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Structure and productivity of inland mangrove stands at Lake MacLeod, Western Australia

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Abstract

Lake MacLeod has the largest area of inland mangroves in the world, where communities of stunted *Avicennia marina* (Forsk) Vierh occur isolated from coastal mangroves. These mangroves exist in extremes of environmental stress, mainly related to high salinity, as a consequence of the extreme environment associated with their location on the margins of a non-tidal salt lake in an arid climate. Characteristics of this unique mangrove system are described, showing an annual productivity of 855 g dry wt m^{-2} and an average biomass of 121.3 t ha^{-1}. These are equivalent levels to open coastal mangroves in sub-tropical Eastern Australia. Phenological patterns showed a maximum production of 3–4 g m^{-2} d^{-1} associated with fruiting during late summer, and minimum leaf loss during the winter period June to September.

Keywords: mangroves, *Avicennia marina*, arid, inland, Lake MacLeod, productivity, structure

Introduction

Lake MacLeod is a large saline coastal lake located approximately 30 km north-north-west of Carnarvon, Western Australia. It has an area of 220 000 ha, of which permanent waters cover *ca* 6 000 ha. The salt lake is episodically inundated by fresh water, allowing development of a unique assemblage of wetland types in Australia (Lane *et al.* 1996). These include permanent saline wetlands and inland mangrove swamps that are maintained by subterranean waterways. The lake is a major migration stop-over and drought refuge area for shorebirds, and is also one of the most important non-tidal stop-over sites in Australia. It also supports Australia's and the World's largest inland community of mangroves and associated fauna. Lake MacLeod is listed on the Register of National Estate and is recognised in the Directory of Important Wetlands in Australia (Lane *et al.* 1996).

Lake MacLeod's mangrove community is the larger of only two inland occurrences in mainland Australia; the other is also in Western Australia, at Mandora Salt Marshes (Beard 1967). The Lake MacLeod mangroves occur as low closed-forest to open scrub/shrubland, forming narrow margins that fringe water bodies at the sinkholes, channels and the central lake. Surrounding areas support low open samphire shrubland. There are two main areas, 7.5 ha at North Cygnet Pond, and 15 ha at South Cygnet Pond (Johnstone 1990). The only mangrove species occurring in Lake MacLeod is *Avicennia marina* (Forsk) Vierh, which is the only mangrove species to reach this far south on the WA coast (Semeniuk 1993).

Mangroves inhabit the intertidal zone of sheltered shores in the tropics or sub-tropics. Those that occur inland, isolated from the ocean, are very unusual and for this reason these rare cases are well described in the literature. Because mangrove seeds or propagules are dispersed by seawater, these inland locations are usually relics of a former sea level, so have geological interest.

Several limestone islands in the Caribbean area have inland saline ponds connected with the ocean by submarine caves, supporting inland mangroves. In Bermuda there are many small mangrove areas, some occurring in inland anachaline ponds that exchange water with the ocean through submarine caves (Thomas, 1993). These occur at sea level, and water salinity is around 35 ‰. Thomas *et al.* (1992) described biotic characteristics of the largest mangrove ponds, finding species variability of mangrove and root biota between ponds, caused by isolation of communities. In the Bahamas, mangroves 50 km inland are described from Inagua by Lugo (1981) at three locations with no apparent connection with the ocean. The island is limestone, and the inland mangrove areas are cut off from the ocean by lithified beach ridges. Evaporation from the large shallow lakes raises salinity to up to 70 ‰, which has the effect of stunting the mangrove trees. Barbuda has inland mangrove ponds 2–4 km from the ocean and separated by Pleistocene beach ridges of 2–4 m in height (Stoddart *et al.* 1973). These inland *Rhizophora* thickets are dense and productive, but tended to be of lower height than the 7 m coastal *Rhizophora* on Barbuda. The distribution was interpreted as a geological relic, caused by sea-level change.

