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Influence of hydrological and environmental conditions on mangrove vegetation at coastal and inland semi-arid areas of the Gascoyne region

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Influence of Hydrological and Environmental Conditions on Mangrove Vegetation at Coastal and Inland Semi-arid Areas of the Gascoyne Region

MASTERS BY RESEARCH THESIS

ENVIRONMENTAL MANAGEMENT

PREPARED BY

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JUNE 2014

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Abstract

Mangrove stands are uncommon within semi-arid climates and rare within inland systems. It is uncertain whether the same environmental variables influence mangroves growing in a semi-arid climate as the trees growing in tropical and sub-tropical areas. Field studies conducted on the ecophysiological responses of the mangrove species *Avicennia marina* are few; however hydrological regimes are considered the key factor influencing mangrove stand zonation, structure and individual tree growth. The Gascoyne region of Western Australia provides a unique opportunity to investigate whether mangroves growing within an inland semi-arid environment display similar growth patterns and ecophysiological responses to their coastal counterparts.

This study investigates the distribution, structure and condition of the mangrove *A. marina* growing at Lake MacLeod and coastal and riverine stands near Carnarvon, Western Australia. Hydrological categories based on freshwater inputs, tidal influences, distance from permanent water sources and sediment elevations were used to investigate the environmental conditions present within specific hydrological regimes. Mangrove tree responses to environmental conditions were evaluated by assessing above-ground biomass, shoot production, water-use efficiency, photosynthesis, specific leaf area, weight and total chloride content. The overarching objective was to determine the environmental factors influencing the presence, morphology and physiological state of *A. marina* growing at inland, coastal and riverine sites in a semi-arid climate.

Soil moisture content, organic matter content, average and seasonal range in sediment EC, and distance from the permanent water sources were found to influence vegetation characteristics at Lake MacLeod. Soil moisture content was highest close to permanent ponds and at lower sediment elevations. Sediment salinity was highest close to pond edges, although the majority of the lake bed is hypersaline due to high evapoconcentration. The environmental gradients are complex at Lake MacLeod as a result of the unique hydrological regime. Seawater supply to permanent ponds is constant via an underground karst system which enters the lake through vents and seepages present along the western edge of the lake bed. It is evident that the constant supply of marine water is the key environmental factor supporting mangrove presence and structure. Average mangrove tree height, basal area, density and canopy cover are greatest near the permanent ponds. Mangrove density and height was also high, though patchy away from the ponds where saline seepages occurred. A high density of stunted mangroves was found on lake shorelines receiving periodic saline flooding via wind surges. Samphire cover was also greatest close to the permanent ponds, demonstrating that both mangrove and Samphire presence and importance is influenced by consistency of water availability.

Sediment conditions were significantly different between inland and coastal sites, with sediment salinity and moisture content higher at Lake MacLeod. The ecophysiological responses displayed by *A. marina* in different categories of hydrological regimes revealed that consistency of water supply, irrespective of salinity, is an important driver of long and short-term productivity, water-use efficiency, leaf size and weight, and tree height.

In general, short and long-term production was inversely proportional to distance from permanent water sources, although it was highly variable due to seepages away from the permanent ponds. Mangrove trees growing at the landward edge of coastal sites were the most water-use efficient (~ -28 δ^{13}C), relative to the inland Lake MacLeod trees (~ -26 δ^{13}C), and was directly linked to water supply not quality. Photosystem health in trees growing at both the riverine stands (yield 0.66 ± 0.01) and inland stands found at greater distances from ponds (yield 0.065 ± 0.02), were significantly lower than all other trees in this study. Relative maximum electron transfer rate was also significantly lower at these sites, suggesting that the riverine trees were affected by other stresses such as herbicides. Mangrove trees near permanent water sources, or that received tidal flushing, displayed larger leaves and lower specific leaf weight, indicating that *A. marina* has the ability to not only tolerate hypersaline conditions but also acclimate to harsh and variable conditions via changes to ecophysiological responses and morphology.

This research has developed a better understanding of how *A. marina* persists at Lake MacLeod and whether these trees are under greater stress as opposed to the mangroves growing at coastal stands. Sediment conditions between coastal and inland sites were significantly different, but it was distance from permanent water sources that influenced mangrove stand features. Therefore, the key environmental variable influencing distribution, structure and ecophysiological state of *A. marina* growing in a semi-arid climate is predominantly water availability.

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USE OF THESIS

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1 Introduction and Study Objectives

Mangroves are marine plants with a growth form that ranges from trees to shrubs and are typically found on the fringes of the ocean (Nybakken and Bertness 2005). A mangrove dominated habitat, referred to as “mangrove forest”, “mangroves” or “mangal”, (Nybakken and Bertness 2005; Duke 2006), consist of single to multi-species communities. They provide important ecosystem functions and services, such as buffering to erosion (Lovelock, Feller *et al.* 2004; Duke and Larkum 2008); filtering nutrients and pollution (Connolly and Lee 2007); and providing spawning, feeding, nesting and nursery areas for a wide variety of organisms (Saenger 1982; Boorman 1999; Johnstone, Burbidge *et al.* 2000).

