must be rejected at all levels in *Avicennia marina* on Mungardobolo Creek and *Rhizophora stylosa* on the Liverpool River. Overall, the transformed variances are quite homogeneous for the species under study on the Liverpool/Tomkinson Rivers system and levels of significance at which the variances are homogeneous are used in later analyses.

Under the experimental design used (Fig. 6.2.2) a series of two-factor nested or hierarchical analyses of variance may be used to examine variation of girths of canopy trees in each of the three species studied between quadrats in each station and between stations on the same waterways. These analyses are provided in Tables 6.3.2 - 6.3.4. Due to "river effect" only accounting in most instances for a very small percentage of total variation it was possible to perform regression analyses on mean girths of canopy trees for each species investigated from all quadrats on the combined tidal waterways throughout

	Liverpool River	Tomkinson River	Mungardobolo Creek
Avicennia marina:	Variances homogeneous at 99% level but not at 95% level.	Variances homogeneous at 95% level.	Variances heterogeneous: not homogeneous at either 95% or 99% levels.
Camptostemon schultzii:	Variances homogeneous at 95% level.	Variances homogeneous at 95% level.	Variances homogeneous at 95% level.
Rhizophora stylosa:	Variances not homogeneous at 99% level. Variances heterogeneous.	Variances homogeneous at 95% level.	Variances homogeneous at 95% level.

TABLE 6.3.1

Results of Cochran's test for homogeneity of intra-quadrat variances of the transformed ($\log_e$) girth measurements for *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* at six stations each on the Liverpool and Tomkinson Rivers and Mungardobolo Creek, N.T.

a wide range of saline conditions. Here no transformation of the data was required. These analyses are provided in Tables 6.3.10 - 6.3.12 and Figs. 6.3.15 - 6.3.17. Regression analyses on girths ($\log_e$-transformed data) of canopy trees for species on individual waterways are provided in Appendix 5.

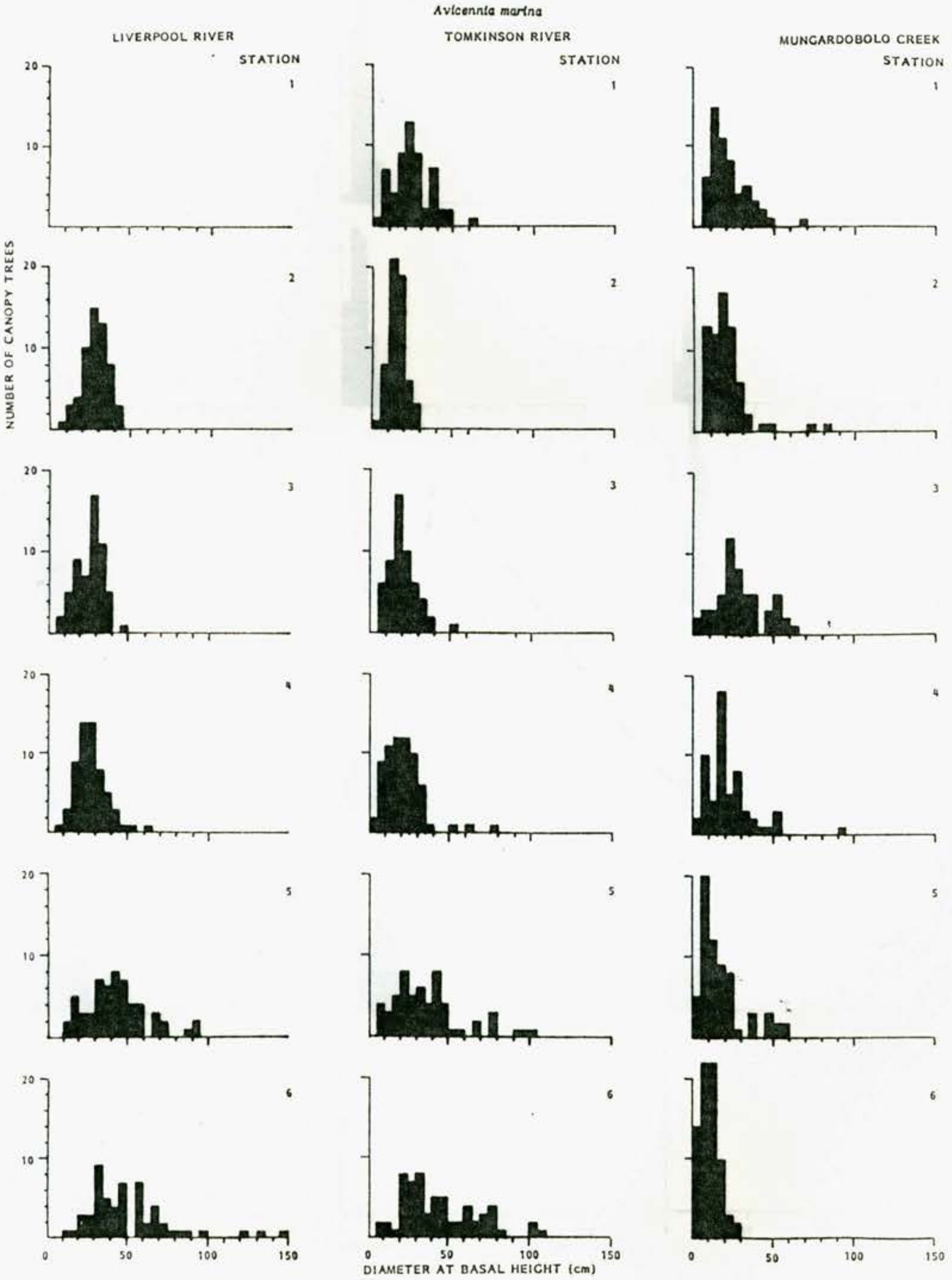

Figure 6.3.1

Incremental size class distribution of girths of canopy trees of *Avicennia marina* on waterways of the Liverpool-Tomkinson Rivers System.

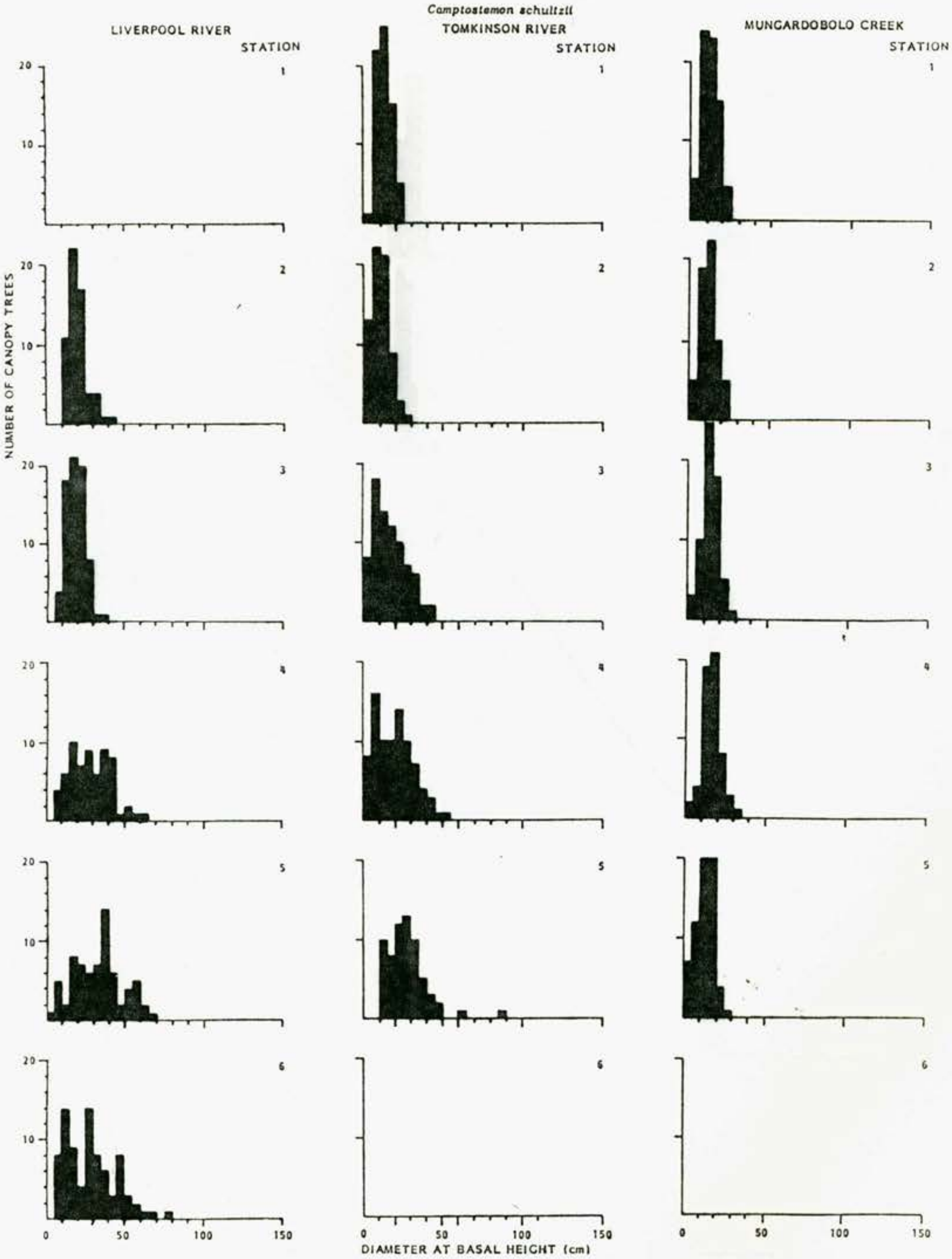

Figure 6.3.2

Incremental size class distribution of girths of canopy trees of *Camptostemon schultzii* on waterways of the Liverpool-Tomkinson Rivers System.

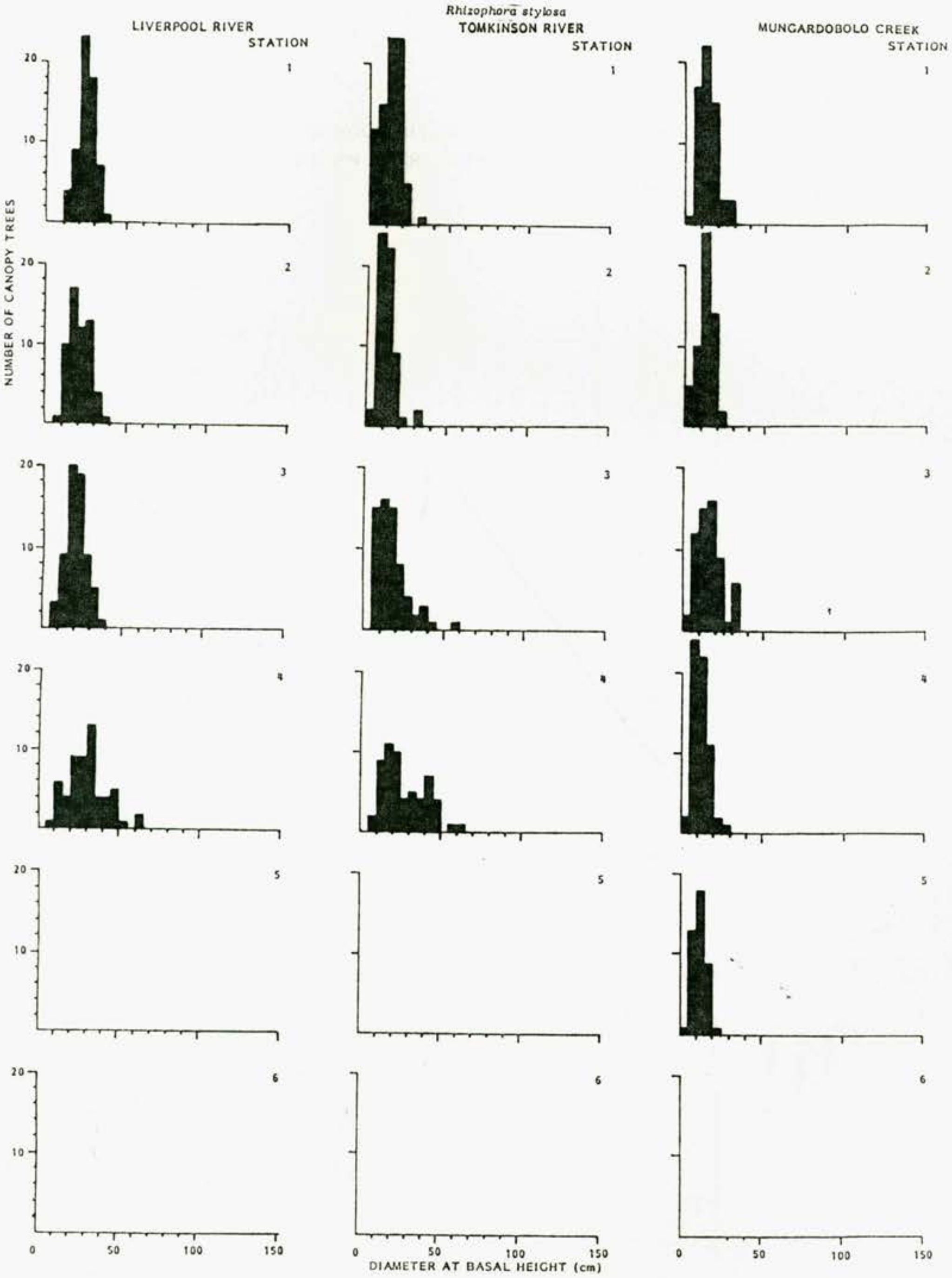

Figure 6.3.3

Incremental size class distribution of girths of canopy trees of *Rhizophora stylosa* on wayerways of the Liverpool-Tomkinson Rivers System.

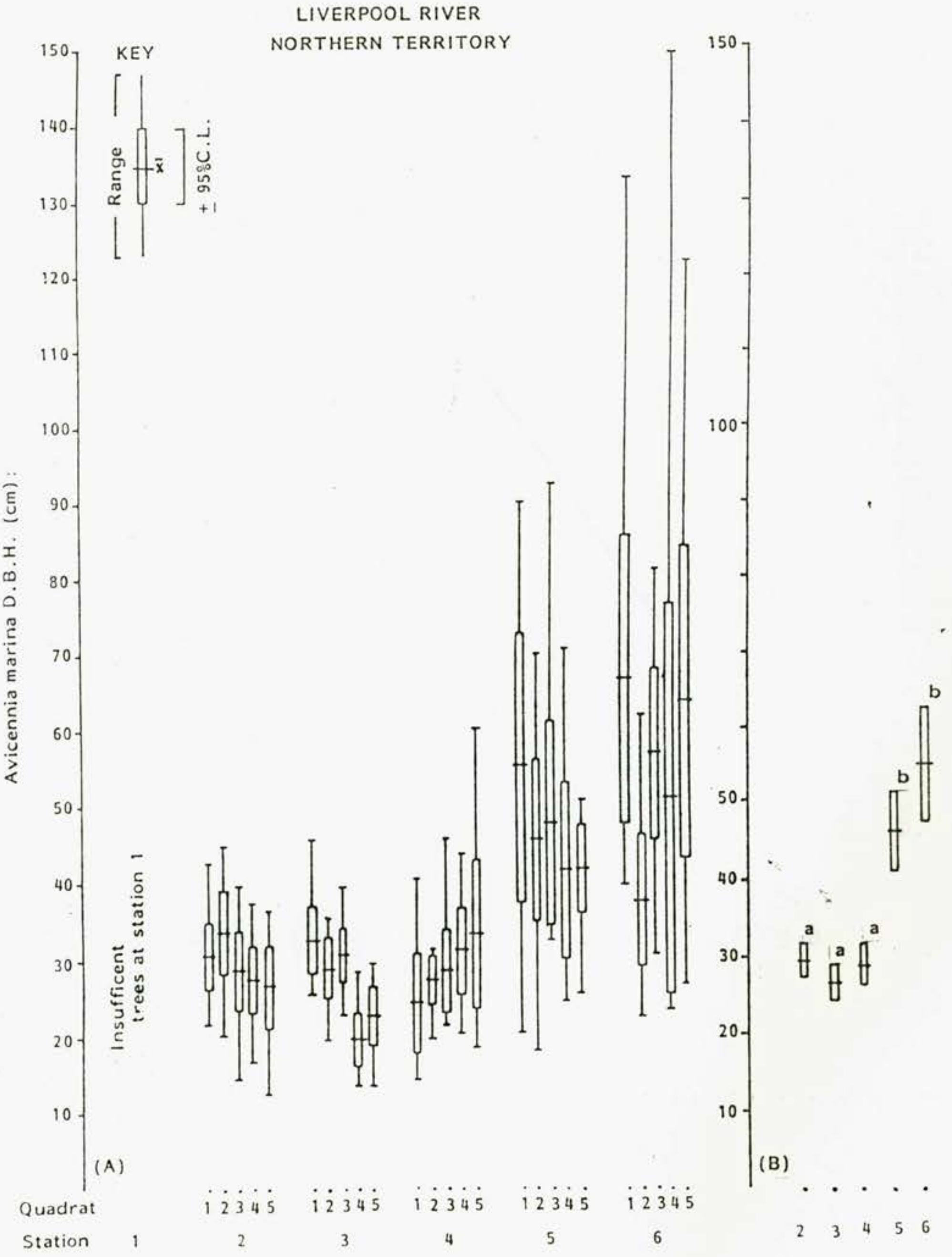

FIG. 6.3.4

Girths of canopy trees of *Avicennia marina* at quadrats and stations on the Liverpool River. Shown are the means, range and 95% confidence limits for stations, values with the same superscript not being significantly different at $p \leq 0.05$ (S.N.K. test- Appendix 1).

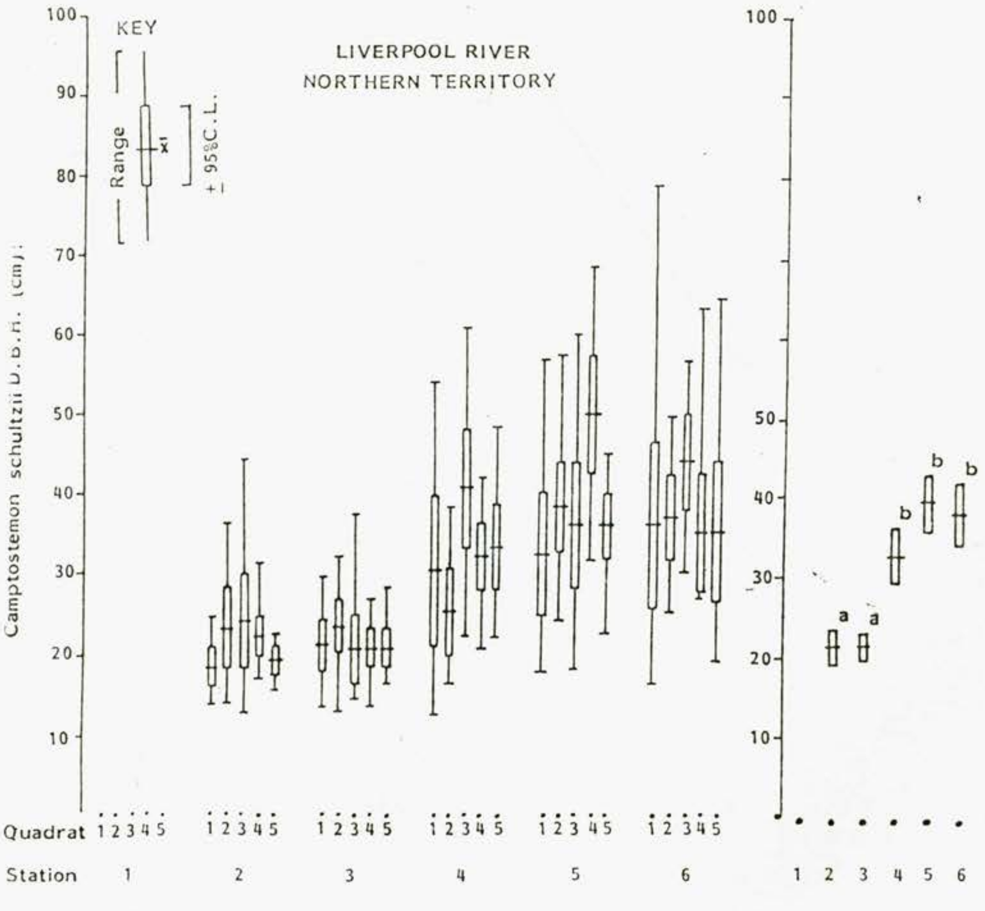

Figure 6.3.5

Girths of canopy trees of *Camptostemon schultzii* at quadrats and stations on the Liverpool River. Shown are the means, range and 95% confidence limits for stations, values with the same superscript not being signficiantly different at $p \leq 0.05$ (S.N.K. test - Appendix 1).