In the South Pacific, Woodroffe (1987) described inland mangroves on a small island of Tuvalu, Nanumanga, where mangroves fringe a water body that

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has no connection with the ocean. Here, inland mangroves, mostly *Rhizophora stylosa*, comprise 9.2 % of the island area.

In the Indian Ocean, Van Steenis (1984) described a unique stand of mangroves (*Bruguiera* sp) on the eastern shore terrace of Christmas Island. The stand is 0.33 ha, 120 m inland and occurs between the elevations of 24 to 37 m above sea level (Woodroffe 1988). Corals in growth position on the terrace were dated to the last interglacial, suggesting that this stand of mangroves has persisted as a shoreline relict during the last 120 000 years of lower sea level. The stand occurs at a freshwater spring, where the mean annual rainfall is 2 000 mm. Large *Bruguiera* here indicate that the genus grows well in fresh water, with good regeneration.

In northern Irian Jaya, Van Steenis (1963) described the mangrove *Sonneratia caseolaris* growing at a freshwater lake around 75 m above sea level. This is attributed to the geological uplifting of northern New Guinea. The same species has been observed growing inland at Timika in southern Irian Jaya, close to the Mile 21 replanting station of Freeport mine (J Ellison, University of Tasmania, personal observation). This location is 10 m above sea level, on a riverbank, and about 10 km inland from the estuarine mangroves.

In Western Australia, Beard (1967) described a large mangrove community 25 km inland of the 80 Mile Beach, at Mandora. The location is a salt creek in limestone, which is lined by mangrove trees of up to 5 m (*Avicennia marina*). There is no tidal connection with the ocean at the site.

These examples all indicate that mangroves occurring inland have been cut off from the open ocean by geological enclosure or sea-level change, most commonly on limestone islands. Thus they would have been isolated from the coastal mangrove genetic pool since the cut off time. The characteristics of inland mangroves at Lake MacLeod are investigated here.

The objective of this study was to establish a baseline survey of the mangroves on Lake MacLeod, to characterise these unique mangroves, and to contribute a starting point for long-term monitoring. Monitoring sites were established at three representative areas of the mangrove margins, at the vents, on an island, and in the southern part of Ibis Pond. Measurements were made of stand structure, crown cover, seasonal production and phenology, annual production, growth rates, and plot biomass.

Methods

Lake MacLeod

Lake MacLeod is situated in the Carnarvon Basin at 23° 36'–24° 38' S, 113° 30'–113° 55' E (Fig 1), and is composed of calcareous marine deposits. It is a former sea embayment that was separated from the sea at the south end by development of sand dunes and mid-Holocene sea-level fall. There are few data on the past sea-level patterns from the region, although a mid-Holocene highstand has been modelled, reaching a maximum of 2 m above present sea level at Exmouth Gulf around 6 000 years BP (Lambeck & Nakada 1990). To the west of the lake is the Tertiary limestone Quobba Ridge, forming high sea cliffs in places, overlain with sand.