Mangrove dominated habitats commonly establish between latitudes 25° N and 25° S (Dawes, Siar *et al.* 1999; Connolly and Lee 2007), and in both tropical and subtropical locations there is high mangrove species diversity (Parida and Jha 2010). Occurrence of mangroves outside these latitudes is normally as a result of warm ocean currents (Nybakken and Bertness 2005), in either subtropical-arid, semi-arid or, more rarely, temperate locations. Within semi-arid and temperate conditions in Australia, mangrove species diversity is reduced, consisting of only a single species *Avicennia marina* (Saenger, Specht *et al.* 1977; Pedretti and Paling 2001).

The interface of marine and terrestrial environments (i.e. intertidal zone) is a challenging ecosystem for most plant species, due to tidal inundation and exposure to variable salinity. However mangrove species are well adapted to this environment (Hogarth 1999). Their root systems allow gas exchange to continue while inundated or subject to anaerobic sediment conditions (Nybakken and Bertness 2005). Salt tolerance strategies are key to their survival; mangroves use either secretion, exclusion, or tolerate elevated salinity of internal fluids to manage the vast range of external salinities to which they are exposed (Hogarth 1999). Vivipary is a common reproductive strategy allowing dispersal of propagules via water flow to suitable recruitment sites (Connolly and Lee 2007).

Saltmarsh plants can be associated with mangroves and consist of herbaceous or low woody vascular plants. The habitats they form are categorised into three main ecosystem groups: shrublands (dominated by chenopods), sedge and rush swamps (upper marsh fringe) and grasslands (poorly developed in Australia) (Adam 2002). Saltmarsh habitats are highly valued for their ecosystem services, which are similar to those that mangrove habitats provide (Boorman 1999). In higher latitudes, saltmarsh is the main community on shorelines, as mangroves are not present (Adam 1991). In lower latitudes, saltmarsh vegetation is most common in the upper reaches of the intertidal zone, with mangroves growing closer to the edge of the ocean or estuary (Ellison and Simmonds 2003). Where rainfall is high (i.e. tropics), mangroves dominate with little or no saltmarsh vegetation. Conversely, within temperate to arid areas or where rainfall is strongly seasonal, saltmarsh vegetation dominates and is supported by sparsely interspersed mangrove trees (Adam 2002). This pattern is evident in Australia (Duke and Larkum 2008). In Northern parts of Australia mangrove stands dominate, and with graduation into temperate and semi-arid regions of Australia saltmarsh communities become extensive but sparse (Hogarth 1999; Connolly and Lee 2007).

1.1 Environmental conditions known to influence mangrove distribution, structure and physiology

Existing plant community structure models highlight that when faced with elevated environmental stress, physical components of the environment (rather than biological interaction) have a high relative importance (Grime 1977; Menge and Sutherland 1987). Globally, the key environmental factors that influence mangrove and saltmarsh presence and importance are debatably salinity, temperature, soil type and freshwater supply (Connolly and Lee 2007). This does not negate the possibility that subsidiary factors are important at the specific site scale (Clough 1993; Matthijs, Tack *et al.* 1999), for example local topography and interactions with the ocean. Most studies on environmental influences on mangroves have been conducted on tropical or subtropical coastlines and have linked high soil salinities to reduced mangrove height, growth and productivity (Dawes, Siar *et al.* 1999; Ajmal Khan and Aziz 2001; Ellison and Simmonds 2003; Connolly and Lee 2007).

Spatial distribution of a mangrove stand reflects flooding regularity and quantity (Bunt 1999; Matthijs, Tack *et al.* 1999) and lower temperatures result in poor species diversity (Saenger, Specht *et al.* 1977). Lovelock et al. (2004) and McKee et al. (2002) researched fringing and dwarf mangroves within tropical climates and they reported lower nutrients, resulting from reduced or no tidal flushing, directly linked to reduced mangrove growth. However, currently no similar studies are available on semi-arid or temperate climates and it is not clear whether the same environmental factors that affect mangrove distribution, structure, and physiology in tropical climates are also relevant in these areas.

River inflow, frequency and extent of tidal flushing have been suggested as being particularly important influences on mangrove and saltmarsh dynamics (Saenger 1982; Nybakken and Bertness 2005). Mangroves existing along coastal shorelines can be exposed to two different hydrological regimes.

1. Mangrove stands present along the coastline, receiving only rainfall and limited surface runoff (Figure 1).
2. Riverine or estuary stands present along riverbanks and at river mouths, receiving significant freshwater flow more regularly and for longer periods of time (Figure 2).

Survival is difficult in the intertidal zone due to extreme variability in salinity gradients, sediment temperature, hydrological exposure, anoxia and osmolarity (Saenger 1982). However, all coastal mangrove systems receive regular flushing via tidal movement which is essential for flushing the root zones and re-establishing suitable temperature, oxygen and salinity levels within the sediment (Naidoo 2010). These conditions enable healthy, lush growth and the mangrove stands are tall, productive systems.