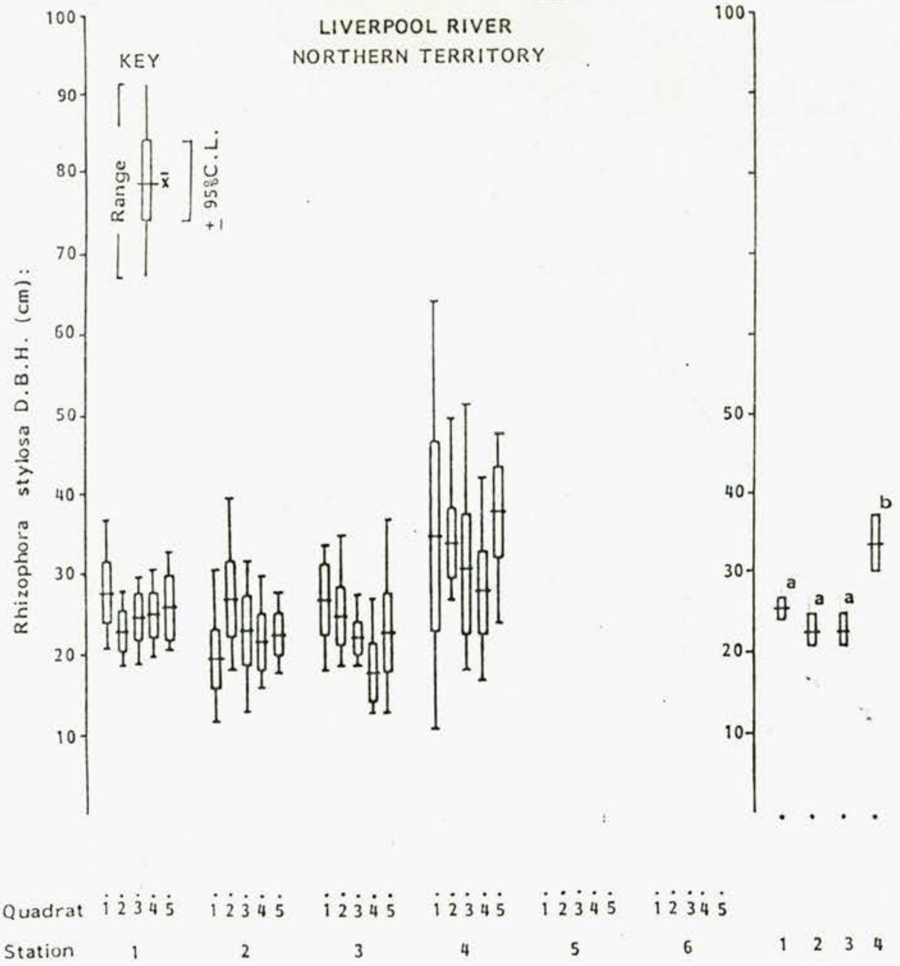

Figure 6.3.6

Girths of canopy trees of *Rhizophora stylosa* at quadrats and stations on the Liverpool River. Shown are the means, range and 95% confidence limits for stations, values with the same superscript not being significantly different at $p \leq 0.05$ (S.N.K. test - Appendix 1).

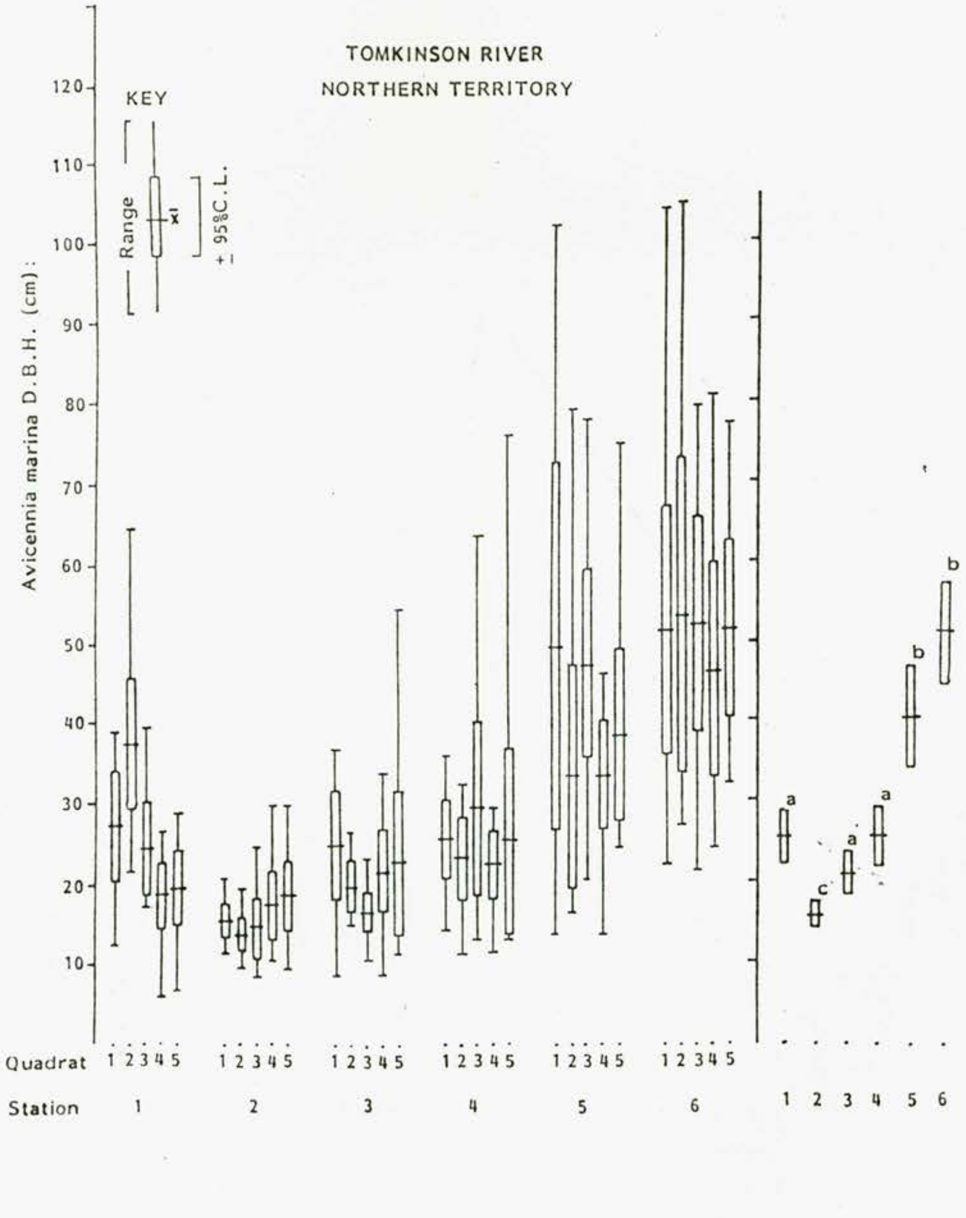

Figure 6.3.7

Girths of canopy trees of *Avicennia marina* at quadrats and stations on the Tomkinson River. Shown are the means, range and 95% confidence limits for stations, values with the same superscript not being signficantly different at $p \leq 0.05$ (S.N.K. test - Appendix 1).

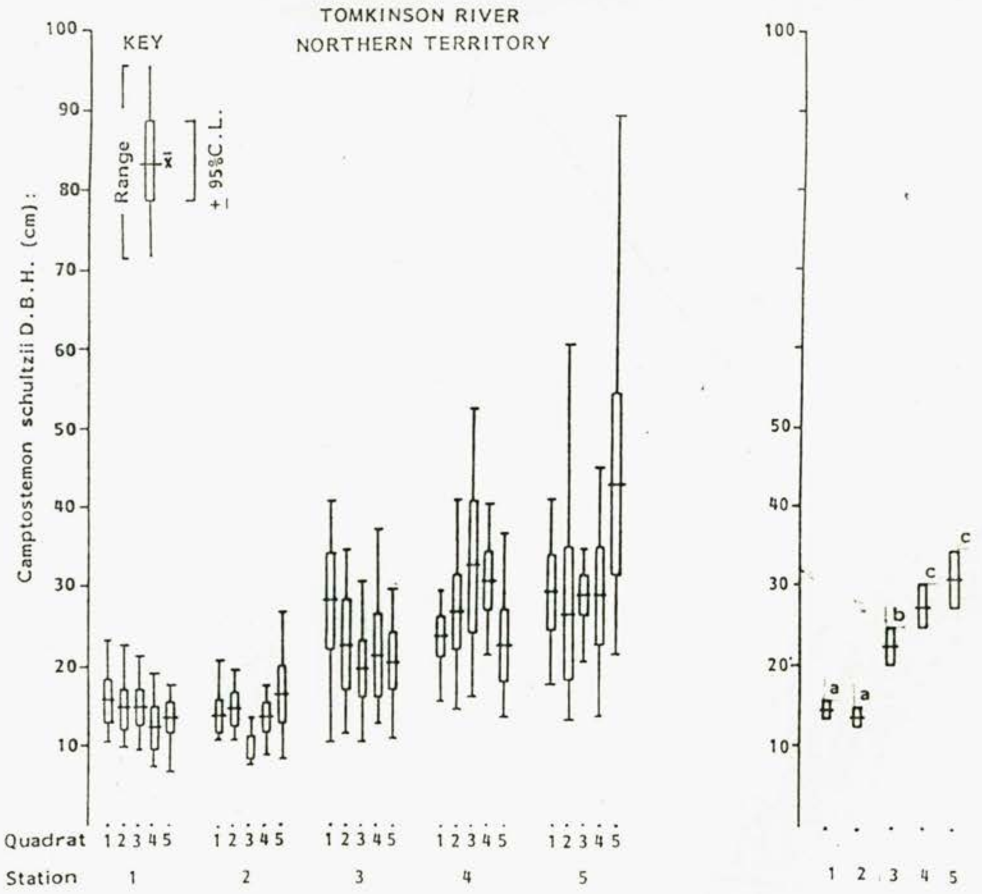

Figure 6.3.8

Girths of canopy trees of *Camptostemon schultzii* at quadrats and stations on the Tomkinson River. Shown are the means, range and 95% confidence limits for stations, values with the same superscript not being significantly different at $p \leq 0.05$ (S.N.K. test - Appendix 1).

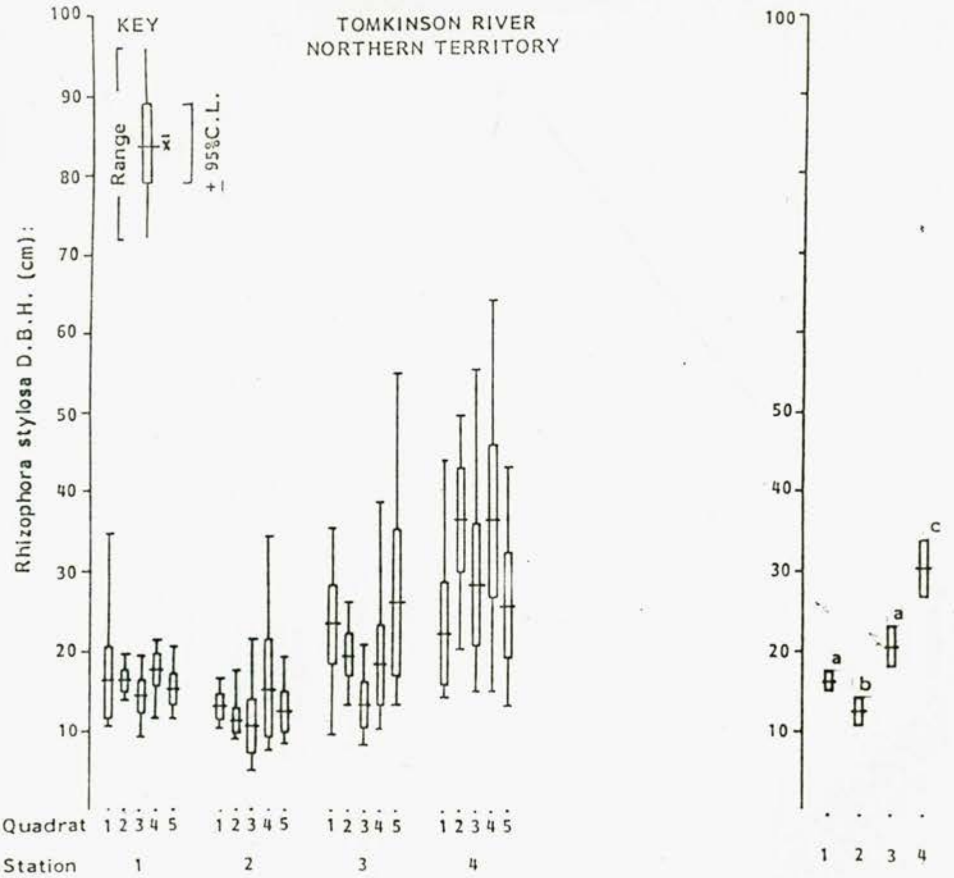

Figure 6.3.9

Girths of canopy trees of *Rhizophora stylosa* at quadrats and stations on the Tomkinson River. Shown are the means, range and 95% confidence limits for stations, values with the same superscript not being signficiantly different at $p \leq 0.05$ (S.N.K. test - Appendix 1).

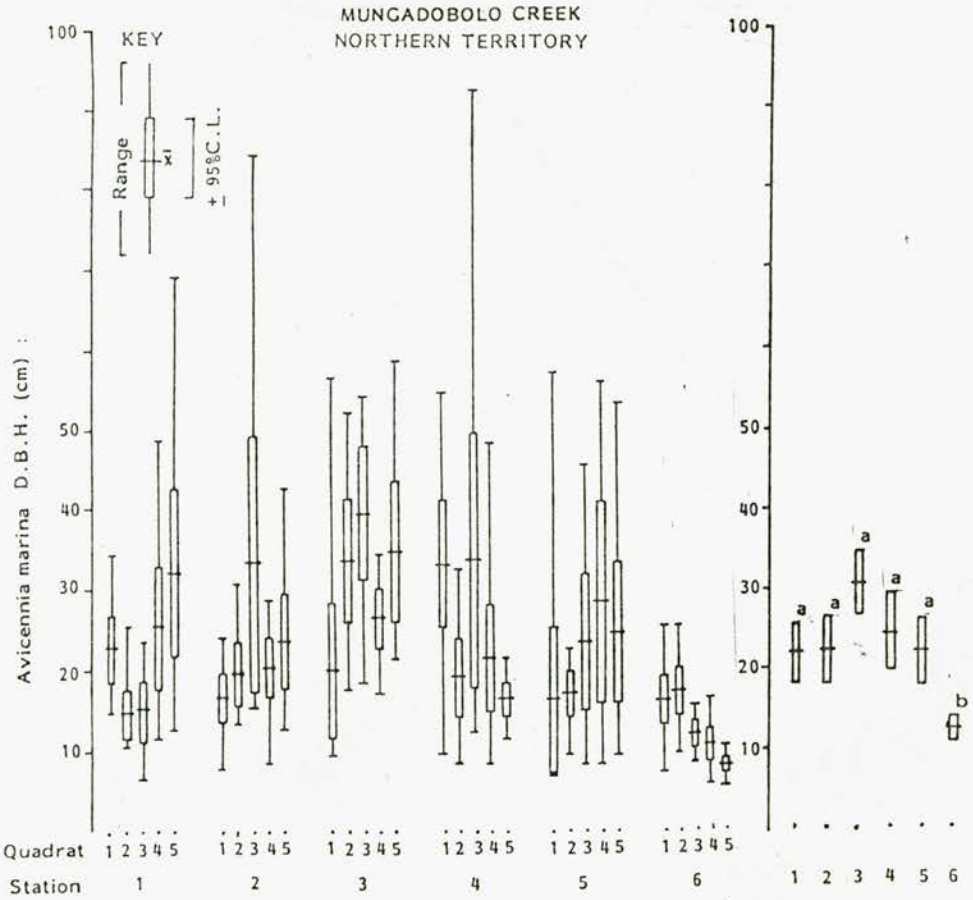

Figure 6.3.10

Girths of canopy trees of *Avicennia marina* at quadrats and stations on the Mungardobolo Creek. Shown are the means, range and 95% confidence limits for stations, values with the same superscript not being significantly different at $p \leq 0.05$ (S.N.K. test - Appendix 1).

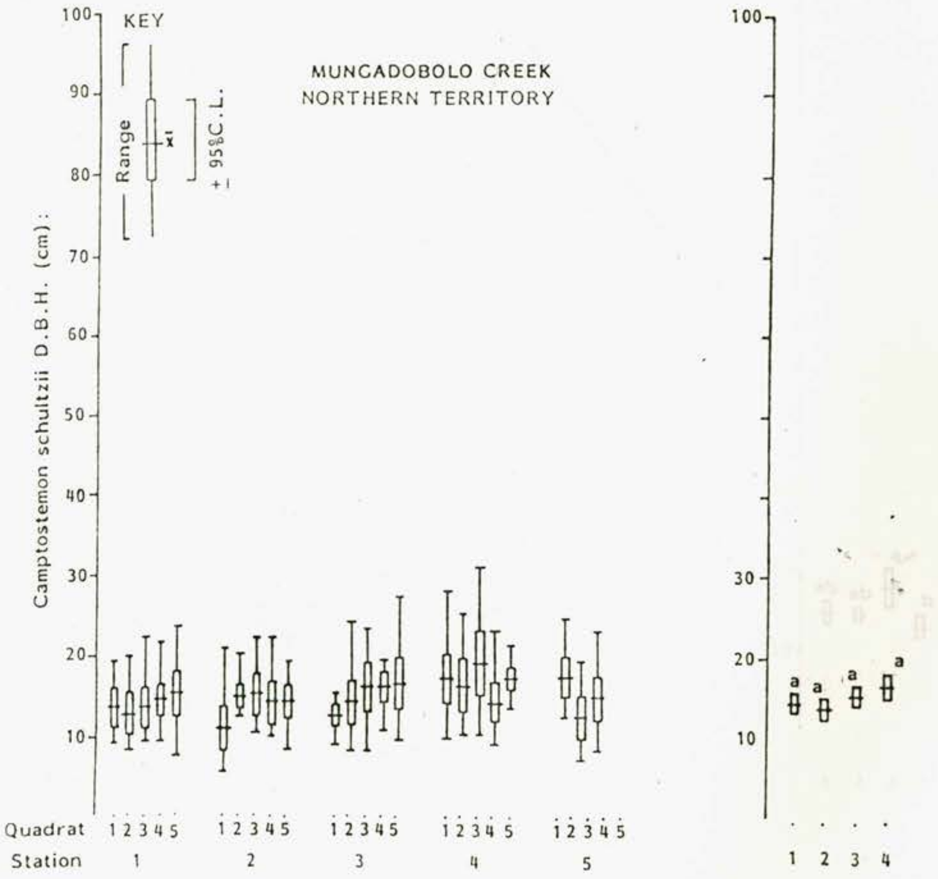

Figure 6.3.11

Girths of canopy trees of *Camptostemon schultzii* at quadrats and stations on the Mungardobolo Creek. Shown are the means, range and 95% confidence limits for stations, values with the same superscript not being signficantly different at $p \leq 0.05$ (S.N.K. test - Appendix 1).