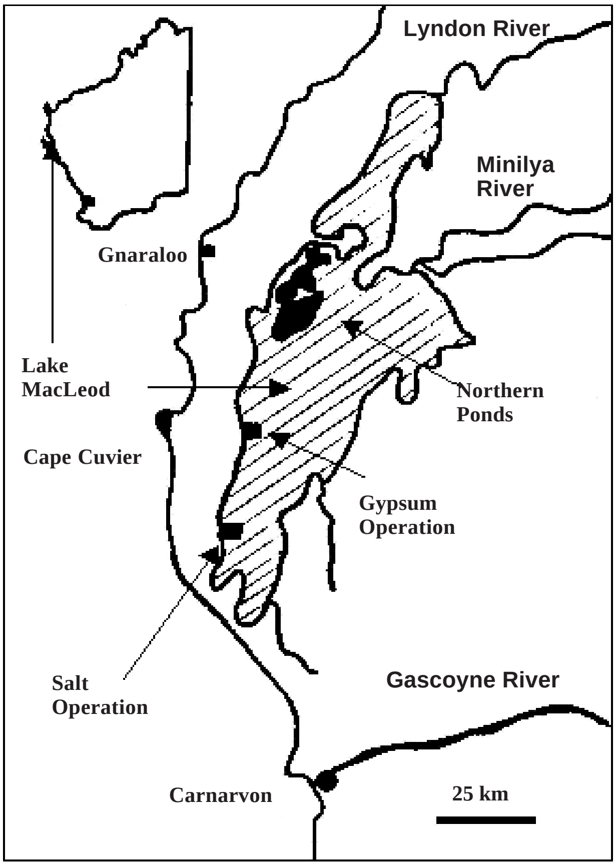

Figure 1. Location of Lake MacLeod and the Northern Ponds.

Ocean water passes underground 18 km through the limestone barrier, driven by a hydraulic head of 3–4 m to rise in sinkholes (“vents”) in the central west part of the lake bed (Handforth *et al.* 1984). The lake surface is at an elevation of 3–4 m below sea level, and consists of Cygnet (north) and Ibis (south) Ponds (Fig. 1). The sinkholes, outflow channels and ponds are permanent, although the southern lake varies in area depending on factors such as rainfall or prevailing winds. The vents are several meters in depth; the central pond is *ca* 1 m deep, and the southern pond *ca* 1.5 m deep. The salinity at the vents is close to seawater, with a salinity gradient rising towards the southern pond.

Freshwater enters Lake MacLeod from several creeks and rivers. Surface inflow from Lyndon and Minilya Rivers is episodic (substantial discharge) or near-seasonal (only the nearby lake-bed inundated). Flooding from the Gascoyne River is infrequent, probably once in ten years, but it can cause the lake to be extensively inundated (such as 1989) or to fill (such as 1980 and 2000). However, the climate is arid. Median and mean annual rainfall at Gnaraloo (see Fig 1) are 203 mm and 230 mm respectively, mostly falling in May–July, and annual evaporation across the site is *ca* 2800–3000 mm (Lane *et al.* 1986).

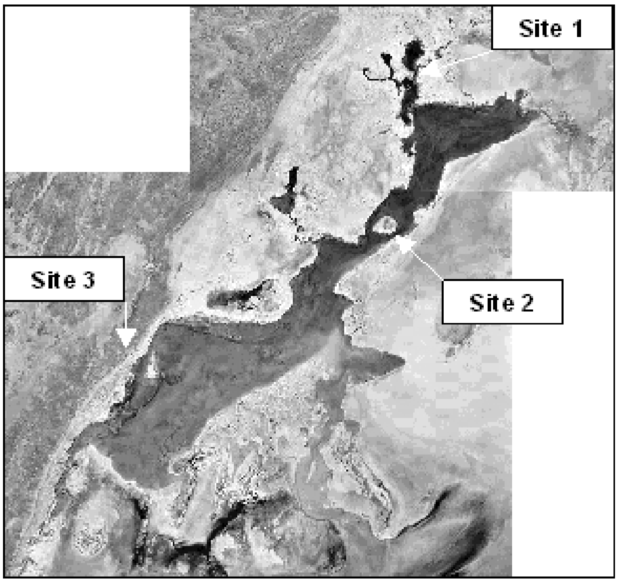

Figure 2. Aerial photograph of Cygnet Pond showing the locations of the three mangrove monitoring sites. Photo 5142 of Minilya (SF49-16) 16/06/95, Western Australian Department of Land Administration.

Monitoring Sites

Permanent plots for monitoring of mangrove community structure were established in December 1997 at three representative sites within the Lake MacLeod mangrove system. The sites (Fig 2) encompass the variability of mangrove types found at Lake MacLeod, of fringing mangroves close to the vents (site 1), on a mid-lake island (site 2), and fringing the main water body at distance from the vents (site 3).

Three replicate permanent monitoring plots, each of 10 x 10 meters, were established at each site location. All trees and seedlings within the plots were tagged and girth measured. Where trees had multiple branches, which occurred in the majority, all were tagged and measured.