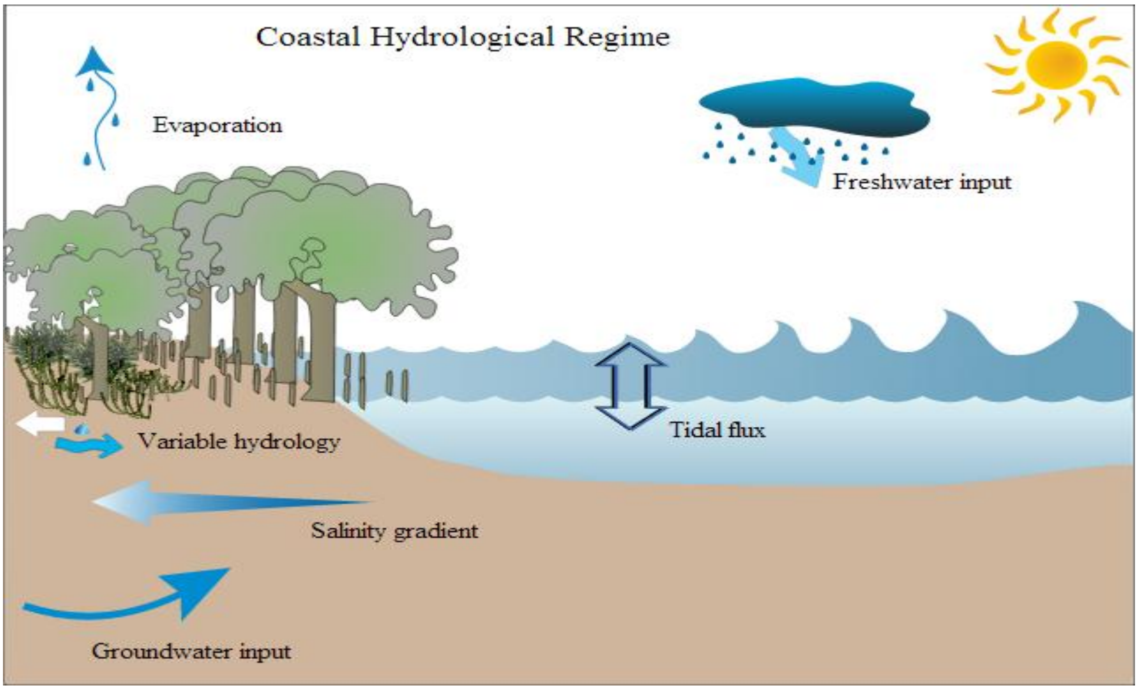

Figure 1: Conceptual diagram outlining potential hydrological regimes present at sites along the coast of the Gascoyne region, Western Australia.

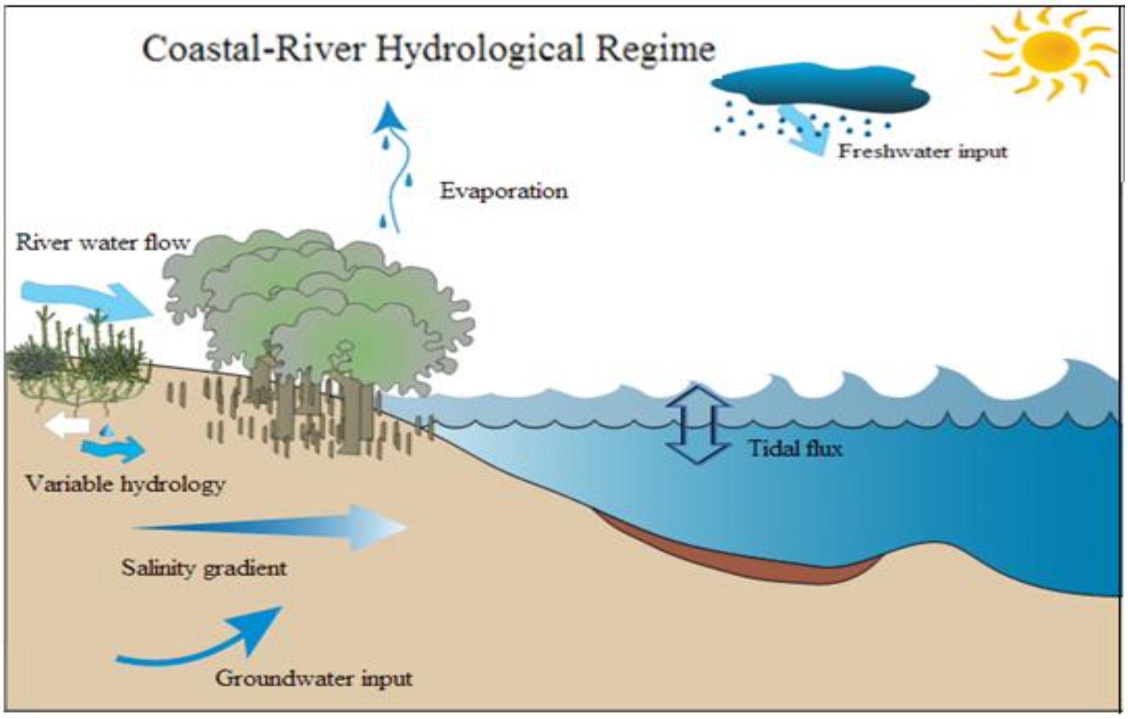

Figure 2: Conceptual diagram outlining potential hydrological regimes present at river sites surrounding Carnarvon, Western Australia.