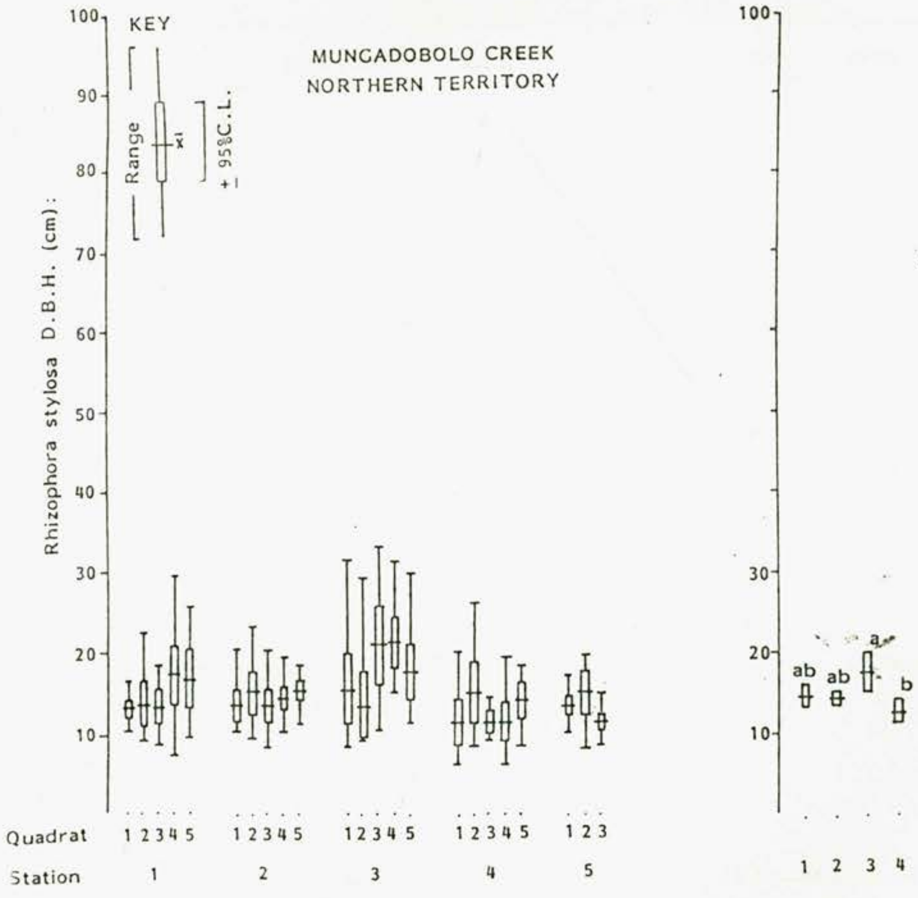

Figure 6.3.12

Girths of canopy trees of *Rhizophora stylosa* at quadrats and stations on the Mungardobolo Creek. Shown are the means, range and 95% confidence limits for stations, values with the same superscript not being significantly different at $p \leq 0.05$ (S.N.K. test - Appendix 1).

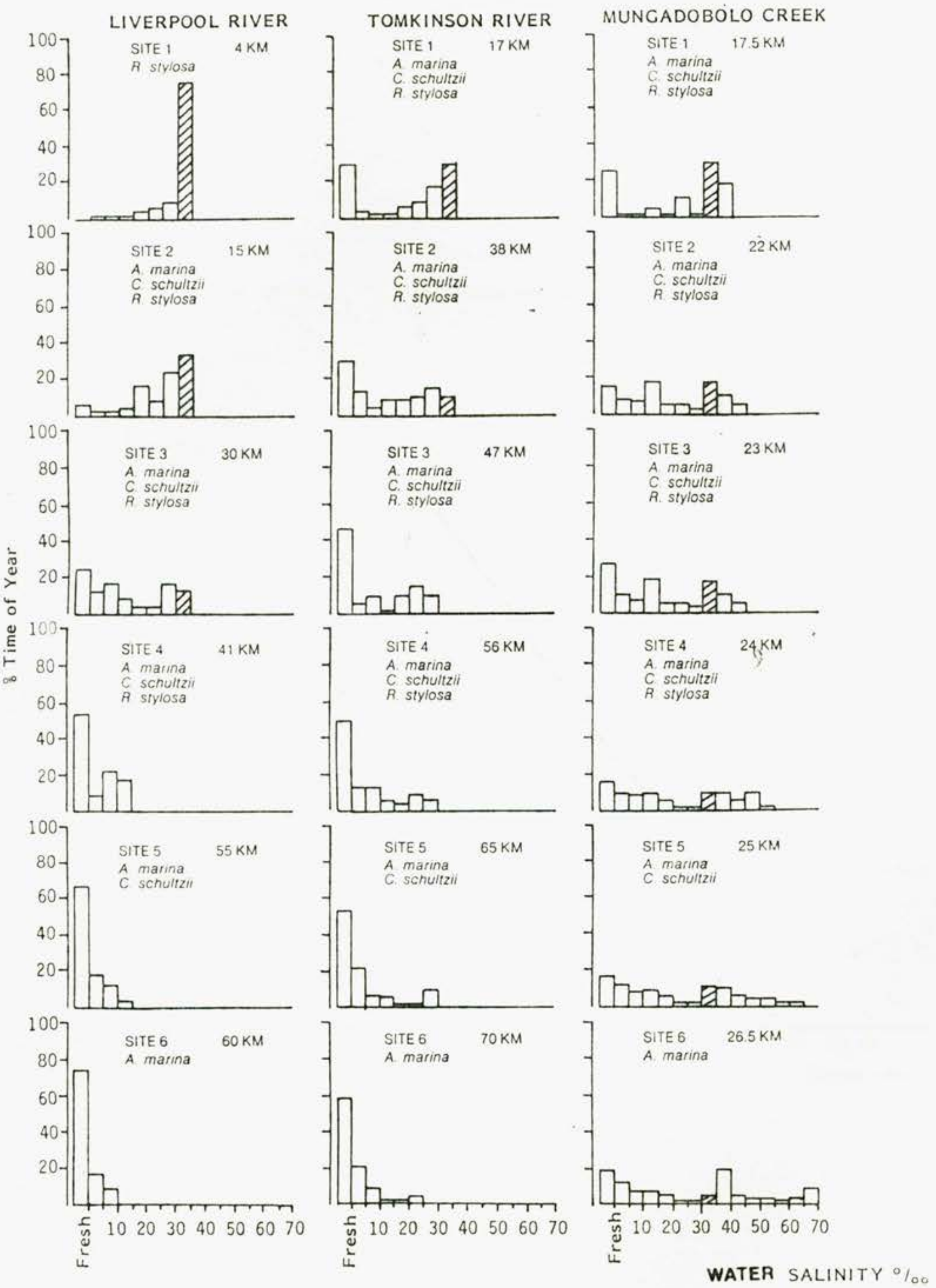

Figure 6.3.13

Percentage time of year for period 1975-79 for species at sites on the Liverpool-Tomkinson Rivers System spent in waters of different salinities (salinity of seawater indicated by cross-hatched column).

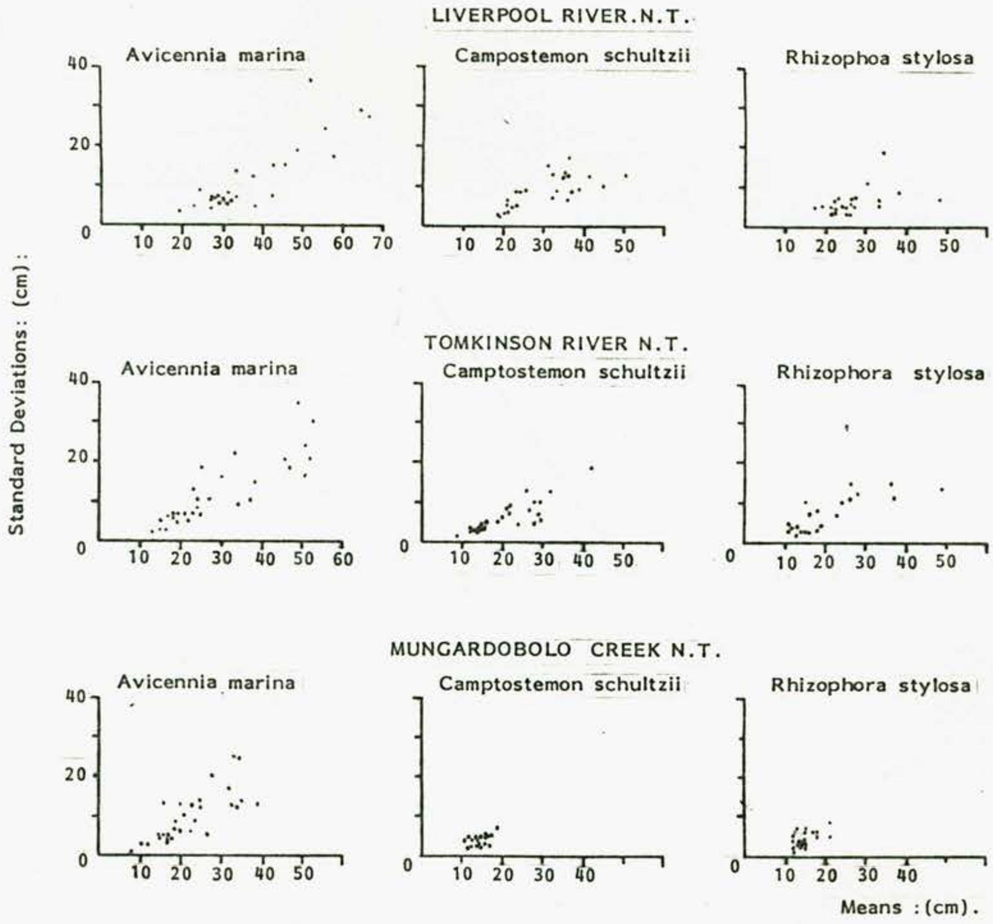

Figure 6.3.14

Relationships between the standard deviations and means of the original girth data of mangrove species examined at each quadrat within each station on the Liverpool-Tomkinson Rivers System, N.T.

TABLE 6.3.2

Summary of analysis of variance of girths (using $\log_e$-transformed data) of canopy trees in *Avicennia marina* at different stations and quadrats within stations on the Liverpool and Tomkinson Rivers and Mungardobolo Creek, N.T. (2 factor; factor A - random, factor B - fixed; random factor nested under fixed factor).

a. LIVERPOOL RIVER

NESTED ANOVA

Source of Variation	SS	d.f.	MS	F
B Stations	17.93	4	4.48	16.86
A Quadrats within stations	5.32	20	0.27	2.68
Residual	22.34	225	0.10	
Total		249		

For Ho: There is no difference in girths of *Avicennia marina* between the five stations on the Liverpool River.

$F = 16.86$

$F_{0.01,4,20} = 4.43$

Therefore reject Ho.

For Ho: There is no difference between girths of *Avicennia marina* at quadrats within stations on the Liverpool River.

$F = 2.68$

$F_{0.01,20,225} = 1.88$

Therefore reject Ho.

TABLE 6.3.2 (cont'd)

b. TOMKINSON RIVER

NESTED ANOVA

Source of Variation	SS	d.f.	MS	F
B Stations	41.39	5	8.28	33.65
A Quadrats within stations	5.91	24	0.25	1.46
Residual	45.26	270	0.17	
Total		299		

For Ho: There is no difference in girths of *Avicennia marina* between the six stations on the Tomkinson River.

$F = 33.65$

$F_{0.05,5,24} = 2.62$

Therefore reject Ho.

For Ho: There is no difference in girths of *Avicennia marina* at quadrats within stations on the Tomkinson River.

$F = 1.46$

$F_{0.05,24,270} = 1.52$

$(24,\infty)$ used from tables

Therefore accept Ho.

TABLE 6.3.2 (cont'd)

c. MUNGARDOBOLO CREEK

NESTED ANOVA

Source of Variation	SS	d.f.	MS	F
B Stations	18.76	5	3.75	5.36
A Quadrats within stations	16.81	24	0.70	3.70
Residual	51.02	270	0.19	
Total		299		

For Ho: There is no difference in girths of *Avicennia marina* between the six stations on Mungardobolo Creek.

$F = 5.36$

$F_{0.05,5,24} = 2.62$

Therefore reject Ho.

For Ho: There is no difference between girths of *Avicennia marina* at quadrats within stations on Mungardobolo Creek.

$F = 3.70$

$F_{0.05,24,270} = 1.52$

$(24,\infty)$ d.f. used from tables

Therefore reject Ho.

N.B. The possibility of committing either Type I or II errors exists here as the variances were not homogeneous at

TABLE 6.3.3

Summary of analysis of variance of girths ($\log_e$-transformed data) of canopy trees in *Camptostemon schultzii* at different stations and the quadrats within stations on the Liverpool and Tomkinson Rivers and Mungardobolo Creek, N.T. (2 factor; Factor A - random, Factor B - fixed; random factor nested under fixed factor.

a. LIVERPOOL RIVER

NESTED ANOVA

Source of Variation	SS	d.f.	MS	F
B Stations	16.55	4	4.14	23.66*
A Quadrats within stations	3.50	20	0.17	2.02*
Residual	19.39	225	0.09	
Total		249		

For Ho: There is no difference in girths of *Camptostemon schultzii* between the five stations on the Liverpool River.

$F = 23.66$

$F_{0.05,4,20} = 2.87$

Therefore reject Ho.

For Ho: There is no difference between girths of *Camptostemon schultzii* at quadrats within stations on the Liverpool River.

$F = 2.02$

$F_{0.05,20,225} = 1.57$

Therefore reject Ho.

TABLE 6.3.3 (cont'd)

b. TOMKINSON RIVER

NESTED ANOVA

Source of Variation	SS	d.f.	MS	F
B Stations	26.54	4	6.63	28.63
A Quadrats within stations	4.64	20	0.23	2.48
Residual	21.05	225	0.09	
Total		249		

For Ho: There is no difference in girths of *Camptostemon schultzii* between the five stations on the Tomkinson River.

$F = 28.63$

$F_{0.05,4,20} = 2.87$

Therefore reject Ho.

For Ho: There is no difference between girths of *Camptostemon schultzii* at quadrats within stations on the Tomkinson River.

$F = 2.48$

$F_{0.05,20,225} = 1.57$

$(20,\infty)$ d.f. used from tables

Therefore reject Ho.

TABLE 6.3.3 (cont'd)

c. MUNGARDOBOLO CREEK

NESTED ANOVA

Source of Variation	SS	d.f.	MS	F
B Stations	1.28	3	0.43	3.40
A Quadrats within stations	2.01	16	0.13	1.59
Residual	14.13	180	0.08	
Total		199		

For Ho: There is no difference in girths of *Camptostemon schultzii* between the five stations on Mungardobolo Creek.

$F = 3.40$

$F_{0.05,3,16} = 3.24$

Therefore reject Ho.

For Ho: There is no difference between girths of *Camptostemon schultzii* at quadrats within stations on Mungardobolo Creek.

$F = 1.59$

$F_{0.05,16,180} = 1.67$

$(15,\infty)$ d.f. used for tables.

Therefore accept Ho.

TABLE 6.3.4

Summary of analysis of variance of girths ($\log_e$-transformed data) of canopy trees in *Rhizophora stylosa* at different stations and quadrats within stations on the Liverpool and Tomkinson Rivers and Mungardobolo Creek, N.T. (2 factor: Factor A - random, factor B - fixed; random factor nested under fixed factor.

a. LIVERPOOL RIVER

NESTED ANOVA

Source of Variation	SS	d.f.	MS	F
B Stations	4.03	3	1.34	8.62
A Quadrats within stations	2.49	16	0.16	2.28
Residual	12.29	180	0.07	
Total		199		

For Ho: There is no difference in girths of *Rhizophora stylosa* between the four stations on the Liverpool River.

$F = 8.62$

$F_{0.05,3,16} = 3.24$

Therefore reject Ho.

For Ho: There is no difference between girths of *Rhizophora stylosa* at quadrats within stations on the Liverpool River.

$F = 2.28$

$F_{0.05,16,180} = 1.75$

(15,120) d.f. used from tables.

Therefore reject Ho.

N.B. The possibility of committing either Type I or II errors exists here as the variances were still not homogeneous at the .99 level.

TABLE 6.3.4 (cont'd)

b. TOMKINSON RIVER

NESTED ANOVA

Source of Variation	SS	d.f.	MS	F
B Stations	18.83	3	6.28	20.93
A Quadrats within stations	4.80	16	0.30	2.37
Residual	11.73	180	0.13	
Total		199		

For Ho: There is no difference in girths of *Rhizophora stylosa* between the four stations on the Tomkinson River.

$F = 20.93$

$F_{0.05,3,16} = 3.24$

Therefore reject Ho.

For Ho: There is no difference between girths of *Rhizophora stylosa* at quadrats within stations on the Tomkinson River.

$F = 2.37$

$F_{0.05,16,180} = 1.67$

$(15,\infty)$ d.f. used from tables.

Therefore reject Ho.

TABLE 6.3.4 (cont'd)

c. MUNGARDOBOLO CREEK

NESTED ANOVA

Source of Variation	SS	d.f.	MS	F
B Stations	2.47	3	0.82	4.30
A Quadrats within stations	3.06	16	0.19	2.09
Residual	16.47	180	0.09	
Total		199		

For Ho: There is no difference in girths of *Rhizophora stylosa* between the four stations on Mungardobolo Creek.

$F = 4.30$

$F_{0.05,3,16} = 3.24$

Therefore reject Ho.

For Ho: There is no difference between girths of *Rhizophora stylosa* at quadrats within stations on Mungadobolo Creek.

$F = 2.09$

$F_{0.05,16,180} = 1.67$

$(15,\infty)$ d.f. used from tables.

Therefore reject Ho.

The results of the nested analyses of variance (Table 6.3.2 - 6.3.4) show in *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa* that in most instances there were significant differences in girths of trees of canopy height between stations on each of the Liverpool and Tomkinson Rivers and Mungardobolo Creek. In each of the three species, mean girths of canopy trees at the stations on each waterway (of Figs. 6.3.4 - 6.3.12) are related to the varying saline conditions shown in Fig. 6.3.13.

In *Avicennia marina*, greatest mean girths, approximately 45-70 cm D.B.H., occurred at upstream sites on the Liverpool and Tomkinson Rivers (Figs. 6.3.4 and 6.3.7). These sites are tidally inundated or flooded by fresh/brackish waters throughout the year (Fig. 6.3.13). Smaller mean girths, typically 20-30 cm D.B.H., occurred at sites (Figs. 6.3.4, 6.3.7 and 6.3.10) inundated by brackish water to seawater in salinity (Fig. 6.3.13). The smallest mean girths (approximately 12 cm D.B.H.) occurred in Mungardobolo Creek at Station 6 (Fig. 6.3.10). The waters at this site range widely in salinity (Fig. 6.3.13) with extremes of interstitial soil salinities of the order of 70$^{\circ}/oo$ being experienced towards the end of the dry season.

In *Camptostemon schultzii*, greatest mean girths of canopy trees, approximately 35-45 cm D.B.H., also occurred at upstream sites inundated by admixtures of fresh/brackish waters on the Liverpool and Tomkinson Rivers (Figs. 6.3.5 and 6.3.8). In more seaward sites and in sites inundated by hypersaline waters (Figs. 6.3.5, 6.3.8 and 6.3.11) mean girths were smaller in the range 15-25 cm D.B.H. Incidentally, in the system of the three waterways in which girths were measured, *Camptostemon schultzii* does not occur in sites inundated by water of salinity greater than about 44$^{\circ}/oo$ with interstitial soil salinities of about 50$^{\circ}/oo$ towards the end of the dry season (Figs. 6.3.11 and 6.3.13).

Similarly in *Rhizophora stylosa*, greatest mean girths of canopy trees, approximately 30-35 cm D.B.H., occurred in sites inundated tidally by admixtures of fresh/brackish waters, while mean girths were smaller, 10-25 cm D.B.H., in sites inundated by waters of brackish to seawater salinities, and were yet smaller, 12-14 cm D.B.H. in sites inundated by hypersaline waters towards the end of the dry season (Figs. 6.3.6, 6.3.9, 6.3.12 and 6.3.13).

These results clearly indicate relationships between mean girths of canopy trees and salinities of waters inundating sites in which they occur. These relationships may be examined further by regression analysis. However, before examining results of such analyses it is worthwhile considering whether there are differences between the three waterways, in mean girths of canopy trees in each species, which are unrelated to differences in salinity of their waters. To examine this, data from sites with similar salinities were selected on the three waterways and in each species the variation in girths of canopy trees were analysed by a nested analysis of variance between quadrats in each station, between stations within waterways and between waterways (Tables 6.3.5 - 6.3.9).

TABLE 6.3.5

Summary of analysis of variance of girths ($\log_e$-transformed data) of canopy trees of *Avicennia marina* at each of two sites on the Liverpool and Tomkinson Rivers and Mungardobolo Creek, N.T. All sites experiencing water salinities of between 35-37‰ and soil salinities 40-60‰ by the end of the dry season. (3 Factors: 2 fixed, one random; random factor nested under one fixed factor, Winer 1971, p.464). Sites used were Liverpool 2 and 3; Tomkinson 1 and 2 and Mungardobolo 1 and 2.

Factor	SS	d.f.	MS	F
Rivers	7.64	2	3.82	1.19 N.S.
Stations (within rivers)	4.55	3	3.19	1.92 N.S.
Quadrats (within stations (within rivers))	11.43	24	1.66	13.95*
Residual	32.12	270	0.12	
Total	55.74	299		

* Significant at 0.05 level.

N.S. Not significant.

Percentage terms from the Mean Square estimate where R = river,

S = Station and Q = quadrat.