Litter fall was measured to quantify vegetative production and phenology. In each plot at each site, two 1 m^2 litter catchers were hung below the mangrove canopy (Saenger & Snedaker 1993). These were emptied each quarter, and the catch oven dried at 60 °C for 2 days, then sorted and weighed. Given the aridity of the Lake MacLeod site, it was possible to empty the litter traps at periods longer than monthly (which was not feasible owing to remoteness and poor access). Trees were re-measured annually, and crown cover and crown density were also estimated in November 1999 to give percent foliage cover (Daubenmire 1959).

Mean tree density and tree height were calculated for each site from the three replicates at each site. Leaf litter data were averaged for the 6 litter catchers at each site, and expressed in dry weight (g) per day for each collection period. Annual variation in production and phenology were analysed from the period September 1998 to September 1999, when collections were most regular.

Biomass was calculated using the allometric relationships established by Clough *et al.* (1997) between stem diameter and above-ground biomass, for the multi-stemmed trees of *Avicennia marin*a found in arid northern WA. Their procedure treats each stem as a discrete tree that shares a proportion of the butt and other elements common to all stems. They measured stem diameters of trees located at Port Hedland, Dampier and Exmouth Gulf, at a height of 10–15 cm above the stem junction, then cut the trees and divided them into leaves, branches, stems and butts. From these measurements they determined an allometric equation that estimates tree biomass from stem measurement (Table 2 of Clough *et al.* 1997); $\log(W) = -0.7506 + 2.299 \log(D)$ where W is dry weight (kg) and D is stem diameter (cm). Clough *et al.* (1997) pointed out that it is largely a question of semantics whether or not the multi-branched architecture of arid mangrove trees should be regarded as multi-stemmed or simply multi-branched. The distinction is irrelevant if the allometric relationship is being used to estimate total above-ground biomass or the above-ground biomass of all woody parts of the tree (trunks and branches); it is potentially an issue only if separate estimates of stem biomass and branch biomass are needed.

Results

The mangroves of Lake MacLeod form a narrow margin around permanent ponds, of usually less than 20 m in width, with dense shrub growth. At all sites a distinct zonation in *Avicennia* physiognomy is apparent. The most developed zone is of tall, dense shrubs fringing the water body (Fig 3). The width of this zone is generally 10 m or less, but at Goat Bay (Site 3) the width extended to 50 m in places. The shrub height and zone width of the taller mangroves is greater on shoreline promontories than bays. Adjacent to the Lake MacLeod water bodies, the density of *Avicennia* pneumatophores is far higher than for *Avicennia* on the open coast (Fig 3), indicating low oxygen levels in the soil and interstitial water. This is also a feature of inland mangroves of Bermuda (Thomas 1993), and could be caused by the lack of aeration of mangrove mud without tidal movement.

Behind the shoreline zone is a sharp demarcation from dense mangrove cover to domination by open salt flat,

Figure 3. *Avicennia marina* forest fringing Lake MacLeod at site 2, showing multi-stemmed architecture, very dense pneumatophores, and an eroding shore.

Figure 4. *Avicennia marina* margin with salt flat at Lake MacLeod, showing scattered stunted trees. Also shown is the variability in pneumatophore height at Site 3.

Table 2

Above ground biomass and foliage cover of mangroves at each plot.

Site/ Plot	Biomass (kg 100 m^{-2})	Crown Cover %	Foliage cover %
1A	1186.9	100	70
1B	1221.8	85	51–68
1C	1849.1	95	66.5
2A	1906.1	90	27
2B	927.3	90	45
2C	1004.6	90	36
3A	2548.8	100	80
3B	1039.2	100	70
3C	1215.9	60	42
Mean	**1212.6**	**90**	**55**

with occasional very stunted mangrove shrubs (Fig 4). Samphires (*Halosarcia* sp) occur in both zones. The sharp demarcation between the two zones would be controlled by micro-elevation, and the relatively stable water levels of the ponds.