Hydrological patterns at a site are influenced by local geomorphology, water quality, quantity and delivery patterns, principally timing and duration of inundation (Phillips, Butcher *et al.* 2005). This in turn affects the variability in salinity, sediment oxygen levels and allochthonous nutrient inputs (Vilarrubia 2000; Lovelock, Ball *et al.* 2009).

Mangrove trees growing at the seaward edge of coastal stands are taller and more robust than landward trees (Dawes, Siar *et al.* 1999; Matthijs, Tack *et al.* 1999; Naidoo 2010). Mangrove tree productivity is enhanced when regular freshwater inflow occurs, stabilising sediment and interstitial water salinity (Connolly and Lee 2007). This leads to larger trees closer to the seaward edge, graduating to smaller trees along the landward edge of the stand (Naidoo 2010).

Although coastal and riverine mangroves are usually periodically inundated with water or situated in waterlogged sediments, drought conditions can still occur due to high salinity and temperature. When salinity and temperature increase in sediments or the water column, mangrove growth can be reduced due to lower water uptake and reduced transpiration and photosynthesis (Parida and Jha 2010). However, dwarfing is also attributed to several edaphic conditions apart from salinity, including nutrient limitation, redox potential, and waterlogging (Naidoo 2010).

Inland mangrove systems are rare globally, with only seven identified by Ellison (1997). These systems have a historical connection to the ocean (Ellison and Simmonds 2003), however maintain a restricted hydrological link to the larger marine environment. Seawater inflow is then thought to maintain similar hydrological conditions commonly found within mangrove habitats (Nybakken & Bertness, 2005). Some examples of inland mangrove systems include geological embayment relics (Ellison and Simmonds 2003) in Bermuda (Thomas, Logan *et al.* 1992), Inagua (Bahamas) (Lugo 1981), 80 Mile Beach at Mandora (Western Australia, (Beard 1967) and Lake MacLeod (Western Australia, Figure 4b; Beard 1967). All reported inland mangrove systems are located in either tropical or subtropical climates except for Lake MacLeod, which endures semi-arid climatic conditions (Ellison 1997).

In contrast to coastal and riverine mangrove systems, most of the inland mangrove systems are exposed to indirect or no tidal fluctuation, have higher evaporation rates, high variability in salinity (with hypersalinity common) and episodic or periodic river water flooding. These factors are likely to result in restricted habitat distribution and cause greater physiological stress to the mangroves, as the frequency and magnitude of either seawater or river water flushing is reduced (Ellison and Simmonds 2003; Naidoo 2010) (Figure 3).

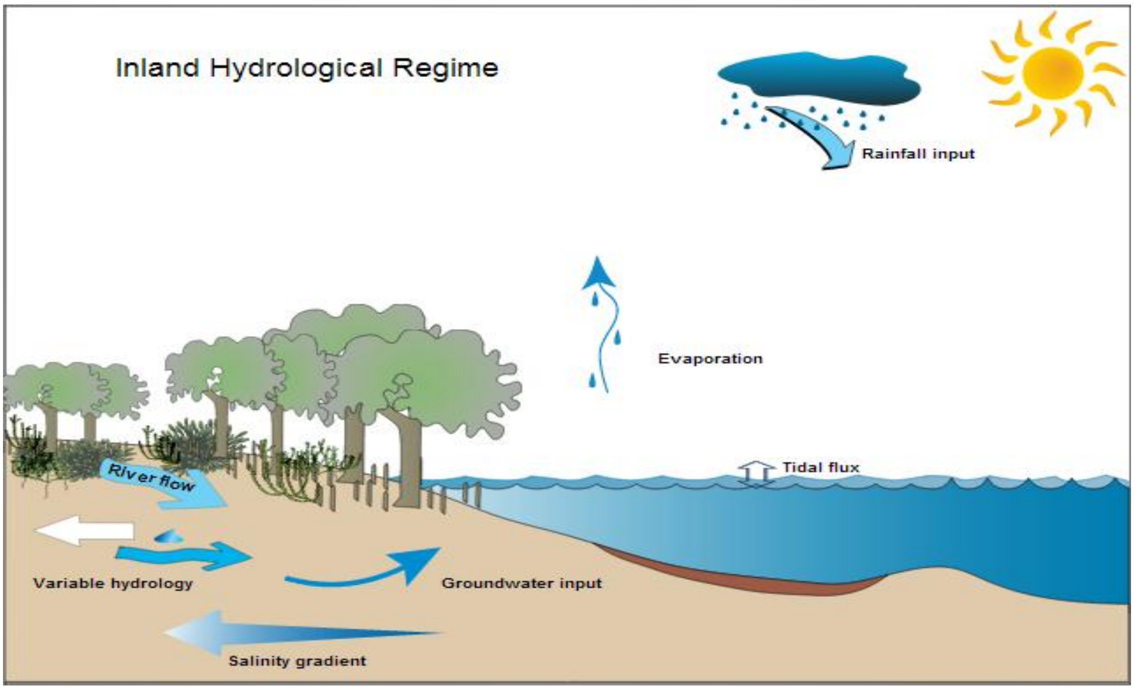

Figure 3: A generic conceptual diagram indicating a probable hydrological regime influencing inland mangrove ecosystems.