σ^2_R = 0.01 = 1.77%

$\sigma^2_{S(R)}$ = 0.08 = 21.57%

$\sigma^2_{Q(S(R))}$ = 0.15 = 43.26%

σ^2_{RES} = 0.12 = 33.40%

Total 0.36 = 100%

TABLE 6.3.6

Summary of analysis of variance of girths ($\log_e$-transformed data) of canopy trees of *Avicennia marina* at two sites each on the Liverpool and Tomkinson Rivers, N.T. These sites experience peak dry season water salinities between 9-18‰ and soil salinities of between 10-25‰ . (3 Factor; 2 fixed, one random, random factor (Quadrats) nested under one fixed factor (Stations), Winer (1971) p.464). Sites used were Liverpool 5 and 6 and Tomkinson 5 and 6.

Factor	SS	d.f.	MS	F
Rivers	0.92	1	0.92	0.38 N.S.
Stations (within rivers)	2.38	2	2.38	2.69 N.S.
Quadrats (within stations (within rivers))	3.53	16	0.88	4.69 N.S.
Residual	33.79	180	0.18	
Total	40.63	199		

* Significant at 0.05 level.

N.S. Not significant.

Percentage terms from the mean square estimate where R = river,

S = station and Q = quadrat.

σ^2_{R} = 0.01 = 4.18%

$\sigma^2_{S(R)}$ = 0.07 = 21.59%

$\sigma^2_{Q(S(R))}$ = 0.07 = 20.01%

σ^2_{RES} = 0.19 = 54.20%

Totals 0.35 = 100%

TABLE 6.3.7

Summary of analysis of variance of girths ($\log_e$-transformed data) of canopy trees of *Rhizophora stylosa* at two sites each on the Liverpool and Tomkinson Rivers and Mungardobolo Creek, N.T. All sites experience water salinities of between 35-37‰ and soil salinities between 40-60‰ by the end of the dry season. (3 Factor, 2 fixed, 1 random, random factor nested under one fixed factor, Winer (1971) p.464). Sites used were Liverpool 1 and 3; Tomkinson 1 and 2, Mungardobolo 1 and 2.

Factor	SS	d.f.	MS	F
Rivers	17.62	2	8.81	4.48 N.S.
Stations (within rivers)	2.45	3	1.97	4.56 N.S.
Quadrats (within stations (within rivers))	2.56	24	0.43	6.24 N.S.
Residual	18.65	270	0.07	
Total	41.29	299		

* Significant at 0.05 level.

N.S. Not significant.

Percentage terms from the mean square estimate where R = river,

S = station and Q = quadrat.

σ^2_R	= 0.07	= 27.33%
$\sigma^2_{S(R)}$	= 0.08	= 30.65%
$\sigma^2_{Q(S(R))}$	= 0.04	= 14.42%
σ^2_{RES}	= 0.7	= 27.57%
Totals	0.25	= 100%

TABLE 6.3.8

Summary of analysis of variance of girths ($\log_e$-transformed data) of canopy trees of *Camptostemon schultzii* at one site each on the Liverpool and Tomkinson Rivers, N.T. These sites experience water salinities of between 9-14‰ and soil salinities of between 10-15‰ at the peak of the dry season. (2 Factor, one fixed, one random, random factor nested under fixed factor, Winer (1971) p.464).

Factor	SS	d.f.	MS	F
Rivers	1.19	1	1.19	2.46 N.S.
Quadrats (within rivers)	1.93	8	0.48	4.50 N.S.
Residual	9.63	20	0.11	
Total	12.75	99		

* Significant at 0.05 level.

N.S. Not significant.

Percentage terms from the mean square estimate where R = river and Q = quadrat.

σ^2_R = 0.01 = 8.83%

$\sigma^2_{Q(R)}$ = 0.04 = 23.65%

σ^2_{RES} = 0.11 = 67.50%

Totals 0.16 = 100%

TABLE 6.3.9

Summary of the analysis of variance of girths ($\log_e$-transformed data) of canopy trees of *Camptostemon schultzii* at two sites each on the Liverpool and Tomkinson Rivers and Mungardobolo Creek, N.T. All sites experience water salinities of between 35-37‰ and soil salinities of between 44-60‰ by the end of the dry season. (3 Factor, 2 fixed, 1 random, random factor nested under one fixed factor, Winer (1971) p.464). Sites used were Liverpool 2 and 3; Tomkinson 1 and 2 and Mungardobolo 1 and 2.

Factor	SS	d.f.	MS	F
Rivers	12.90	2	6.45	110.47*
Stations (within rivers)	0.09	3	0.06	0.11 N.S.
Quadrats (within stations (within rivers))	3.25	24	0.51	7.28 N.S.
Residual	18.83	270	0.07	
Total	35.08	299		

* Significant at 0.05 level.

N.S. Not significant.

Percentage terms from the mean square estimate where R = river, S = station and Q = quadrat.

σ^2_R = 0.06 = 31.98%

$\sigma^2_{S(R)}$ = 0.02 = 11.21%

$\sigma^2_{Q(S(R))}$ = 0.43 = 21.92%

σ^2_{RES} = 0.07 = 34.88%

Totals = 0.20 = 100%

In *Avicennia marina*, variation in mean girth of canopy trees is not significantly related to differences between waterways either in sites experiencing slightly hypersaline conditions in the dry season (Table 6.3.5) in all three waterways or in sites tested on the Liverpool and Tomkinson Rivers experiencing only brackish waters in the dry season (Table 6.3.6). Indeed, components of the total variation attributable to differences between waterways is very low in both analyses; 4.2% and 1.8% respectively. The only significant variation in either analysis is that between quadrats within stations within waterways in the first analysis (Table 6.3.5).

Similarly in *Rhizophora stylosa* there is no significant variation in mean girths between the three waterways in the sites tested experiencing slightly hypersaline conditions in the dry season (Table 6.3.7). However in *Camptostemon schultzii* there is significant variation between the three waterways in mean girths of canopy trees in the sites tested experiencing slightly hypersaline conditions in the dry season (Table 6.3.9), though in smaller analyses involving sites inundated only by admixtures of fresh/brackish waters on the Liverpool and Tomkinson Rivers no such significant variation between the two waterways shows up (Table 6.3.8).

Accordingly the relationship of mean girths of canopy trees and peak interstitial soil salinities measured in the dry season was directly examined in each species for all quadrats on the three tidal waterways using regression analysis (Tables 6.3.10, 6.3.11 and 6.3.12). Separate analyses for each species on each waterway were also performed using soil and water salinities during the peak of the dry season (Appendix 5).

Similar results in general were derived using water and interstitial soil salinities, and therefore in Tables 6.3.10-6.3.12 only relationships to interstitial soil salinities, the more immediate environment of the roots of the trees, are given.

In all three species, mean girths of canopy trees were inversely related to interstitial soil salinity (Figs. 6.3.15-6.3.17). In each of the three species, there was a significant linear relationship between values of mean girth and soil salinities during the dry season for the quadrats, with the inverse linear relationship giving a better fit to the data than a second order polynomial for *Camptostemon schultzii* (Fig. 6.3.16) and *Rhizophora stylosa* (Fig. 6.3.17). For *Avicennia marina* which colonizes sites throughout a broader saline gradient the second order polynomial provided a slightly better fit to the data than the inverse linear relationship (Fig. 6.3.15).

For *Avicennia marina* on the combined Liverpool-Tomkinson-Mungardobolo tidal complex which encompasses the entire range of saline conditions over which the species occurs, the best fit linear and second degree polynomial regressions were

$$y = 53.71 - 0.61x$$

and $$y = 64.48 - 1.265 + 0.008x^2$$

where y = mean tree girth (cm) in each quadrat and x is the peak dry season interstitial soil salinity ($^{o}/oo$).

The second degree polynomial was a significantly better fit than the linear regression (Table 6.3.10), indicating that throughout the entire range of soil salinities under which *Avicennia marina* occurs that the relationship between girth of trees (that have attained forest canopy heights) and peak dry season interstitial soil salinities was curvilinear.

TABLE 6.3.10

Analysis of variance of linear and parabolic regression (Snedecor and Cochran, 1967) of mean girths of canopy trees of *Avicennia marina* on peak dry season interstitial soil salinities from quadrats on waterways within the Liverpool-Tomkinson Rivers system, central Arnhem Land, N.T.

Avicennia - all rivers combined (using soil salinity ‰):

Source	SS	d.f.	MS	F
Regression on x	7948.07	1	7948.07	113.54**
Regression on x and x^2	8515.94	2	4257.97	66.60**
Deviations from linear regression	5819.36	83	70.00	
Deviations from parabolic regression	5243.49	82	63.93	
Curvilinearity	567.37	1	567.37	5.88**
Total	13768.43	84		

** Significant at 0.05 level.

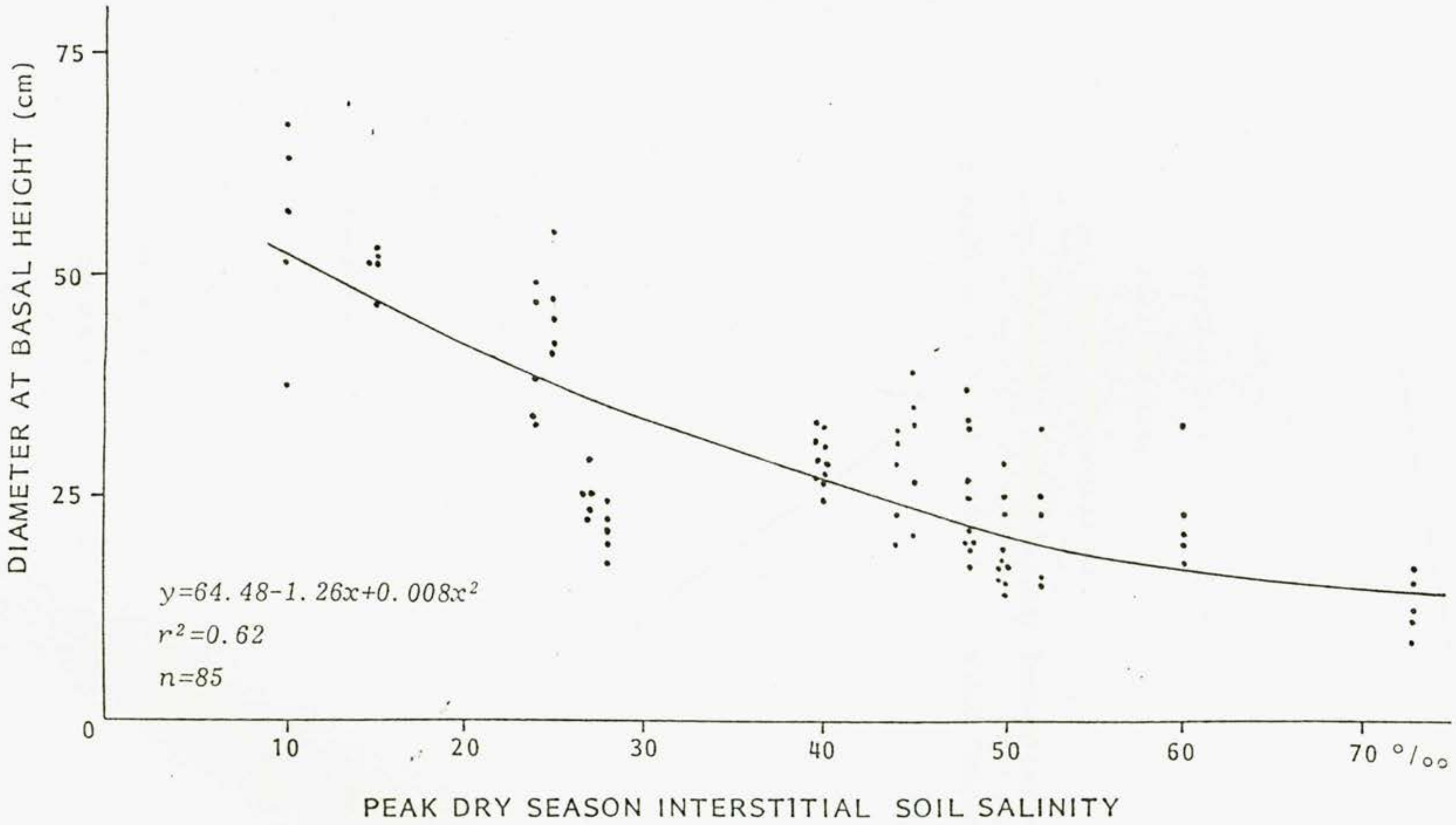

Figure 6.3.15

Relationship between mean girths of canopy trees of *Avicennia marina* against peak dry season interstitial soil salinities from quadrats on the Liverpool-Tomkinson Rivers System.

For *Camptostemon schultzii* on the combined Liverpool-Tomkinson-Mungardobolo tidal complex which encompasses the entire range of saline conditions over which the species occurs, the best fit linear and second degree polynomial regressions were

$$y = 44.84 - 0.57x$$

and $$y = 44.32 - 0.53x - 0.0005x^2$$

where y = mean tree girth (cm) in each quadrat and x is the peak dry season interstitial soil salinity (‰).

The second degree polynomial was not a significantly better fit than the linear regression (Table 6.3.11) indicating that throughout the entire range of soil salinities under which *Camptostemon schultzii* occurs that the relationship between girth of trees (that have attained forest canopy height) and peak dry season interstitial soil salinities was linear.

Camptostemon: All rivers combined (using soil salinity ‰)

Source	SS	d.f.	MS	F
Regression on x	4000.03	1	4000.03	125.09**
Regression on x and x^2	4000.65	2	2000.32	61.65**
Deviations from linear regression	2174.52	68	31.99	
Deviations from parabolic regression	2173.90	67	32.45	
Curvilinearity	0.62	1	0.62	0.02 N.S.
Total	6174.55	69		

** Significant at 0.05 level.

N.S. Not significant at 0.05 level.

TABLE 6.3.11

Analysis of variance of linear and parabolic regression (Snedecor and Cochran, 1967) of mean girths of canopy trees of *Camptostemon schultzii* on peak dry season interstitial soil salinities from quadrats on the combined Liverpool and Tomkinson Rivers and Mungardobolo Creek, central Arnhem Land, N.T.

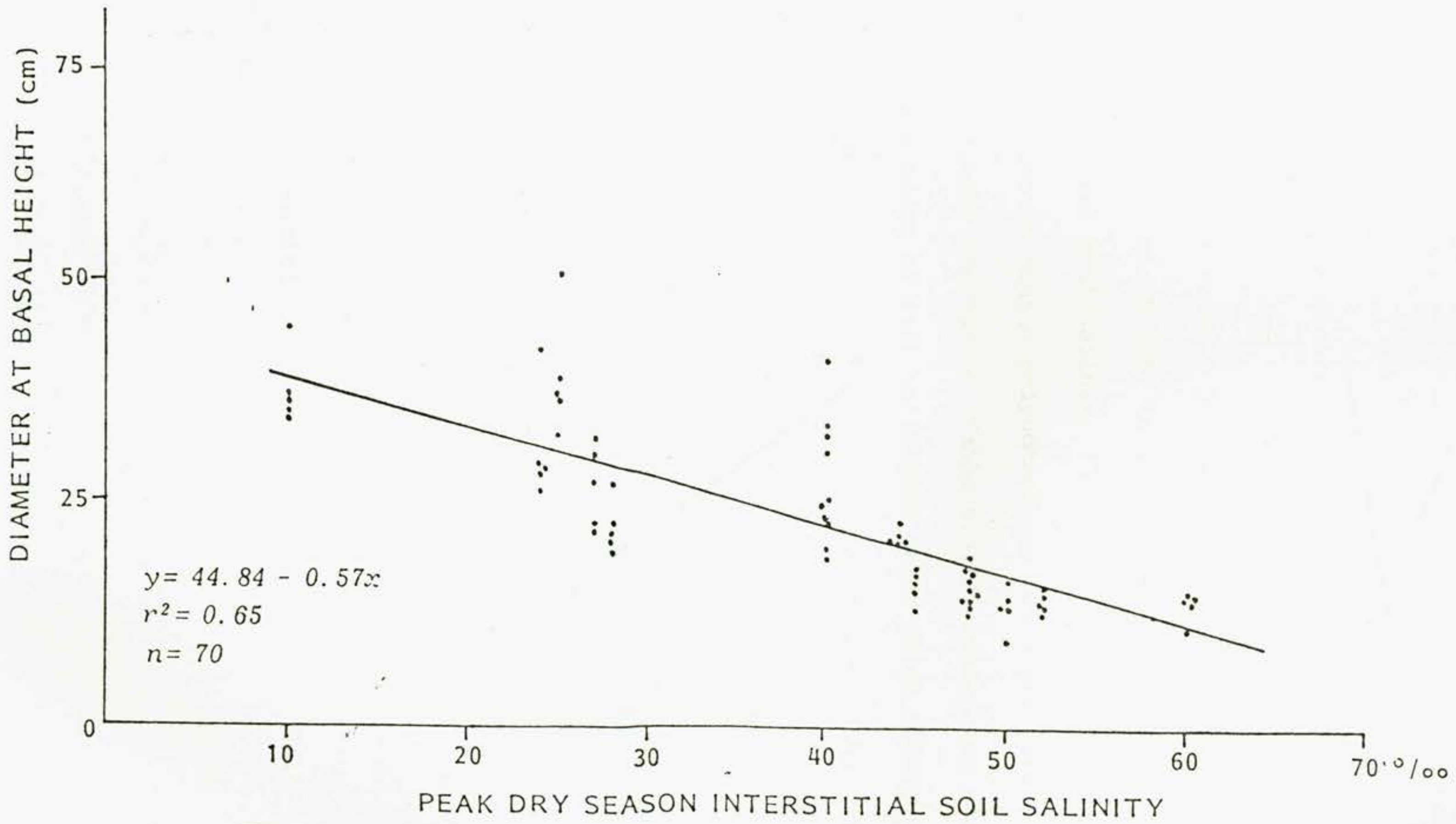

Figure 6.3.16

Relationship between mean girths of canopy trees of *Camptostemon schultzii* against peak dry season interstitial soil salinities from quadrats on the Liverpool-Tomkinson System.

For *Rhizophora stylosa* on the combined Liverpool-Tomkinson-Mungardobolo tidal complex, which encompasses the entire range of saline conditions over which the species occurs the best fit linear and second degree polynomial regressions were

$$y = 41.18 - 0.48x$$

and $$y = 29.85 + 0.08x - 0.007x^2$$

where y = mean tree girth (cm) in a quadrat and x is the peak dry season interstitial soil salinity ($^{o}/oo$).

The second degree polynomial was not a significantly better fit than the linear regression (Table 6.3.12) indicating that throughout the entire range of soil salinities under which *Rhizophora stylosa* occurs that the relationship between girth of trees (that have attained forest canopy height) and peak dry season interstitial soil salinities was linear.

Rhizophora: All rivers combined (using soil salinities $^{o}/oo$)

Source	SS	d.f.	MS	F
Regression on x	1140.86	1	1140.86	37.94**
Regression on x and x^2	1169.32	2	584.66	19.42**
Deviations from linear regression	1744.24	58	30.07	
Deviations from parabolic regression	1715.78	57	30.10	
Curvilinearity	28.46	1	28.46	0.95 N.S.
Total	2885.11	59		

** Significant at 0.05 level.

N.S. Not significant at 0.05 level.

TABLE 6.3.12

Analysis of variance of linear and parabolic regression (Snedecor and Cochran, 1967) of mean girths of canopy trees of *Rhizophora stylosa* on peak dry season interstitial soil salinities from quadrats on the combined Liverpool and Tomkinson Rivers and Mungardobolo Creek, central Arnhem Land, N.T.