At site 3 (Goat Bay), mangroves of the zone 2 salt flat margin type had unusual variability in pneumatophore height (*ca* 5–60 cm; Fig 4). This could be due to periods of stationary higher water levels, when the lake floods. In places (*i.e.* adjacent to Plot 1C), *Halosarcia* grows in dense mats over the top of *Avicennia* pneumatophores.

Community structure and biomass

Site descriptions (Table 1) indicate the variable characteristics of these mangrove communities. Biomass of each 100 m^{2} plot at Lake MacLeod, using the 1999 stem diameter data and allometric determinations of Clough *et al.* (1997) are given in Table 2.

Site 1 is a taller promontory of older trees, with branches densely overhanging the water. There are no seedlings under the dense canopy. Plot 1C is adjacent to a patch where mangrove trees have recently died. Here *Halosarcia* samphires are densely growing over the *Avicennia* pneumatophores.

Site 2 mangroves occur on a low island central in the pond, where inundation occurs during strong southerly winds. The mangrove margin is narrow, and landward of this (inside the island) is unvegetated salt/mud flats. The exposed nature of site 2 is reflected by the lower heights of trees (Table 1). There is evidence of bank erosion, with horizontal *Avicennia* roots draping over the edge of the bank into open water (Fig 3). Some eroded sediment has been re-deposited among the mangroves within the plots.

At Goat Bay (Site 3), mangroves vary between a narrow margin at plot 3A, to up to a 50 m margin at plot 3C. Plot 3A is largely one multi-stemmed tree, with heavy shading and no samphire growth. Plot 3C has a large amount of dead timber, which pre-dates the monitoring period.

Crown cover

Crown cover values (Table 2) are high, showing that while the mangrove margins are narrow the trees have dense growth. However, foliage cover is particularly low at the island site 2, to give an overall mean of 55%.

Seasonal production and phenology

Averaged production in dry weight g m^{-2} d^{-1} from each site is shown in Figs 5–7, and the total annual production of litter from the Lake MacLeod sites is given in Table 1.

Discussion

Comparing the seasonal productivity and phenology data (Figs 5–7), all sites showed minimum productivity during the winter period of June to September and maximum production during the spring period of August to December. The exception is the high productivity at Site 1 during late summer (March to June). This was caused by heavy fruiting as opposed to leaf production. Phenological patterns are very similar

Table 1

Stand structure data and annual litter production for mangrove monitoring sites at Lake MacLeod.

Site	Tree density m^{-2}	Tree height (m) December 1997	Tree height (m) February 1999	1997–1999 Mortality %	Annual production (g dry wt m^{-2})
1	0.57	3.85	4.05	2.5	1077
2	0.31	2.47	2.46	0	659
3	0.50	2.94	3.10	4.0	829
Mean	**0.46**	**3.09**	**3.20**	**2.1**	**855**

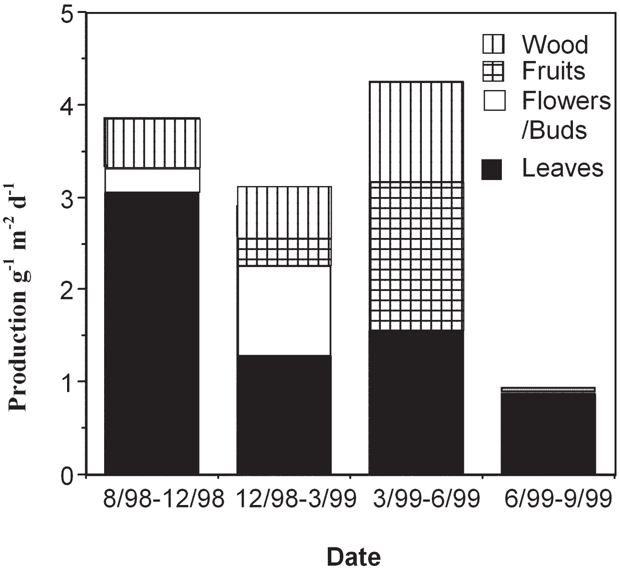

Figure 5. Mangrove litter production, Lake MacLeod site 1.