Patterns in inland mangrove growth relative to hydrological conditions are likely to follow that of coastal systems, however previous work has suggested inland plants are shorter than their coastal counterparts, with more obvious, discrete ecotones athwart the stands (Ellison, 1997; Ellison & Simmonds, 2003).

1.2 Mangrove traits and ecophysiological responses to environmental stress

Mangroves possess morphological, anatomical, physiological and reproductive features that allow survival under high and variable salinity levels (Saenger 1982; Stewart and Popp 1987; Ball 1988a). Morphological features of mangroves that aid survival in the intertidal zone are well studied; these features generally function to minimise water loss and improve water-use efficiency (WUE) (Naidoo 2010). Most mangrove species possess aerial root morphologies such as stilt, pneumatophore, knee and buttress roots. Gas exchange occurs even in anoxic sediments due to aerenchyma tissue and lenticels within the roots, as well as tidal movement (Hogarth 1999). This specialised root structure and function is paramount to the survival of mangroves within hypoxic environments (Ball 1988a). The root systems cope well with temporary inundation, although prolonged flooding has been directly linked to mangrove mortality (Ellison 2001). Ideally, flooding in mangrove stands should range from seasonally tidal or near-permanent (Krauss, Lovelock *et al.* 2008). Water movement and flushing of sediment surrounding the root zone helps to maintain an acceptable level of aerobic conditions (Saenger 1982).

Leaf anatomy and morphology are reliable measures linked to the environmental conditions experienced by mangrove trees (Liang, Zhou *et al.* 2008; Parida and Jha 2010). Adaptation to drought stress, resulting from harsh osmotic relations, is commonly displayed as lower specific leaf area, thicker leaves and cuticles and heavier specific leaf weight (Lugo, Cintron *et al.* 1982; Naidoo 2010; Naidoo, Hiralal *et al.* 2011). Sobrado (1999) identified that individual leaf area and weight ratios in the dry season were 24% and 20% lower in low and high salinities respectively, relative to the wet season. Therefore, specific leaf area is a good indicator of environmental stress in mangroves (Lugo, Cintron *et al.* 1982; Medina and Francisco 1997).

Depending on age, salt tolerance and environmental salinity, mangrove species utilise either one or all three of the following salt regulation strategies; exclusion, excretion and salt accumulation. These salt regulation strategies involve roots, salt glands on leaves and physiological processes within the leaves (Hogarth 1999). It is unclear how each individual species manages salt regulation, and further physiologically based studies are needed to elucidate the exact mechanisms of ion regulation that mangroves utilise to adapt to highly saline environments. Some mechanisms are known to be more dominant in certain species than others (Hutchings and Saenger 1987); this is dependent on salt tolerance and species morphological adaptations. Salt secreting species such as *Avicennia* have higher salt permeability at the root zone, with ion regulation also controlled within leaves via salt glands on the leaf cuticle (Medina and Francisco 1997; Hogarth 1999). The mechanism used by a species to control ion movement and accumulation influences leaf ion content. Suarez & Medina (2006) found that increased salinity reduced K^+ uptake and increased Na^+ concentration in tissue water content of leaves on mangroves (*A. germinans*). The efficiency with which each mangrove species tolerates high and fluctuating salinities determines mangrove species global distribution, stand zonation and anatomical features (Banerjee 1993; Sobrado and Ball 1999).

Ecophysiological responses of mangroves are primarily driven by hydrological regimes and salinity, although factors such as light and temperature can also influence responses (Hutchings and Saenger 1987). It is expected that with increased drought stress and higher salinity, mangrove trees will display higher WUE, lower productivity and reduced photosynthetic rate. These ecophysiological responses directly affect the structure and condition of mangroves (Medina and Francisco 1997; Wei, Yan *et al.* 2008; Naidoo 2010). However, there are no ecophysiological studies relating to mangroves at inland locations within a semi-arid climate, and few quantitative studies on mangroves in natural hypersaline conditions (Sobrado and Ball 1999; Naidoo 2010). Previous studies of WUE reveal that environmental factors such as light intensity (Sobrado and Ball 1999), atmospheric CO_2 concentration (Krauss, Lovelock *et al.* 2008), water stress (Naidoo 2006; Naidoo 2010), temperature (Ball 1988a), nutrients (Lovelock, Feller *et al.* 2004; Martin, Bruhn *et al.* 2010) and salinity (Medina and Francisco 1997; Naidoo, Hiralal *et al.* 2011) alter the stable carbon isotope ratio within plants (Farquhar, Ehleringer *et al.* 1989; Wei, Yan *et al.* 2008).

The mangrove habitat is an evaporative saline environment that requires mangroves to conserve water to maintain favourable carbon, water and salt relations (Martin, Bruhn *et al.* 2010). Riverine and coastal fringing mangroves generally display lower WUE than scrub or dwarf mangrove trees growing along landward edges of mangrove stands (Cheeseman and Lovelock 2004; Naidoo, Hiralal *et al.* 2011). Typically dwarfed mangrove trees experience infrequent tidal inundation and high evapotranspiration rates, producing hypersaline sediment conditions (Naidoo, Hiralal *et al.* 2011). These conditions prevent water uptake via osmotic drought and hence the dwarfed trees are more WUE (Naidoo 2010).