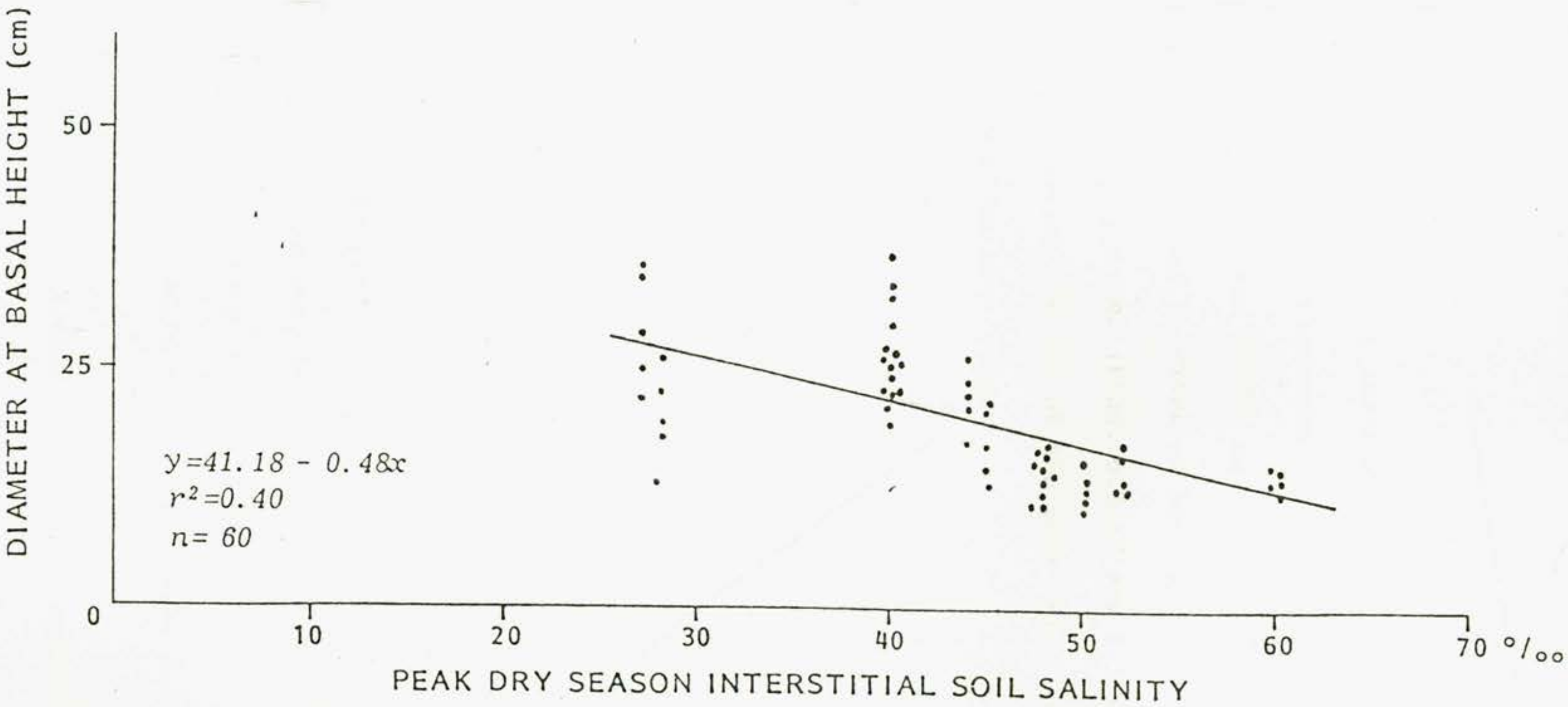

Figure 6.3.17

Relationship between mean girths of canopy trees of *Rhizophora stylosa* against peak dry season intersitial soil salinities from quadrats on the Liverpool-Tomkinson Rivers System.

6.3.2 BASAL AREA

Bole basal areas are related to peak dry season high tide water and soil salinities for the three mangrove species under investigation. The relationships they show with water salinity are not simple inverse ones and differ in form between the species (Figs. 6.3.18 and 6.3.19). For instance the form of the relationship in *Rhizophora stylosa* is converse to that in *Avicennia marina.*

In *Avicennia marina* maximum basal areas of the order of 25 m^2/hectare are attained in sites at both extremes of the range of dry season water salinities (Figs. 6.3.18 and 6.3.19) while in sites inundated by seawaters for 30% of the year (Fig. 6.3.13) basal areas of between 3-9 m^2/hectare occur.

In *Camptostemon schultzii* basal areas were greatest (≃10 m^2/hectare) in sites inundated by admixtures of fresh/brackish waters throughout the year with a gradual reduction (≃2-4 m^2/hectare) in sites inundated by seawaters for considerable periods of the year. A further reduction to around 2 m^2/hectare predominated in sites inundated by increasingly hypersaline waters during the latter half of the dry season (Figs. 6.3.18 and 6.3.19, Appendix 4).

In the stilt-rooted *Rhizophora stylosa* maximum basal areas of about 30 m^2/hectare occurred in sites inundated by seawaters for at least 75% of the year while in sites influenced by increasingly hypersaline waters very low basal areas (≃1-3 m^2/hectare) occur with a slight increase (≃10 m^2/hectare) occurring at sites influenced by fresh/brackish waters throughout the year (Figs. 6.3.18, 6.3.19, Appendix 4).

6.3.3 DENSITY

Stands of *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa* show considerable variations in density throughout the range of saline gradients encountered in this study area in terms of both canopy trees and individuals irrespective of their height (Fig. 6.3.20). As with basal areas, patterns of relationship with water salinities differ in the three species, but with densities *Camptostemon schultzii* and *Rhizophora stylosa* show similar patterns.

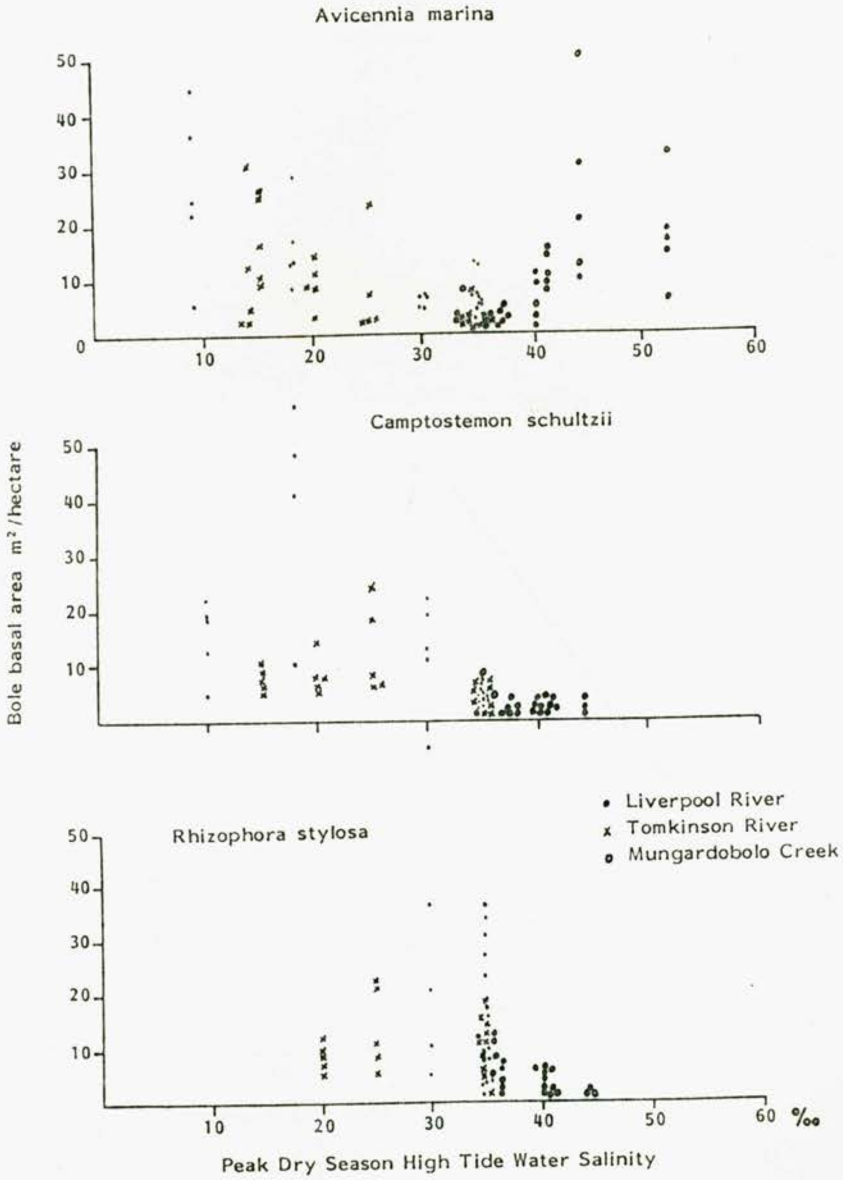

Figure 6.3.18

Summed bole basal areas of canopy trees of *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* at quadrats within stations on the Liverpool-Tomkinson Rivers System.

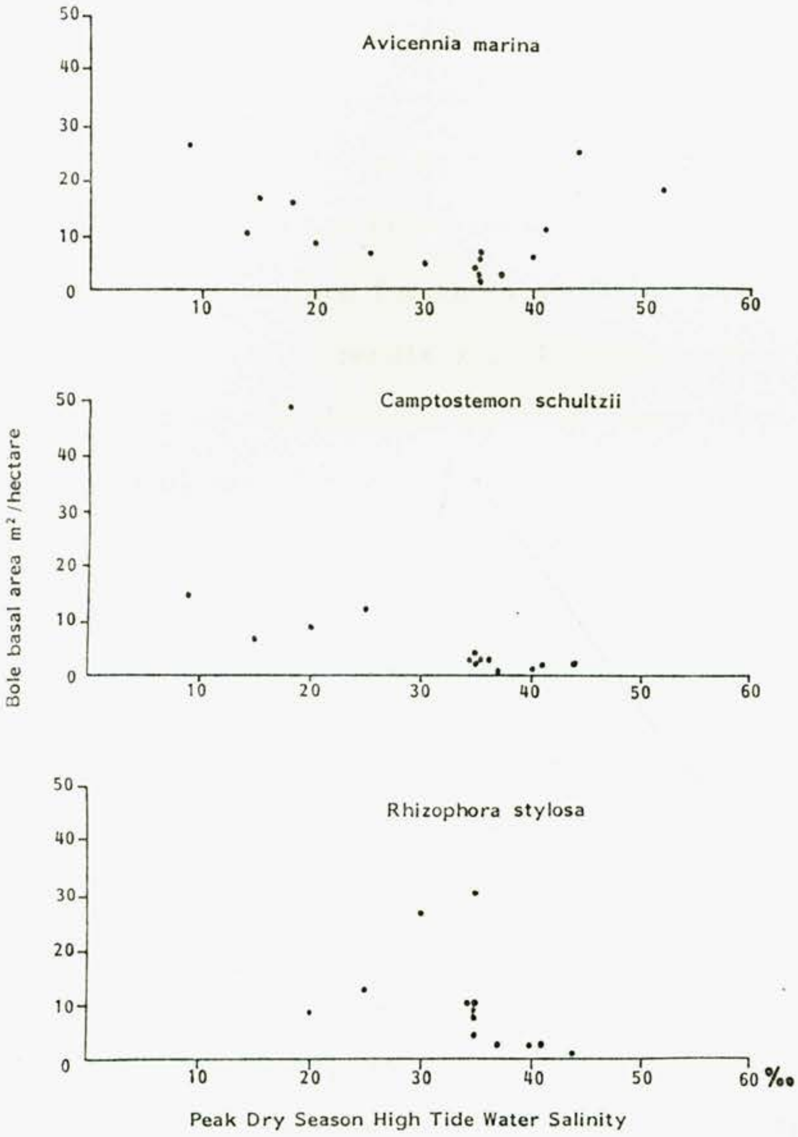

Figure 6.3.19

Summed bole basal areas of *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* at stations on the Liverpool-Tomkinson Rivers System.

In stands of *Avicennia marina*, densities show no systematic change with water salinity for sites either inundated by admixtures of fresh/brackish waters throughout the year or admixtures of fresh/brackish/seawater and slightly hypersaline waters up to 40^{o}/oo by the end of the dry season. At Station 6 on Mungardobolo Creek which is briefly influenced by freshwaters during the wet season but has hypersaline waters up to 70^{o}/oo by the end of the dry season (Fig. 6.3.13) mean densities of 3,130 trees/shrubs/hectare at "all inclusive heights" and 1,206 trees/hectare for trees attaining the scrub canopy height occur (Fig. 6.3.20, Appendix 3). *Avicennia marina*, although occurring in a thicket of thin-stemmed trees of canopy height $\leq$ 3.5 m, is here influenced by only five other mangrove species, all occurring as herbs and low shrubs (*Acanthus ilicifolius*, *Aegialitis annulata*, *Camptostemon schultzii*, *Excoecaria agallocha* and *Xylocarpus australasicus*) due to the extreme seasonal hypersaline conditions. In other sites, trees of the species grew taller and considerably more mangrove species occurred (Appendix 7).

In stands of *Camptostemon schultzii* greatest densities occurred at sites receiving admixtures of fresh/brackish waters throughout the year and also at sites receiving considerable seawater inundation towards the end of the dry season. At sites receiving either more than 75% freshwater inundation throughout the year or hypersaline waters towards the end of the dry season noticeable decreases in densities occurred (Fig. 6.3.20, Appendix 3).

In stands of *Rhizophora stylosa* greatest densities were found at sites influenced by seawater salinities for at least 75% of the year with lower densities in sites with lower or higher water salinities at this season (Figs. 6.3.13, 6.3.20, Appendix 3).

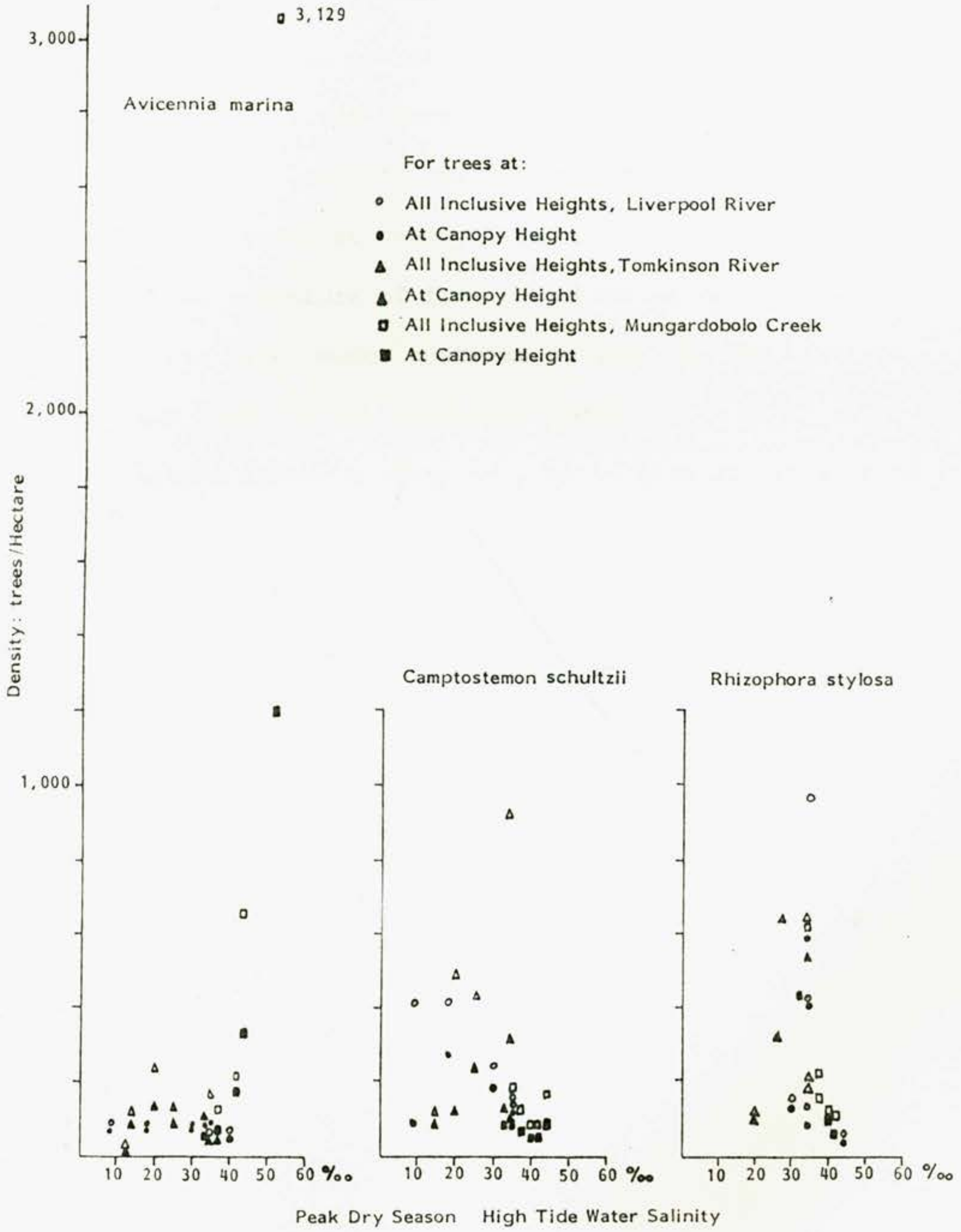

Figure 6.3.20

Densities of trees and shrubs of *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* at "all inclusive heights" and for canopy trees at stations on the Liverpool-Tomkinson Rivers System.

6.3.4 CANOPY HEIGHT

Throughout saline gradients encountered in the study area, all mangrove species show considerable variations in canopy heights. These variations may influence species densities at different sites. Observed canopy heights are given in Appendix 7.

For the species investigated, *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa*, it was found that all

a. attain greatest canopy heights (20-25 m) at sites inundated by an admixture of fresh/brackish waters throughout the year. These sites occur upstream of km35 on the Liverpool River and km40 on the Tomkinson River.

b. attain canopy heights only up to 10 m at sites inundated by seawater (35‰) for at least 30% of the year.

c. show a gradual reduction in canopy height from around 10 to 3 m at sites only briefly influenced by freshwaters during the wet season but inundated by seawaters and increasingly hypersaline waters (≃45-60‰) towards the end of the dry season.

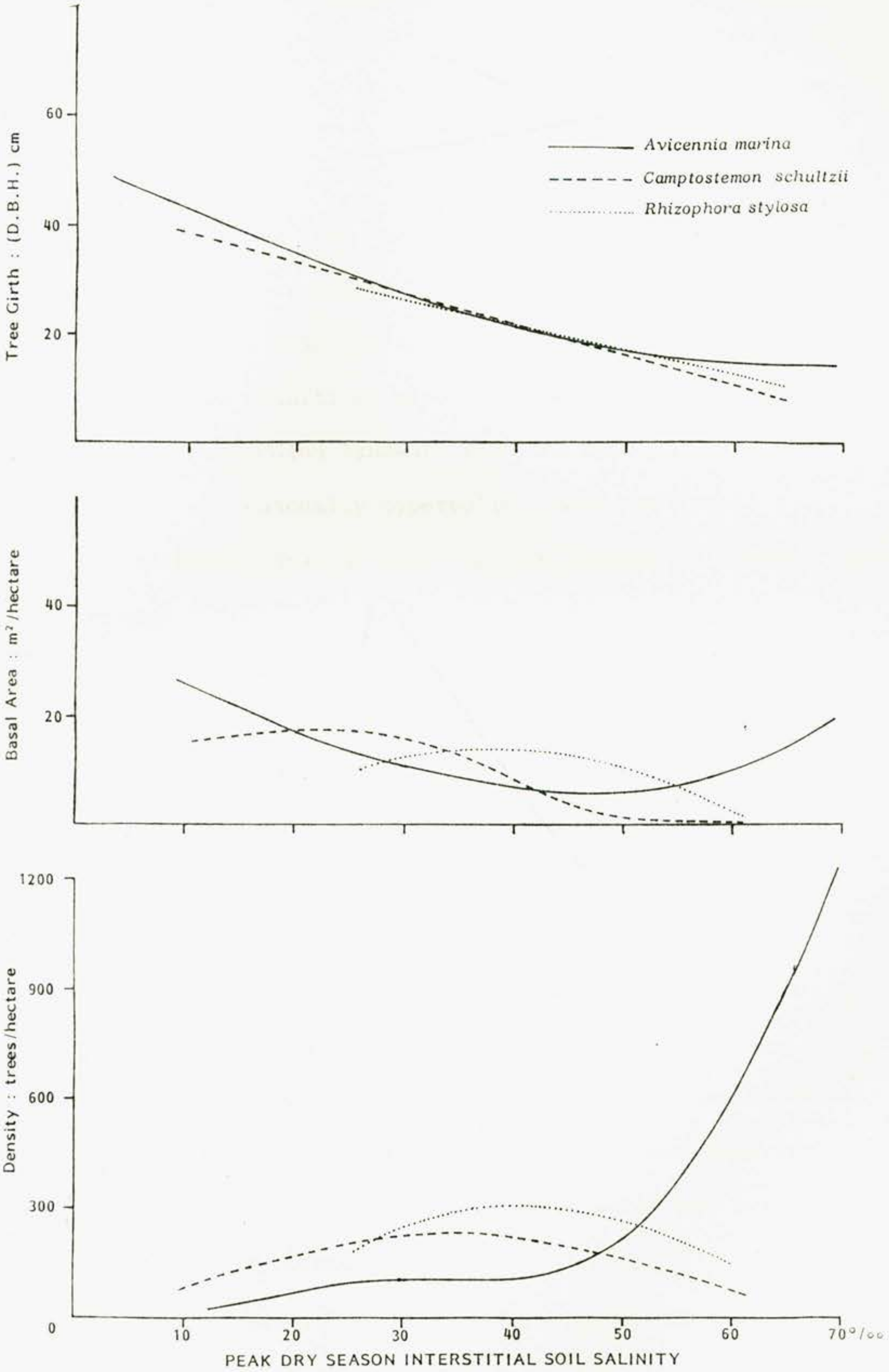

Figure 6.3.21

Idealized representation of girths, basal areas and densities for canopy trees of *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* against peak dry season (1979) interstitial soil salinities on the Liverpool-Tomkinson Rivers System.