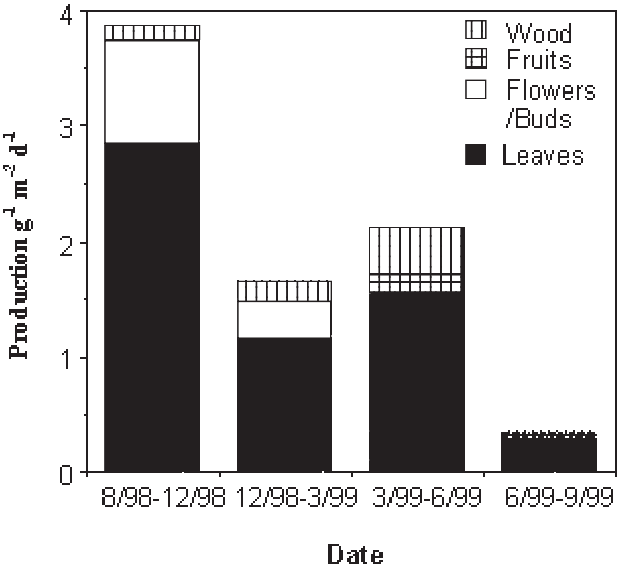

Figure 6. Mangrove litter production, Lake MacLeod site 2.

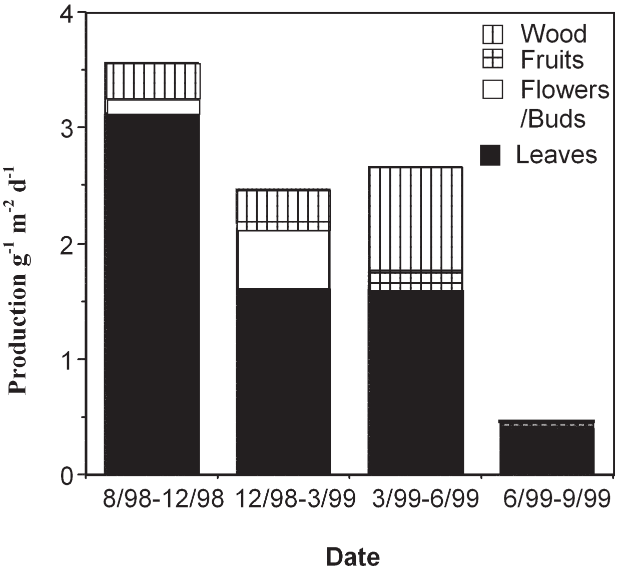

Figure 7. Mangrove litter production, Lake MacLeod site 3.

between sites. Sites 1 and 3 closely correspond, while site 2 differs only in showing slightly later commencement of fruiting. Site 1 showed the highest fruit productivity, which occurred over a longer period, resulting in the highest annual production of sites (Table 1). This may reflect more equable conditions at site 1, being the closest of all sites to the vents, also demonstrated by the taller mean tree heights (Table 1).

Litter productivity over the year is also similar between sites. All sites recorded a maximum leaf production of around 3–4 g m^{-2} d^{-1} in the spring/summer period August to December. The average annual production for MacLeod mangroves of 855 g dry wt m^{-2} is surprisingly high, given the stunted stature of the trees and environmental stresses at the site. However, the mangrove margin is narrow and dense, so this production rate is over a very limited area compared with coastal mangroves. While there are few studies of *Avicennia* productivity in Australia (Saenger & Snedaker, 1993), a similar result was found for a 4 m stand in Queensland by Duke *et al.* (1981). Mackey & Smail (1995) found annual litter fall of subtropical *Avicennia marina* in the Brisbane River, southern Queensland, to be 831–922 g dry wt m^{-2} over two years of measurement. Of this, leaf fall accounted for 47% of the total litter fall, reproductive litter 30%, and woody litter 23%. By comparison, during measurement of the Lake MacLeod mangrove production in the September 1998 to September 1999 period, leaf fall accounted for 68% of the total litter fall, reproductive litter 20%, and woody litter 12%.