Medina & Francisco (1997) developed a conceptual model of the interactions between salinity, nutrients and freshwater availability, based on edaphic and climatic conditions within arid coastal and riverine mangroves. Their model highlighted that WUE of mangrove plants increased at higher salinity, while photosynthesis and productivity decreased. Therefore, habitats with higher salinity are likely to have smaller plants, that use less water physiologically (due to limited water availability) to maintain productivity. Not all mangrove species however respond the same way to higher salinity, therefore only absolute values of $\delta^{13}C$ ratios within the same species can be compared (Wei, Yan *et al.* 2008).

Mangrove photosystems regulate photosynthesis depending on environmental conditions. Photosystem response to salinity and light are interrelated and are key in influencing the daily variability in photosynthetic rate for mangroves (Krauss, Lovelock *et al.* 2008). Increased light (difference between predawn and midday) reduces the efficiency of photosystem II (PSII) over and above any changes to water availability or salinity levels (Sobrado 1999). However, down regulation of PSII occurs when trees are exposed to hypersaline conditions, along with other environmental stressors (Larcher, Wagner *et al.* 1990; Kathiresan and Bingham 2001). Ion deficiency and accumulation, particularly for potassium (K^+), sodium (Na^+) and chloride (Cl^-), within photosynthetically active tissues also influences the photosynthetic metabolism (Krauss, Lovelock *et al.* 2008). Interestingly, Ball et. al. (1987) revealed that the decrease in photosynthetic rate of *A. marina* at increased salinity, was due to salinity-induced K^+ deficiency, rather than toxic effects of Na^+ and Cl^- accumulation.

Chlorophyll *a* fluorescence is a well utilised method for investigating photochemical processes within PSII. This can provide information on photosynthetic capacity and efficiency (Ralph and Gademann 2005). Portable fluorometers allow *in situ* measurements of these processes. Rapid light curves (RLC) measure the actual photosynthetic rate by plotting electron-transport rate versus irradiance to calculate the relative maximum electron transfer rate (rETRmax) during photosynthesis (Ralph and Gademann 2005). The photochemical efficiency of PSII is determined by dark-adapting leaves before a light pulse. This measure indicates the amount of light energy converted by PSII and represents the stress level of a plant (Naidoo 2010). It is expected that trees growing within extreme and highly variable hydrological regimes will display lower rETRmax and maximal fluorescence than those growing in a more consistent regime (Naidoo 2006).

Temperature, salinity and aridity are key environmental factors influencing growth and survival of individual mangrove species (Clough 1993). At a regional scale temperature and aridity are the prominent factors influencing mangroves, whereas at the local scale salinity is the most influential factor. Tropical and subtropical mangrove trees are larger, have higher production rates and larger above-ground biomass than the same species in a temperate or semi-arid climate (Naidoo 2010). The local hydrological regime and salinity level are the principal abiotic factors affecting mangrove tree growth and productivity (Wei, Yan *et al.* 2008; Naidoo 2010). It is common to see reductions in above-ground biomass with increased elevation and distance from water. There is a distinct gradient in sediment salinities that can become hypersaline due to increased variability and harsher environmental conditions (Saintilan 1997; Dawes, Siar *et al.* 1999; Ross, Ruiz *et al.* 2001; Suarez and Medina 2006).

1.3 Significance and objectives of the study

Recent interest lies in the environmental influences responsible for mangrove tree productivity and ecophysiological responses (Naidoo 2010; Naidoo, Hiralal *et al.* 2011); however few studies exist on mangroves at the climatic and physiological extremes of their geographical range. Central ecophysiological paradigms are focused around inundation depth, duration and frequency, salinity gradients and geomorphological characteristics (Krauss, Lovelock *et al.* 2008). Research is required across a broader range of salinities (Wei, Yan *et al.* 2008) including rare locations such as inland systems with unique hydrological regimes. These inland mangrove systems may receive limited freshwater inflows, no tidal influence and restricted links to the ocean (Ellison 1997). It is not known if mangroves growing in inland systems display similar morphological features, growth patterns and ecophysiological responses to their coastal counterparts.

A unique opportunity exists to assess the largest inland mangrove system in the southern hemisphere; Lake MacLeod in the semi-arid Gascoyne region of Western Australia, and compare it to nearby coastal and riverine mangrove systems growing in a semi-arid climate. Coastal mangrove stands within a semi-arid climate are rare and research is needed on relating the environmental and mangrove vegetation characteristics of this habitat to coastal and riverine habitats.

This study investigated the distribution and structure of *A. marina* in relation to hydrological and sediment conditions existing at the semi-arid, inland mangrove system at Lake MacLeod. In addition, the productivity, water-use efficiency (WUE) and morphological traits of *A. marina* growing in the three different hydrological regimes (inland, coastal and riverine) of the Gascoyne were compared. This research is expected to highlight key environmental variables associated with *A. marina* distribution, structure and physiological condition within these semi-arid climatic conditions and enable comparison with more common studies of sub-tropical/tropical mangrove systems.