6.4 DISCUSSION

Macnae and Kalk (1962) observed that mangroves are tallest along borders of tidal creeks where the ground-water level rises and falls daily with the tides and soils are regularly aerated. These authors note that away from creeks heights of any mangrove species may drop rapidly and in permanently waterlogged centres of mudflats, where conditions are practically anaerobic mangroves are dwarfed to a low scrub. Such conditions also exist on tidal waterways in this study area and proceeding landward from the bank in either an estuarine, fresh-brackish or seasonally hypersaline inundated locality one is confronted either by gradual or abrupt changes in species composition and structure.

In particular, species of mangrove occurring along portions of waterways dominated by seasonally brackish water, where canopy heights of riverside trees attain 15-18 metres, canopy height is progressively reduced further inland under different regimes of tidal inundation. Similarly for mangrove species growing along banks of waterways that become seasonally hypersaline where canopy heights might only be 3.5 metres, there is still a further reduction in canopy heights of the species as one traverses inland from the bank.

In this study it was also found that in bankside vegetation, girths and canopy heights of various species of mangroves growing in tidal waterways varied with variations in water and soil salinities prevailing in the dry season.

In his description of salt flats in Western Australia, Macnae (1968) observed species changes and increasing scrubbiness with increasing soil salinities. He reports dwarfed *Avicennia marina* growing at soil salinities of 90‰ .

Cintron *et al.* (1978) report a rapid increase in mangrove tree mortality beyond a soil salinity threshold of about 60^{o}/oo , and that mangrove tree height (of a number of North American species) is inversely proportional to soil salinity between 17 and 72^{o}/oo . They also postulate that mangrove growth is limited by soil salinities higher than 90^{o}/oo .

With regard to structure, various studies in south-east Asia, in particular Fox (1970), provide detailed data on mangrove swamps from forestry viewpoints. However it needs to be emphasized that these forests have been selectively logged for building materials, charcoals, etc., by local indigenes over countless generations. Nearer the survey area Paijmans and Rollet (1977) provide considerable structural and ecological detail on the mangroves of Galley Reach in Papua New Guinea. Pool *et al.* (1977) and Cintron *et al.* (1978) have examined the structure of North American mangrove forests, but as opposed to this study, provide only overall figures of basal area and density for forests at different localities. Ball (1980) provides structural details of mangrove forests in southern Florida by species. However her detailed study of girths, basal area and densities concerns patterns of secondary succession in contrast to this study on pristine mangrove vegetation.

Concurrent with increases in canopy heights of the three species investigated at sites receiving considerable fresh/brackish water, and also with decreases in their canopy heights with increasingly hypersaline waters, a gradual loss of other mangrove species occurs from fringing riverside vegetation associations. Losses of these species may be attributed to the varied tolerances of individual mangrove species to either excessive freshwater, seawater or increasingly hypersaline water inundation. Variations of density of stands of the three species are considered to be partly related to whether or not other mangrove species or species from freshwater plant complexes are also present. Density of individual mangrove species within a vegetation association fringing tidal waterways is a complex issue influenced by relative sizes of individuals of the species in question, the presence and population structures of other mangrove or strand species and physio-chemical conditions.

Large fluctuations in tree densities of the species investigated, at sites influences by what appear to be "similar" seasonal salinity regimes may be a result of another mangrove species being slightly more successful in establishment. Densities of the species studied fluctuated considerably throughout the saline gradients encountered. An idealized plot of densities of the three species studied is provided in Fig. 6.3.21, showing each species to peak in density at different soil salinities. Such a finding is perhaps not unusual. However, peak density for *Avicennia marina* is attained in waters that become seasonally hypersaline. Highest densities occurred at sites where this species occurred in nearly monospecific stands. For trees attaining canopy height, the highest density recorded for any station was 1,206 trees/hectare (Mungardobolo Site 6). Here with only thin-stemmed, stunted thickets of *Avicennia marina* (canopy height ≤ 3.5 m) most other mangrove species are presumably excluded from establishment by the extremely hypersaline soil and water salinities (50-60°/oo) that occur towards the end of the dry season.

For *Rhizophora stylosa*, peak density occurs at sites subjected to inundation by seawater for at least 75% of the year - a saline condition not tolerated by most mangrove species. Here a density of 588 trees/hectare was attained for trees reaching the canopy height (Appendix 3). *Camptostemon schultzii* for the most part tends to maintain a more consistent density throughout sites experiencing salinities between 20-35°/oo towards the end of the dry season. No sharp peaks in density seemed to occur as was observed in either

Rhizophora stylosa or *Avicennia marina*. Fig. 6.3.21 is considered to summarize adequately for each of the three species the variation of density of its stands in relation to extremes of salinity occurring in different portions of the waterways studied.

There is little doubt that variations in tree density in each of the three species can be related to water and soil salinities. However, to what extent varying regimes of salinity influence density through competition from other mangrove species in the field or by the direct action of the overall admixture of environmental and physico-chemical conditions has not been elucidated.

Basal areas attained by a species are likely to reflect the relative proportions of sites occupied by its individuals as against those of other species of tree, shrub or herb. Thus they would be expected to be high in sites where nearly monospecific stands of the species occur, as in the seasonally hypersaline sites where *Avicennia marina* occurs with high basal areas; and those sites at the true estuary to the Liverpool-Tomkinson Rivers System which experience seawater salinities for over 75% of the year. Here *Rhizophora stylosa* attains high basal areas in nearly monospecific stands. Basal areas of a species may also be high in sites where its stands consist of several individuals with large girths even though the stands are far from being monospecific, as in the occurrence of *Avicennia marina* in sites where waters remain fresh to slightly brackish in the peak of the dry season. For the three species studied, an idealized graph of basal area fluctuations (excluding the basal area of *Camptostemon schultzii* at Quadrat 5, Station 4, Liverpool River) in relation to extremes of seasonally varying salinity is shown in Fig. 6.3.21. Overall, it is shown that each species peaks in basal area at a different salinity. Pool *et al.* (1977), however, report for the south coast of Puerto Rico, an extreme environment characterized by high evaporation causing high seasonal soil salinities, that mangrove areas are characterized by short canopies and low basal areas.

Achievement of large girths by all three species may be attributed either to fast growth rates or long life spans or a mixture of the two. The only consistent pattern the three species show in their occurrence over the extremely wide range of salinities of sites in the study area is the inverse relationship between mean girth of canopy individuals and the peak dry season soil salinity of the sites in which they occur. In this study there is no evidence to suggest whether this variation may be primarily attributed to variation in life span of canopy trees or to variation in growth rates of the trees between the sites. This is a matter for future investigation, as are possible competitive interactions of species of mangroves across the range of extremes in salinities observed between sites. Only when there is further evidence on these matters can the general patterns of variation of mean girth, basal area and density with site salinity in stands of each of these three species be explained further. Meanwhile, in the following chapter daily and seasonal variations of plateau values of stem xylem pressure potentials, in particular for the three species discussed at length in this chapter, are explored over a range of environmental conditions including various soil and water salinities.

CHAPTER 7

Daily and seasonal variations of plateau values of stem xylem pressure potentials of selected mangrove species on tidal waterways in central Arnhem Land, Northern Territory.

7.1 INTRODUCTION

Salinity effects on plants have a dual nature, for salts change both the water relations and the electrolyte balance of plant tissues. As Greenway (1973) remarks "salt accumulation in the environment lowers its water potential with an almost inevitable decrease in water potential of the plant tissues". Mangroves, although occurring in a dynamic saline environment (McMillan, 1974), must like all other plants transpire pure water when stomata are open, allowing net uptake of carbon dioxide in photosynthesis. Many mangrove species however, unlike many mesophytes, experience rapidly fluctuating and sometimes extreme water potentials in the root environment from which this water must be obtained (cf. Miller *et al.*, 1975).

Within the plant, water potential will, in general, lie between that of the root medium and that of the air, and its precise value in each part of the plant will depend, as Cowan and Milthorpe (1968) have shown, on the rate of transpiration and on a number of resistances to water flow. Major resistances are that of the stomata which can be modified by the plant with others occurring in the xylem pathway and at the site of uptake of water from the soil.

Measurement of the water potential of a small shoot provides an approximation of the water potential affecting the leaves. The pressure chamber technique for measuring water potentials of small shoots is usually attributed to Scholander *et al.*, (1962), and has been widely used as shown in the review of Ritchie and Hinckley (1975) of the measurement of water potentials of xylem sap. If the xylem fluid is very dilute, the pressure used to reach end-point in the pressure chamber is essentially equivalent (but opposite in sign) to the water potential of the leaves, but if the xylem sap has an appreciable concentration of solutes the osmotic potential due to these must be added to it to arrive at the total water potential value. In the case of mangroves the xylem solute concentration, although small, is not negligible (cf. Scholander *et al.* 1965) although it was not measured in the present study. For this reason the values obtained with the pressure chamber are termed "xylem pressure potential" throughout.

In this study, investigations of the following problems are reported: whether xylem pressure potential shows daily or tidally controlled fluctuations (cf. Lewis and Naidoo 1970); and whether the lowest xylem pressure potential is correlated with salinity in wet and dry seasons. The possibility was also considered that knowledge of lowest dry season xylem pressure potential values might assist in generating hypotheses about the variation in growth of mangroves along salinity gradients, as described in the previous chapters.

Measurements of xylem pressure potentials of mangrove species were obtained during the wet and dry seasons of 1977, on the Liverpool-Tomkinson and Blyth-Cadell River Systems in Arnhem Land, Northern Territory. Investigations were undertaken to determine the daily (or other short-term) cycles of xylem pressure potentials in *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* in the wet and dry seasons; and following this to observe the xylem pressure potential in the middle of the day - the time at which it was lowest - in these species at sites along gradients of salinity in the wet and dry seasons. A number of additional observations of daytime xylem pressure potentials of fifteen other mangrove species in the study area are included.

7.2 METHODS

For the mangrove species studied xylem pressure potentials were determined for leafy shoots using a pressure chamber ("Scholander bomb"). Shoots were cut from the trees at 1.3 metres and were selected to suit the 6.4 mm orifice of the bomb. For each measurement the pressure chamber (shielded from the sun) was transported to each tree in a boat. After a stem had been sharply cut it was immediately inserted into the bomb. The bomb was closed and inflow of nitrogen started within 10 to 30 seconds of cutting in most cases. On four occasions, usually because of mechanical difficulties and problems of containing the leaves on the shoot within the chamber, it was 30-45 seconds before final closure of the chamber. Nitrogen gas from cylinders was used in the pressure chamber and the end point of measurement was the pressure in MPa required to initiate xylem sap flow from the cut stem. This pressure with its sign changed to negative, is termed the "xylem pressure potential".

Measurements were undertaken during the late wet and late dry seasons of 1977. The positions of all trees used were marked on maps, and the trees tagged with aluminium labels for rediscovery the following season. The same individual trees were used for both wet and dry season measurements. All trees were near the riverbank and were flooded by spring high tides during periods of measurement.

Measurements on one tree of each of *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* at the 30-km mark upstream on the Blyth River, were made at approximately three-hourly intervals for thirty-eight and forty hours in wet and dry seasons respectively. Observations were not continued longer because of fatigue. Tidal fluctuations were determined with a Foxboro tidegauge fixed to a tree at the 30-km mark; air and water temperatures were recorded with thermocouples and Grant multipoint recorders.

On the Liverpool-Tomkinson System five trees of each of the same three species were selected at Stations 1 (17 km), 4 (56 km) and 6 (68.5 km) on the Tomkinson River, Stations 5 (25 km) and 6 (26 km) on Mungardobolo Creek and Station 6 (60 km) on the Liverpool River. Station locations are provided in Appendix 2. These stations encompassed a wide range of saline conditions in which the three species occur. Measurements of xylem pressure potential (one measurement for each species at each of five quadrats within each station) were undertaken during the late wet and late dry seasons. All measurements were made between 1000 and 1600 hours over the plateau periods of the lowest daily xylem pressure potentials. For some of the fifteen other mangrove species studied (*Ceriops tagal* var. *australis*), *Excoecaria agallocha, Xylocarpus australasicus*), measurements were made as late as 1750 hours but only on specimens receiving full afternoon sun. Sunset was at 1819 hours in May 1977 and 1829 hours in October 1977 (Nautical Almanac 1977).

7.3 RESULTS

7.3.1 Daily cycles in xylem pressure potentials of *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa* during the wet and dry seasons on the Blyth River, Northern Territory

Figures 7.1 a and b show a steady increase in xylem pressure potentials (for all three species and in both seasons) from about midday to midnight or shortly after, roughly steady values from then until just before dawn, and then a more rapid decrease till about midday. After this the steady increase till midnight and the plateau in the small hours were repeated until observations were terminated. Tidal fluctuations followed a different pattern from fluctuations in xylem pressure potential, with approximately 2.1 and 2.6 tidal cycles in the

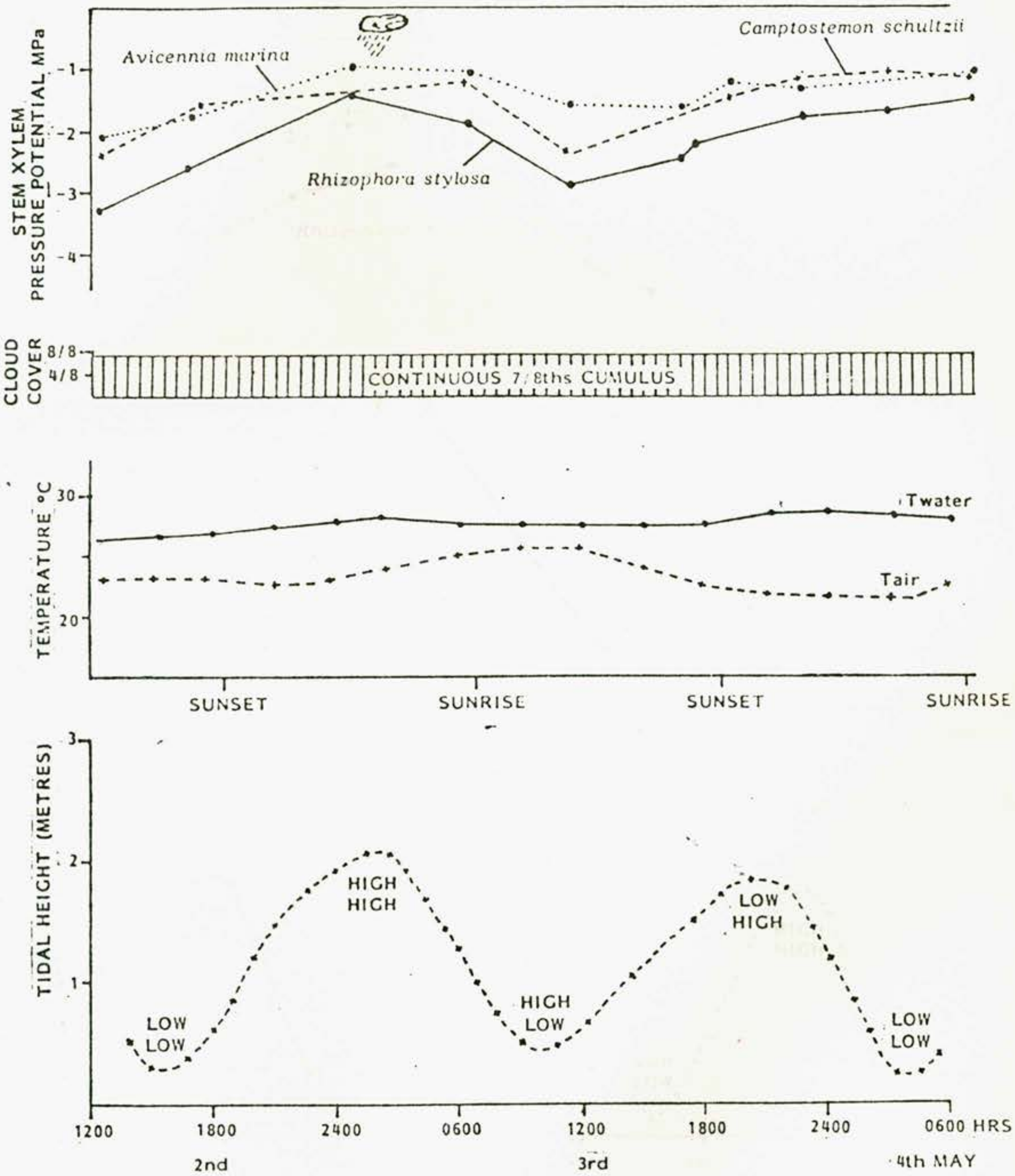

FIG. 7.1a

Daily variation in xylem pressure potentials of *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa;* air and water temperatures and tidal cycles at km30, Blyth River, Arnhem Land, Northern Territory during the late "wet" season 2-4th May, 1977.

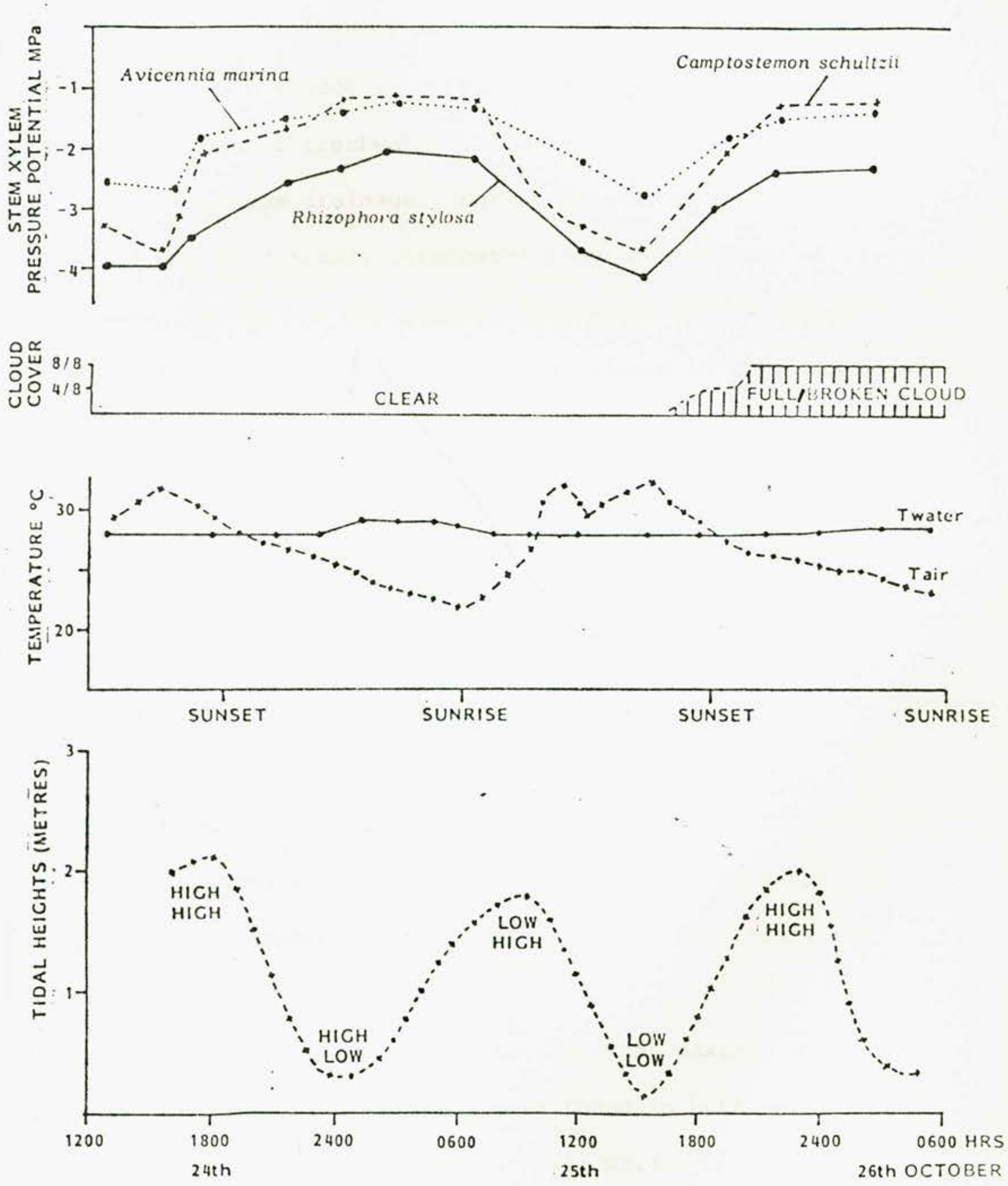

FIG. 7.1b

Daily variation in xylem pressure potentials of *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa;* air and water temperatures and tidal cycles at km 30, Blyth River, Arnhem Land, Northern Territory during the late "dry" season 24-26th October, 1977.

wet and dry-season periods of measurement respectively, compared with about 1.5 cycles of xylem pressure potential in the same period on each occasion. There were only very slight variations in water temperature (27°C and 28-29°C) and water salinity (2‰ and 8‰ during the wet and dry seasons respectively).