This above-ground mangrove biomass from Lake MacLeod *Avicennia marina* (Table 2) is equivalent to 121.3 t ha^{-1}. This result is compared with published above-ground biomass results for *Avicennia marina* of similar height ranges in Australian temperate latitudes (Saenger & Snedaker 1993) in Fig 8. While results are similar, *Avicennia* trees stunted by aridity as opposed to temperature are of heavier biomass, which is to be expected given the butt and multi-branched architecture of these trees (Clough *et al.* 1997).

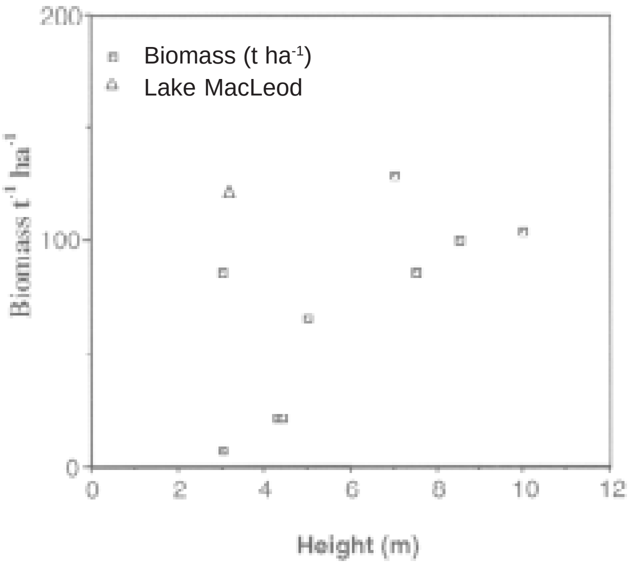

Figure 8. Biomass of *Avicennia marina* at Lake MacLeod compared with *Avicennia* biomass/height records from temperate Australia (data from Saenger & Snedaker, 1993)

Mangrove margins at a number of locations had areas of previous mangrove mortality, although rates over the monitoring period 1997–1999 were 0–4% (Table 1). Adjacent to the vents, there are sections of shoreline where mangrove trees either appear to be unhealthy, with low leaf cover, or the trees are dead. At site 3 (Goat Bay), there is several hundred meters of largely dead mangroves. Occurrence of dead timber in Plot 3C is reflected by the low foliage cover (Table 2). This tree death occurred before December 1997, and may have been caused by storm damage. The broken canopy and relatively large size of trees in this plot may have weakened them to further storm damage. The recorded mortality of 6% in this plot was likely a result of Cyclone Vance in March 1999.

There are several other possible causes of mangrove death at Lake MacLeod. These include salinity stress, as shown at the Embley River estuary in the Gulf of Carpentaria where death of *Avicennia marina* occurred following a series of drier than normal wet seasons, and consequent high soil salinities (Conacher *et al.* 1996). Change in lake water level could also cause mortality, either by increasing salinity stress with a drop in water level, or causing inundation stress with raised water level. Such effects would be documented by continued monitoring at these sites.

In summary, the mangroves of Lake MacLeod are unique, being one of the world's larger inland mangrove areas. Despite their extreme habitat, on the margins of a non-tidal salt lake in an arid climate, these mangroves have high productivity. Rates of primary production, measured by litter fall and mangrove biomass per unit area, are equivalent to mangroves of similar height in normal coastal situations.

The spatial extents of mangroves at Lake MacLeod are obviously controlled by water conditions, particularly water surface elevation that determines the inner margin of mangroves with the salt flat. Water salinity controls mangrove physiognomy, indicated by the stunted architecture of trees more distant from the water's edge. Pneumatophore heights in some areas indicate stress from periods of inundation during higher lake levels, and previous mortality events are apparent from before the period of this study. Having established this baseline study, future monitoring will elucidate these mortality events.

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