It is expected that trees at the semi-arid inland system of Lake MacLeod will display a range of mangrove plant sizes, canopy and density based on gradients in hydrology and salinity. According to Medina & Francisco (1997), the semi-arid, evaporative inland marine system of Lake MacLeod, with its lack of tidal flushing, will support small mangrove plants of lower canopy cover and basal area where sediment salinities are highest. In the physiological comparisons, Lake MacLeod mangroves are expected to have greater WUE, but lower productivity, than both coastal and inland mangrove trees due to reduced freshwater inflow, absence of tidal flushing and higher sediment salinities due to evapoconcentration. However, the landward edge of coastal mangrove stands is expected to have trees with similar physiological status to the inland mangroves.

The comparisons outlined above will further our understanding of the growth, structure and ecophysiological responses of mangroves under the variable conditions of Lake MacLeod and Carnarvon areas. This will also contribute to our understanding of the natural recovery of Lake MacLeod mangrove stands and the strategies required for mangrove monitoring and recovery processes.

1.4 Thesis structure

This thesis presents the results of research on mangrove dominated stands containing *Avicennia marina* and Samphire species within the Gascoyne region of Western Australia. This work was supported by Rio Tinto and Dampier Salt Ltd. The research results fill some high priority knowledge gaps highlighted from the Lake MacLeod Report produced by Edith Cowan University for Dampier Salt Ltd. This thesis aims to increase knowledge on the persistence of a unique inland marine mangrove system found within a semi-arid climate zone.

This thesis is divided into five main chapters:

- Chapter 1 is a general introduction which describes the structure, morphological and ecophysiological features of mangroves growing in a semi-arid climate.
- Chapter 2 describes all aspects of the study region.
- Chapter 3 investigates the environmental drivers which influence presence and importance of mangrove dominated vegetation at an inland marine system Lake MacLeod.
- Chapter 4 investigates and compares morphological features and the ecophysiological state of mangroves in relation to environmental conditions found at coastal and inland locations within a semi-arid climate.
- Chapter 5 is an overall thesis discussion and conclusions resulting from the research undertaken.

2 Chapter two - Study Region

This chapter describes the region and study sites where the research was conducted. Climate, land use, hydrology and vegetation types are described. This information provides background into the site selection and the context of the study.

2.1 Location and Climate

This study was conducted in the Gascoyne region, mid-west Western Australia, an area of 138,000 km² at inland mangrove stands, Lake MacLeod and coastal fringing and riverine mangrove stands, near the township of Carnarvon (Figure 4). The climate of this region is semi-arid with low but variable rainfall, high evaporation and extreme, episodic climatic events such as cyclones.

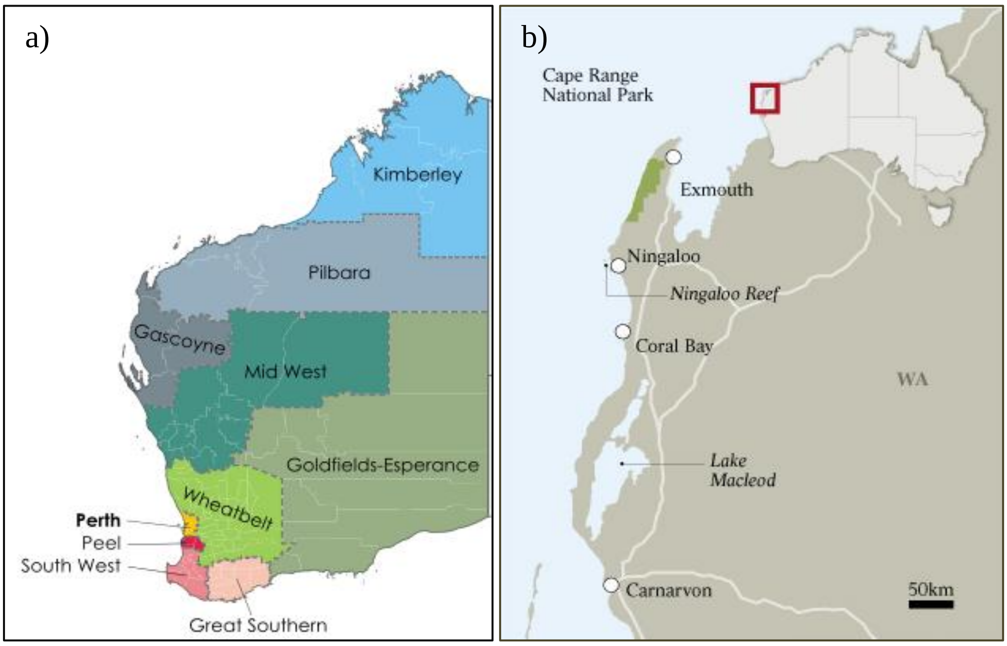

Figure 4: a) Gascoyne region within the mid-west of Western Australia. b) Carnarvon township and Lake MacLeod's location within the Gascoyne region.