Seasonal differences in tidal cycles with the shorter cycle occurring in the wet season is attributed to the influence of the considerable influx of freshwaters into the tidal portions of the river from areas of upstream drainage. During periods of heavy flooding tidal cycles may be entirely eliminated from the waterway as floodwaters flow seaward. During the dry season, freshwater inflow diminishes resulting in tidal cycles which, although delayed in time and amplitude, are more in tune to tidal cycles of the adjacent Arafura Sea. Negligible changes in water salinity are found in this portion of the waterway which remains slightly brackish throughout most years. The maximum daily air temperature recorded was 32.6°C - during the dry season - a period without much noticeable cloud cover. This compares with a daily maximum temperature of 25.5°C during the late wet season measurements when considerable cloud cover was in evidence. Cloudiness during this period was estimated at 7/8ths cumulus. Light rain from a cloudburst fell immediately prior to readings being taken at 0100 hours (3.5.77) and measurements of stem xylem pressure potentials for *Avicennia marina* could not be obtained.

From Figs. 7.1 a and b it is seen that maximum nocturnal xylem pressure potentials ≃-1.0 Mpa were found in both seasons for *Avicennia marina* and *Camptostemon schultzii* whilst *Rhizophora stylosa* varied from -1.5 Mpa in the "wet" to -2.3 Mpa during the "dry" season. Minimum daily xylem pressure potentials were more extreme for all three species in the "dry" season and occurred around 1130 hours during May in the late wet season and around 1500 hours during October in the late dry season.

Although stem xylem pressure potentials fluctuated more during the late dry season in all species, potentials in *Rhizophora stylosa* always remained more negative (-½ to -1 Mpa) than those in *Avicennia marina* or *Camptostemon schultzii* in the "wet" season; and than those observed in *Avicennia marina* in the dry season. However when compared to xylem pressure potentials observed in *Camptostemon schultzii*, xylem pressure potentials observed at the same hour in *Rhizophora stylosa* were more negative (≃ -1 to -1½ Mpa) during the late "dry"season.

Avicennia marina, closely followed by *Rhizophora stylosa,* showed the largest daily fluctuations of xylem pressure potentials in the late "dry" season. However the form of the curve in *Avicennia marina* has a longer nocturnal plateau with more rapid rises and falls in pressure potential. In the late "wet" season, *Rhizophora stylosa* shows the largest daily fluctuation in xylem pressure potential, closely followed by *Avicennia marina*, whereas *Camptostemon schultzii*, although possessing least fluctuations throughout both seasons, has a longer nocturnal plateau in the late "dry" season. Lowest (most negative) xylem pressure potentials occurred during the dry season (≃1500 hours), with -3.7 Mpa for *Avicennia marina,* -2.6 Mpa for *Camptostemon schultzii* and -4.1 Mpa for *Rhizophora stylosa*.

7.3.2 Seasonal Measurements of daily plateau values of xylem pressure potentials of mangrove species on the Liverpool-Tomkinson Rivers System

Daytime plateau values of xylem pressure potentials (measured between 1000-1600 hours) of trees of *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa* are shown in Fig. 7.2 in varying conditions of salinity at stations along the Liverpool-Tomkinson Rivers system. Some measurements for other species obtained in the estuary of

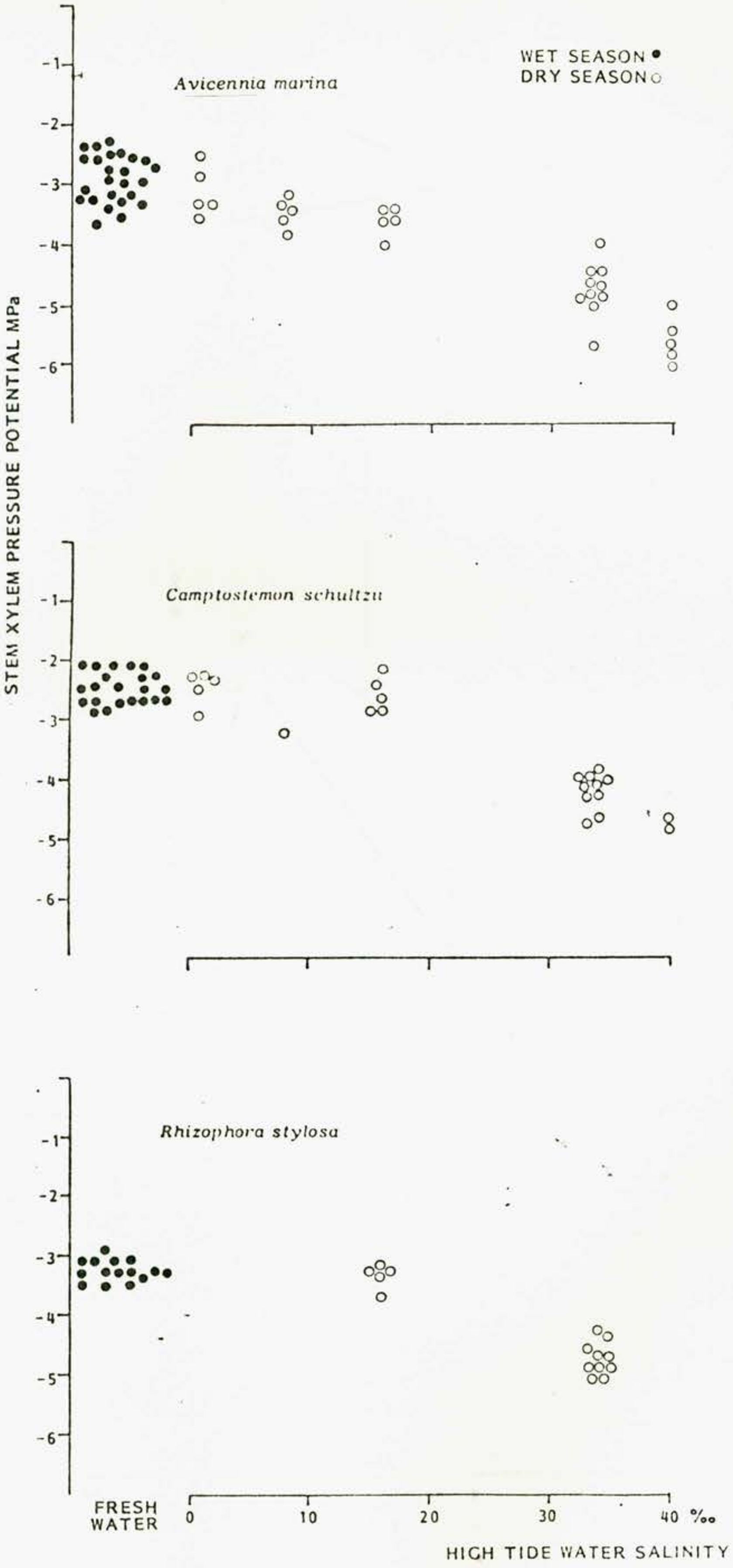

FIG. 7.2

Daytime plateau values of stem xylem pressure potentials for trees of *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* in varying conditions of salinity at stations along the Liverpool-Tomkinson Rivers System, N.T. (stems measured between 1000-1600 hours).

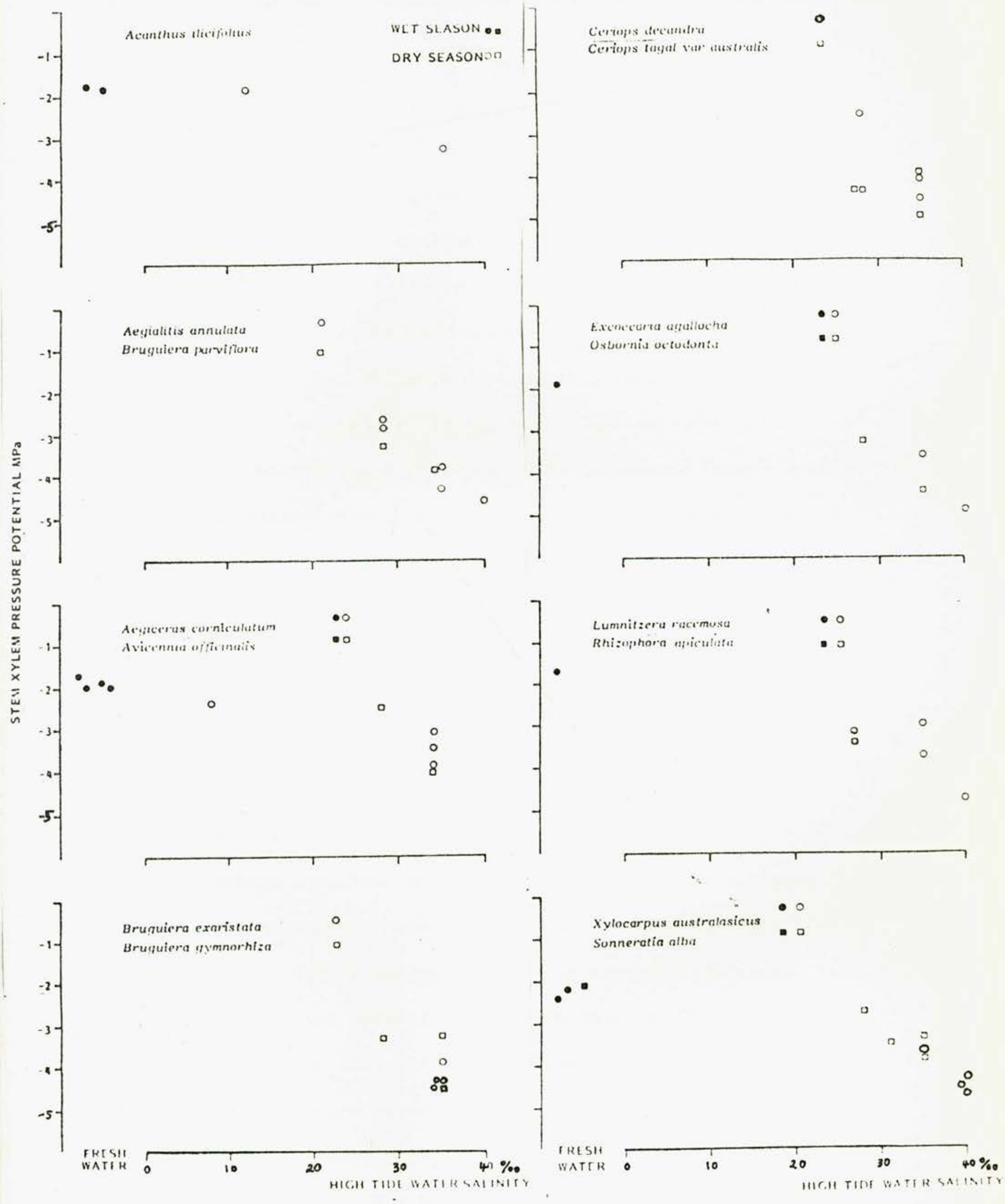

FIG. 7.3

Daytime plateau values of stem xylem pressure potentials for mangrove species in varying conditions of salinity on the Liverpool-Tomkinson Rivers System, N.T. (measurements taken between 1000-1600 hours).

the Liverpool River (10 km upstream) are given in Fig. 7.3. In each group (where late wet season and late dry season values are shown) the same trees were measured in each season. Each graphed value represents a single measurement (data provided in Appendix 6).

All sites were under freshwater inundation during the late wet season (2.5.77) and the uppermost site on the Liverpool River remained fresh in the late dry season (22.10.1977) also. At all sites in the "wet" and in the freshwater site in the "dry" season the species studied showed daytime xylem pressure potentials between -2 and -3.6 Mpa, with *Rhizophora stylosa* tending to the more negative values. *Camptostemon schultzii* remained least negative whilst *Avicennia marina* spanned almost the entire range. *Rhizophora stylosa* was absent from the uppermost (freshwater) station on the Liverpool River, the two uppermost seasonally brackish stations on the Tomkinson River and the uppermost seasonally hypersaline station on Mungardobolo Creek.

Apart from Station 6 on the Liverpool River, sites on the Liverpool and Tomkinson Rivers and Mungardobolo Creek had increased in salinity as the dry season progressed. The daytime xylem pressure potentials in *Camptostemon schultzii* did not differ from the freshwater (and wet season) values at values up to $17^{o}/oo$ and up to this salinity those for *Rhizophora stylosa* were also all (except one) within the wet season range. At the highly saline stations on Mungardobolo Creek, during the dry season, all the species showed much more negative xylem pressure potentials than in the site (sampled during the dry season) on the Liverpool River where waters remained fresh throughout the year (km60). The lowest daily xylem pressure potentials recorded were -6.1 MPa for *Avicennia marina* and -4.9 MPa for *Camptostemon schultzii* in waters of salinity $40^{o}/oo$ and -5.1 MPa for *Rhizophora stylosa* (water salinity $34^{o}/oo$) in Mungardobolo Creek. The values recorded for *Avicennia marina* at the Tomkinson River sites with high tide water salinities of $8^{o}/oo$

and 15-17^{o}/oo in the late dry season ranged between those for freshwater and those for extreme salinity. There was a statistically significant correlation between daytime xylem pressure potential and water salinity in each species ($r^2 = 0.8429$ $p \ll 0.001$; $r^2 = 0.8198$ $p \ll 0.001$; $r^2 = 0.8264$ $p \ll 0.001$; in *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa,* respectively). Although data are too few for detailed analysis the xylem pressure potential values for all the other species (Fig. 7.3) appear to fit a similar pattern.

7.4 DISCUSSION

Adaptations thought to be important in the maintenance of a salt balance by mangroves include as Clough *et al.*, (1982) have summarized:

a) The capacity of the roots to discriminate against NaCl.

b) The possession by some species of specialized salt secreting glands in their leaves.

c) The accumulation of salt in leaves and bark.

d) The loss of salt when leaves and other organs are shed.

Apart from the possession of salt secreting glands by a few species, all these adaptations occur to varying degrees in all mangrove species.

Among these four, the capacity of the roots to discriminate against salt is pre-eminent in influencing xylem pressure potential. Measurements of the sodium chloride concentration and osmotic potential of the xylem sap of mangroves indicate, as Scholander *et.al.*, (1962, 1965); Atkinson *et al.*, (1967) and Scholander, (1968) have shown, that sodium chloride is largely excluded from the xylem and that species with salt-secreting glands in their leaves have the capacity to exclude 80-85% of the sodium chloride in seawater whereas those species without such glands are more efficient, excluding 95-98% of sodium chloride in seawater. It might thus be expected that salt-excreting species (eg. *Avicennia marina*) would tend to have somewhat less extremely low pressure potentials than those without, at a given water or soil salinity. The data for *Rhizophora stylosa* agree with this but the data for *Camptostemon schultzii* do not, indicating that factors other than the physiology of the roots must predominate in the determination of xylem pressure potential (e.g., stomatal behaviour).

Maintenance of turgor in living plant cells requires at least that the intracellular osmotic potential must be more negative than the osmotic potential of the substrate. In the xylem in equilibrium with such living cells, in the absence of large concentrations of solutes, this is shown as a negative xylem pressure potential. Additionally, daily patterns of change in water potnetial in woody plants have been shown by many workers (for example Klepper, 1968; Wolff *et al.*, 1977; Losch *et al.*, 1982), with more negative values occurring in the middle of the day reflecting loss of water from the plant during transpiration. Both these aspects are evident in the results reported here.

Turner and Long (1980), reported that in rapidly transpiring leaves water potentials of uncovered leaves measured in a pressure chamber were 0.2-0.7 MPa lower than water potentials of leaves covered with a plastic sheath from just prior to excision to the completion of the experiment. These researchers found that the error in the water potential of uncovered leaves arose from rapid water loss in the first thirty seconds after excision. They also found that the degree to which the water potentials were lowered depended on:

1. The rate of transpiration
2. The leaf water potential at the time of excision
3. The species
4. Whether the species was growing in a glasshouse or in the field.

The measurements reported here were made in 1977, and plastic bags were not used to cover the shoots at excision: it is likely therefore that errors exist in the values of xylem pressure potentials recorded. These errors are likely to be small at night when transpiration rates would have been low; and greater in the daytime, especially in the late dry season. The error involved is likely to be small since in nearly all cases the shoot was enclosed in the "bomb" within thirty seconds of excision. Compared to the herbaceous species (e.g., jojoba, cotton) used by Turner and Long (1980), mangrove species examined here are likely to have low transpiration rates in view of their tendency to xeromorphy (cf. Saenger 1982).

Although this study was undertaken prior to Turner and Long's experimental findings it was found in a preliminary test with *Camptostemon schultzii* (at the beginning of the dry season, June 1977 that shoots from the same tree and "bombed" within thirty seconds of excision provided a xylem pressure potential of -4.4 MPa whereas a similar shoot excised and left in the sun for fifteen minutes before being enclosed in the chamber developed a much more negative potential of -5.1 MPa. Thus it was held to be imperative (in this study) that the boat containing the pressure chamber was situated immediately adjacent to the shoots of each species before excision.

Daily cycles of xylem pressure potential with most negative values in the middle of the day and least negative at night are shown in Fig. 7.1, the two seasonal sets of observations from the Blyth River. Scholander (1968) found for a number of mangrove species values between -2.7 and -5.7 MPa with the more negative values occurring during the daytime when presumably the evaporative loss from leaves is greatest (cf., e.g., Allaway *et al.*, 1981 who showed a correlation between increasing xylem sap flow rate and increasingly negative xylem pressure potential in small shoots of several coral island woody strand species). Attiwill and Clough (1980) also reported findings for *Avicennia marina* in Victoria similar to those for the three species in the Northern Territory in Fig. 7.1. Air temperature is also correlated with xylem pressure potential: this may be partly due to high temperatures in the daytime being related to a lowering of the water potential of the air (and thus leading to increased transpiration), and partly to the correlation of both temperature and xylem pressure potential (via stomatal behaviour) with time of day.

No evidence was obtained supporting an effect of tidal cycle on xylem pressure potential - the fluctuations in xylem pressure potential had a period close to twenty-four hours while the tidal cycles observed were considerably shorter (Fig. 7.1). Lewis and Naidoo, (1970) reported that tides influence the apparent transpirational rhythms of *Avicennia marina* in South Africa but if this had been so in the trees observed here an effect on xylem pressure potential would have been expected. In the Blyth River study water salinity was only slightly brackish, varying from $2^{o}/oo$ in the late wet season (May) to $8^{o}/oo$ in the late "dry" season (October). Here all water potential values are between zero and -0.5 MPa, however the night-time maximum xylem pressure potential was -1 to -1.3 MPa in *Avicennia marina* and *Camptostemon schultzii* and lower still in *Rhizophora stylosa*. Since salinity and xylem pressure potential are strongly negatively correlated (in the long term; cf. Fig. 7.2) it might be that in a site and at a time of year where large tidal fluctuations of salinity occur (cf, upstream portion of Mungardobolo Creek during the late dry season) some tidal influence on xylem pressure potential would be detectable. Further work is required on this aspect.

In the late "wet" and late "dry" seasons both *Avicennia marina* and *Camptostemon schultzii* had only slightly negative plateau values, suggesting recovery of plant water potential to some equilibrium value at night. This has been used as a criterion for absence of water stress (cf., Roberts *et al.*, (1981) referred to in Losch *et al.*, (1982)), but in *Rhizophora stylosa* the xylem pressure potential did not reach the same value in the "dry" as in the "wet" and also only achieved "plateau" values for a short period during the night; this could be interpreted as evidence of water stress. However the data are far from sufficient to assist in explaining variation in mangrove growth which had been hoped for (cf., Chapter 6) and for this more detailed physiological investigations would be required.

In the late "dry" season xylem pressure potential in *Rhizophora stylosa* was 3.5 to 3.6 MPa more negative in the middle of the day than the water potential of the surrounding slightly brackish water: in *Avicennia marina* it was 3 to 3.2 MPa and in *Camptostemon schultzii* it was 2.2 to 2.3 MPa more negative. In the late "wet" season however these negative differences were somewhat reduced with xylem pressure potentials in *Rhizophora stylosa* 2.9 to 3.3 MPa; in *Avicennia marina* 2.4 to 2.6 MPa and in *Camptostemon schultzii* 1.7 to 2.1 MPa more negative than the potential of the water inundating bases of the trees. This degree of difference may well be due to the effect of daytime transpiration on top of

(a) the water potential of the surrounding water

(b) whatever the night-time activity is (eg, cell growth)

that causes the xylem pressure potential to be more negative than the water potential of the water inundating the tree bases.

Although only surface water salinity was measured at the Blyth River site it has been shown (Chapter 3) that interstitial soil salinities are slightly higher at any site than surface waters inundating substrates on flood tides. However, as the Blyth River site was only slightly brackish throughout the year, differences in interstitial soil salinities from surface tide water would be negligible and still not account for xylem pressure potentials of all three species being more negative than the water potential. Perhaps soil salinity at the root interface where salt exclusion occurs (i.e. endodermis) is considerably higher than the overall interstitial soil salinity at any site due to salts, after exclusion, being concentrated around the endodermis? This a problem arising from studies reported on in this Chapter that requires specialized investigation.

In Fig. 7.4 it is shown that in order to extract freshwater from seawater a mangrove species need only attain an osmotic potential (i.e., total water potential in this case) of about -2.5 MPa as seawater contains approximately 35 grams solute/litre - mostly sodium chloride.

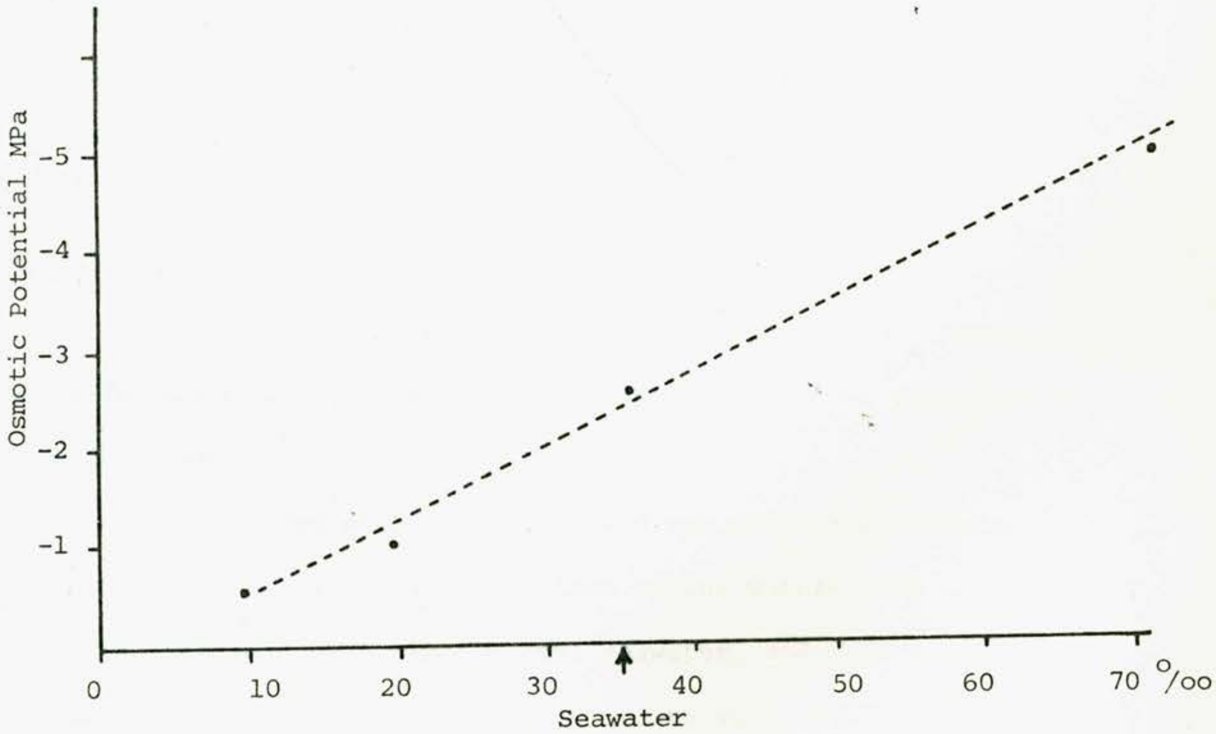

Fig. 7.4 Osmotic potential of saline waters - adapted from Rozema (1975).

However in seawater salinities mangrove species in Figs. 7.2 and 7.3 typically attained xylem pressure potentials of -4 to -5 MPa. It is apparent then that all mangrove species maintained much lower xylem pressure potentials in the middle of the day than was required to extract freshwater from seawater. Conversely at sites inundated by freshwater - with essentially no saline stress in either wet or dry seasons - mangrove species occurring at such localities (viz *Avicennia marina, Camptostemon schultzii*) again maintained considerably lower xylem pressure potentials (≃ -2 to -3 MPa) than required for extraction of this freshwater (cf., Fig. 7.2)).

In maintaining much lower xylem pressure potentials in the heat of the day than is required to extract freshwater from saline waters of various concentrations it is possible that some species - *Avicennia marina, Osbornia octodonta, Ceriops tagal* var.*australis, Rhizophora stylosa* and *Aegialitis annulata*, in particular, may be leaving their stomata open and transpiring, whereas other species may be partially closing their stomata at internal water potentials closer to that of the substrate (e.g., *Acanthus ilicifolius, Lumnitzera racemosa* and *Xylocarpus australasicus* - Fig. 7.3). Again there is scope for much further physiological work on the water relations of these species.

Scholander *et al.* (1965) found sap pressures of mangroves high enough to extract freshwater from saline waters with a salt concentration about 2.5 times normal seawater, and Cintron *et al.* (1978) consider that the limits of mangrove growth with respect to soil salinity appears also to be at 2.5 times the concentration of salt in normal seawater (≃90^{o}/oo). The findings reported here also show that these mangrove species have xylem pressure potentials which would be in equilibrium with 2 to 2.5 times seawater, but these xylem pressure potentials apparently result from transpiration (since they occur in daytime) together with a root environment slightly more concentrated than seawater. In mangroves growing in seasonally saline areas of 90‰ as Cintron *et al.* (1978) relate, then it could be expected that their xylem pressure potential might be as low as -8 MPa or more if they transpire. In this regard, although not a part of this study, it would be very interesting to observe plants in such conditions and especially to enquire into the osmotic concentrations of their cytoplasm and vacuoles and whether the diurnal rhythm of their stomatal opening (and transpirational stream) differs markedly from mangroves growing under the same climatic regime in less saline habitats.

CHAPTER 8

CONCLUSION

When the survey reported in this thesis began, it was apparent that, in terms of the distribution of species of mangroves, the coastline of northern Australia was one of the least studied portions of the entire Indo-Pacific region. The Indian Ocean, Timor and Arafura Seas each have shores on this coast, and knowledge of the distributions of many mangrove species along it is clearly important in the biogeography of mangroves of the whole region.

In elucidating distributional patterns and biogeographical questions in mangroves, this study has only been partially successful. Its findings reiterate the complexity of distributional problems and the need to examine all species distributions individually. Following Chapter 1, in which a generalized account of the river systems and variations in environmental factors such as climate, tides, oceanic currents is provided, Chapter 2 examined distributions of individual mangrove species and suggested that local climatic factors appeared largely responsible for much of the present variation in species diversity. Other workers, including Fosberg (1961, 1975), Macnae (1966,1968), Chapman (1970, 1975, 1976), Zahran (1975, 1977) and Cintron *et al.* (1978) have also stressed that increasing climatic aridity results in a reduction of floristic diversity of mangroves in both tropical and sub-tropical regions.

In Chapter 2 it was also suggested that for many mangrove species recorded in only central and eastern portions of the survey area and which fruit mostly in the wet season, eastward flowing currents might preclude their colonization of western portions of the survey area.

However the direction of surface currents is often reversed for considerable periods during cyclonic storms. It is postulated that the floating fruits and disseminules of those mangrove species with restricted discontinuous distributions across the northern coastline of the Northern Territory could theoretically reach all regions of the survey area. That all species recorded in this survey do not occur at all sites is then of considerable interest.

Successful establishment of any species at any site then within its geographic range is considered (as Saenger *et al.*, (1977) so aptly put it) to depend on the complex interrelation of historical, environmental, biological and chance factors. In addition problems of species' distributions are further complicated by microclimate which may allow establishment of a species under cover of other species in harsh climatic environments. Under seasonally arid conditions it has been shown that, in soils and other substrates of tidally inundated areas, concentrations of salt may build up to well above those normally occurring in seawater. Occurrence of some species of mangroves and not others in arid areas may be related to variation between species in their salt tolerance and mechanisms for regulating salts in or excluding them from water entering their tissues.

As discussed in a recent review by Mizrachi *et al.*, (1980), different mechanisms regulating salts in or excluding them from water entering tissues, operate in different mangrove species. However there does not seem to be any evidence that "salt-excluding" species (i.e., *Excoecaria agallocha*, *Lumnitzera racemosa* and *Xylocarpus australasicus*) occur less in arid hypersaline sites than "salt-excreting" species and only *Aegialitis annulata* and *Avicennia marina* (both salt-excreting species) occur in more extremely hypersaline sites than them.

In this study it is clearly apparent that there may be a strong connection between degrees of climatic aridity, salt-tolerance and geographical distribution of species of mangroves. Species which only occur in sites where salinities rarely if ever exceed those normally occurring in seawater are confined to relatively few areas in the seasonally less arid portions of the area surveyed across northern Australia. *Bruguiera sexangula, Xylocarpus granatum, Lumnitzera littorea, Sonneratia caseolaris* and *Ceriops tagal* are species with such geographical and ecological occurrences within the survey area. Other species, which occur in sites where salinities exceed those normally found in seawater, invariably occur much more widely in the survey area.

It is apparent that an ability to tolerate extremely high salinities, even for quite limited periods of the year and a wide range of salinities, would provide certain species with advantages in establishment throughout tidal waterways in this survey area. Such species are likely to be more ubiquitous in occurrence than those species that can tolerate salinities only slightly greater than seawater (35^{o}/oo) or largely fresh/brackish waters. Thus the limits of salt tolerance by the various species, particularly seedlings, may be an important factor in helping to explain distribution, abundance and structure of different mangrove communities in this survey area. Additionally, it is apparent that most fruiting occurs during the "wet" season when tidal inundation is more pronounced and a greater range of sites is available for colonization. If the timing of fruiting and thus dispersal of fruits and disseminules are of paramount importance in colonization and establishment then establishment and early growth of seedlings may be particularly critical for survival of many mangrove species in the survey area. This suggestion could be investigated by detailed observations of these phases of the life cycle in the field.

The occurrence of individual species of mangrove is related to subtle variations in seasonal climatic aridity and seasonal variation in water salinities in tidal waterways. Tidal systems on the northern coastline of the Northern Territory were floristically more diverse than those in the Kimberley, Joseph Bonaparte Gulf and Gulf of Carpentaria regions. It was found that the most diverse mangrove flora in the survey area occurred in the Arnhem Bay/Gove region of the Northern Territory - an area receiving some rainfall in most months of the year - and the least diverse flora occurred in seasonally arid sites around the southern portion of the Gulf of Carpentaria and Joseph Bonaparte Gulf. However for some sites in the wettest region of the survey area (c. 1500 mm/annum) (Daly River, Port Keats, Moyle River) very few mangrove species occurred but this finding could be more related to seasonality of rainfall and the considerable aridity experienced by these sites during the dry season.

The distributions of species of mangroves in northern Australia show certain trends. *Heritiera littoralis* is totally absent from the Northern Territory but is present on the east Queensland coast. *Bruguiera sexangula, Ceriops decandra, Ceriops tagal, Nypa fruticans, Rhizophora apiculata, Rhizophora lamarckii, Sonneratia alba* and *Sonneratia caseolaris* all occur at sites across the northern coastline of the Northern Territory and down the east Queensland coastline, but remain unrecorded at any site within the larger portion of the Gulf of Carpentaria. Other species, *Bruguiera gymnorhiza, Bruguiera parviflora, Camptostemon schultzii, Lumnitzera littorea, Scyphiphora hydrophyllacea* and possibly *Xylocarpus granatum* are represented only by straggly trees/shrubs at few sites within the Gulf.

The reduction in floristic diversity in most of the Gulf of Carpentaria is not attributable to "latitudinal sifting" of species as all the Gulf lies within the geographic ranges of all these species. The Arnhem Bay/Gove region at the north western extremity of the Gulf with twenty-two species recorded, has the most diverse mangrove flora of any region in the Northern Territory. Likewise, the Port Musgrave region on the north-eastern shores of the Gulf of Carpentaria with twenty-seven recorded species (pers. obs.) is also particularly diverse in species when compared to other sites detailed by Bunt and Williams

(1980) and Bunt *et al.* (1982) in north-eastern Queensland.

The pattern of high numbers of species for mangroves at sites near the northern limits of the Gulf of Carpentaria and extremely low numbers of species recorded from sites further within this Gulf, frequently only eight to eleven species, poses a number of problems.

The prevailing sea currents flow east along the northern coastline of the Northern Territory into and around the Gulf of Carpentaria during the "wet" season, when the fruiting of most mangroves occurs. The currents thus pass the Arnhem Bay/Gove region, deflect across the Gulf entrance to the Port Musgrave region in Queensland and then move southwards in a clockwise direction around the Gulf. Floating disseminules of the various mangrove species should then retain viability over such small sea journeys (when contrasted to the distributional spread of many of the species throughout islands in the Pacific Ocean), and seem likely to reach all sites within the Gulf of Carpentaria. Circumstantial evidence for this is the restricted local occurrences of species like *Acanthus ilicifolius*, *Bruguiera parviflora*, *Camptostemon schultzii* and *Lumnitzera littorea* in extremely sheltered habitats in southern parts of the Gulf. It is suggested that propagules of many other species also reach these shores but that they do not become established due to the considerable climatic aridity experienced in this region during the "dry"season.

A situation analogous to that in the Gulf of Carpentaria exists in the distribution of mangroves in the Cambridge and Joseph Bonaparte Gulfs on the north-west coast of Australia. Numbers of species of mangroves commonly recorded on particular waterways in these Gulfs range between only seven to thirteen species (Thom *et.al.*, 1975; Wells, 1982) while further south at sites in the Kimberley region of Western Australia between thirteen to fifteen mangrove species are frequently recorded (Semeniuk *et al.*, 1978; Wells, 1981).

Of the thirteen species occurring in the Cambridge and Joseph Bonaparte Gulfs, *Camptostemon schultzii, Rhizophora stylosa* and *Sonneratia alba* are infrequently encountered and then only as straggly trees or shrubs in contrast to their considerable abundance in adjacent tidal waterways of the Kimberleys (Wells, 1981).

Also, both *Bruguiera parviflora* and *Bruguiera exaristata* are less frequently encountered amongst the mangrove vegetation around Cambridge or Joseph Bonaparte Gulfs than at localities further south in the Kimberleys.

It might be expected that there would be fewer mangrove species in the Kimberley region, lying at higher latitudes than the Cambridge and Joseph Bonaparte Gulfs. Such is not the case. The increase in number and abundance of species in the Kimberleys and the floristically and structurally depauperate mangrove scrubs fringing waterways entering the two latter mentioned gulfs may relate to subtle differences in seasonal aridity as shown in the Climatic Averages, N.T., W.A. (1975).

The south-east trade winds that blow rather consistently across the hot, dry interior of the continent during the "dry" season (Gentilli, 1971) are considered by this writer to be most important in their effects on species numbers and structure of the mangrove vegetation along both the north-west coast of Australia and throughout the lower portions of the Gulf of Carpentaria. These drying winds blow straight into the mangrove scrubs fringing the low level plains abutting these gulfs and many species of mangroves with more humid climatic requirements are thus excluded from establishment in such seasonally arid regions. In the Kimberley region, which is also subject to considerable climatic aridity, the more diverse mangrove flora occurs in scattered pockets beneath cliffs of drowned river valleys. Such vegetation is often shielded from the sun's direct rays for a larger portion of the day (particularly in the months of the dry season during the winter due to the aspect of the overhead cliffs, and is also protected from the desiccating effects of the south-east trade winds by the Mitchell Plateau.

Population structure of certain species of mangroves varies with the extent of seasonal variaton of soil salinity. From investigations into variations in girth, basal area and density along seasonal salinity gradients in the Liverpool-Tomkinson River system, it was found that in *Avicennia marina*, *Camptostemon schultzii* and *Rhizophora stylosa* there is an inverse relationship between mean girth of canopy individuals and the peak dry season soil salinity of the sites in which they occur. In this study there is no evidence to suggest whether this variation may be primarily attributed to variation in life span of canopy trees or to variation in growth rates of trees between sites. Variations in density and basal area over the range of seasonal salinities between sites were less consistent between the three species.

Basal areas and densities of these three species were found to be high at sites where nearly monospecific stands of the species occur, as in seasonally hypersaline sites (*Avicennia marina*), those sites in the true estuary of the Liverpool-Tomkinson Rivers System which experience seawater salinities for over 75% of the year (*Rhizophora stylosa*) and upstream brackish water sites (*Camptostemon schultzii*). Overall it was shown that each species examined peaked in basal area and density at different salinities.

In all three species individuals attain greatest canopy heights (20-25 m) at sites inundated by admixtures of fresh/brackish waters throughout the year and obtain canopy heights only up to ten metres at sites inundated by seawater for at least 30% of the year. Individuals of all three species also show a gradual reduction in canopy heights from around ten to three metres at sites only briefly influenced by freshwaters during the wet season but inundated by seawaters and increasingly hypersaline waters (45-60°/oo) towards the end of the dry season.

It is possible that sizes attained by mature individuals of *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa* may be controlled by seasonal variation in water potential. A statistically significant correlation between xylem pressure potential and salinity was found in the three species. Here lowest xylem pressure potential inversely correlated with water salinity but was not dependent on site. In an examination of daily and seasonal variations of plateau values of stem xylem pressure potentials of selected mangrove species, there was no evidence of an effect of tidal cycle on xylem pressure potential. Late in the dry season, *Avicennia marina* showed the largest daily fluctuations in xylem pressure potentials, closely followed by *Rhizophora stylosa*. The lowest (most negative) xylem pressure potentials recorded in *Avicennia marina, Camptostemon schultzii* and *Rhizophora stylosa* were during the "late dry" season.

Although varying with species it was found that xylem pressure potentials 2-2.5 MPa below that of the surrounding water were maintained and that differences were more extreme during the "dry" than the "wet" season. Also no correlation was found in variations in xylem pressure potential with the physiological difference between species excreting and those not excreting salts from their leaves, nor was there any evidence of physiological disorder at extremes of range/season except for lack of overnight recovery of xylem pressure potential in *Rhizophora stylosa*.

The findings reported here show that some mangrove species may develop xylem pressure potentials which would be in equilibrium with 2 to 2.5 times seawater, but that these xylem pressure potentials apparently result from transpiration (since they occur in daytime) together with a root environment slightly more concentrated than seawater. These findings agree with those of Scholander *et al.*, (1965) who found sap pressures of mangroves high enough to extract freshwater from saline waters with a salt concentration about 2.5 times normal seawater and those of Cintron *et al.*, (1978) who consider that the limits of mangrove growth with respect to soil salinity appears also to be at 2.5 times the concentration of salt in normal seawater.

Overall, this thesis provides new distributional and ecological information for mangrove species in tidal waterways of the Kimberley region (Western Australia) and throughout the Northern Territory. This information should also be of use to researchers working in the field of mangrove ecology as detailed studies on changes in floristics, girth, density, basal area and numerous other investigations can be undertaken within this survey area without having to be apprehensive about the findings because of known but unquantified man-induced regimes of disturbance. Such disturbances have been detailed by Christensen (1982) and include charcoal production, boatbuilding, fodder, forestry, exploitation, thatch collection and reclamation activities which are widespread throughout most of the African, Middle-East, Indian and South-East Asian coastlines. In addition the regions surveyed at the confluence of the Indian Ocean, Timor and Arafura Seas now provide the extreme distributional limits for many species that are widely distributed throughout the entire Indo-Pacific region.

It is considered that detailed palynological investigations of ancient mangrove swamps in the survey region need to be undertaken before any attempt is made to speculate further on reasons for the non-occurrence of many mangrove species from sites across this northern coastline of Australia.

It is suggested that differences in water relations between the various mangrove species are related to mechanisms of salt balance and leaf morphology in different climatic regions. More detailed physiological work is needed, especially on root response to salinity, and on stomatal behaviour and the influence of salinity on photosynthesis, and future investigations made in this area may significantly help to unravel some of the patterns of zonation and distribution of the various plant species considered as mangroves.

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