Lake MacLeod in the Gascoyne region is in a transitional climate zone; between temperate winter-dominated rainfall and tropical summer-dominated rainfall. Mean temperatures range from 17°C - 35°C in summer and 10°C - 20°C in winter, evaporation rates range from 2400 mm – 3600 mm per annum and rainfall is on average 200 mm – 300 mm per annum (Bureau of Meteorology 2013). Rainfall is irregular and ephemeral (Russell 2004) though it generally falls during the temperate winter months (May – July). Prior to and during the first year of this study, the area was wetter than the previous 68 years (1945 - 2013) average of 230 mm, where in 2011, 399 mm and in 2010, 367.6 mm of rain fell. This significantly increased freshwater influx to water bodies within the area causing flooding of the Gascoyne River and associated wetlands, Lake MacLeod (Bureau of Meteorology 2013).

This region is within the global southeast trade wind belt, winds prevail from the south for most of the year. During summer, there is a strong sea breeze that increases in strength in the afternoon. Average summer wind velocities are 25 km/hr, with gales of 40 – 50 km/hr occurring regularly. During winter, weaker southerlies (average velocity of 15 km/hr) occur without the complication of a strengthening sea-breeze and gales become less frequent (Logan 1982; Bureau of Meteorology 2011). The combination of high solar radiation levels, low erratic rainfall and strong winds significantly contribute to the extreme evaporation rates in the region, which peak during October to March (average ~ 1788.4 mm) and decrease in winter (average ~ 1096.9 mm). These environmental factors are pivotal to the hydrological regime experienced at Lake MacLeod and impact vegetation distribution, structure and composition (Phillips, Butcher *et al.* 2005).

2.2 Land use

The land surrounding Lake MacLeod and Carnarvon is managed as pastoral properties, with mining activities including salt and gypsum production also occurring. National (e.g. Cape Range, Kennedy Range) and Marine Parks (e.g. Ningaloo, Shark Bay) are also located within this region. Lake MacLeod has also been proposed for listing under the Ramsar International Convention on Wetlands as a Wetland of International Importance based on it being an important habitat to a diverse range of bird species including transequatorial migratory waders (Gascoyne Development Commission 2010). Additionally Lake MacLeod is listed in the Directory of Important Wetlands in Australia (DIWA) as a nationally significant wetland (DEC 2009).

Land use surrounding Carnarvon is dominated by irrigated horticulture with approximately 2000 ha of the river levee and flood plains utilised for this industry, beyond these areas is an extensive pastoral industry (Waddell, Thomas *et al.* 2012). The Carnarvon boat harbour is designed to accommodate recreational fishing boats and commercial fisheries such as prawn trawlers and scallop vessels (Department of Transport 2014).

2.3 Inland Environment - Lake MacLeod

2.3.1 Origin and Morphology

Lake MacLeod is an expansive and complex wetland covering 2,000 km^2. It is approximately 18 km inland and extends roughly parallel to the coast for around 120 km to the north from Carnarvon (DEC 2009). Originally a marine embayment, Lake MacLeod was separated from the Indian Ocean approximately 6000 years ago by the continual accretion of dune ridges to the south of the basin (Russell 2004). The lake bed is 3–4 metres below sea level and is predominately dry throughout the year (Phillips, Butcher *et al.* 2005), although a number of areas have permanent water. Lake Macleod is unique, complex and has eight main wetland types (Environment Australia 2001). These include a mix of distinct ‘inner wetlands’ with permanent water (sinkholes, channels, ponds, marshes) along the western extent, with ‘flood out marshes’ at the river mouths to the northeast of the greater lake area (DEC 2009).

2.3.2 Hydrology

Water input into the Lake MacLeod system is directly from rainfall, via runoff from river systems or through seepage of marine waters. The main lake bed experiences episodic surface water input from the Lyndon and Minilya Rivers in the northeast, plus indirect inputs from the Gascoyne River to the south via smaller tributaries including Cardabia and Boolathana Creeks. River water input is irregular and variable; with the lake becoming inundated only following heavy rainfall events associated with cyclones.

The Lake MacLeod system is separated into three ‘ponds’ Ibis, Cygnet and Chirrida Ponds (Figure 5), which are fed by the seepage of marine water through a unique subterranean coastal limestone karst system. Seawater is pushed into the saline ponds through the Cygnet seepage face; this is a hydrological structure critical for maintaining the Lake Macleod evaporite system. Lying along the north western side of the lake basin, the Cygnet seepage face discharges seawater through porous surfaces - ranging from cavernous openings metres in diameter to smaller holes less than 1 mm across (Shepherd 1991). The outlets termed ‘vents’ facilitate flow from hydrostatic pressure initiated by tidal movement and is maintained due to lower elevation of the lake bed compared to the sea (Phillips, Butcher *et al.* 2005). Water discharged from the seepage face display chemical properties similar to seawater upon discharge into the ponds, increasing in concentration with distance from the vents due to evaporation. Water sources entering the Lake MacLeod system differ (fresh or saline) resulting in dynamic water and sediment chemical properties. This produces extreme and harsh conditions for flora and fauna existing within and surrounding the system, and it is thought that many species are surviving at the edge of their tolerance range (Ellison 2001; Ellison and Simmonds 2003). This seawater input is constant and seawater continually overflows from the ponds onto the surrounding 'spill sheets', which are flat expanses of sediment that the water discharged from the vents sits on. The water is moved over these spill sheets by wind.

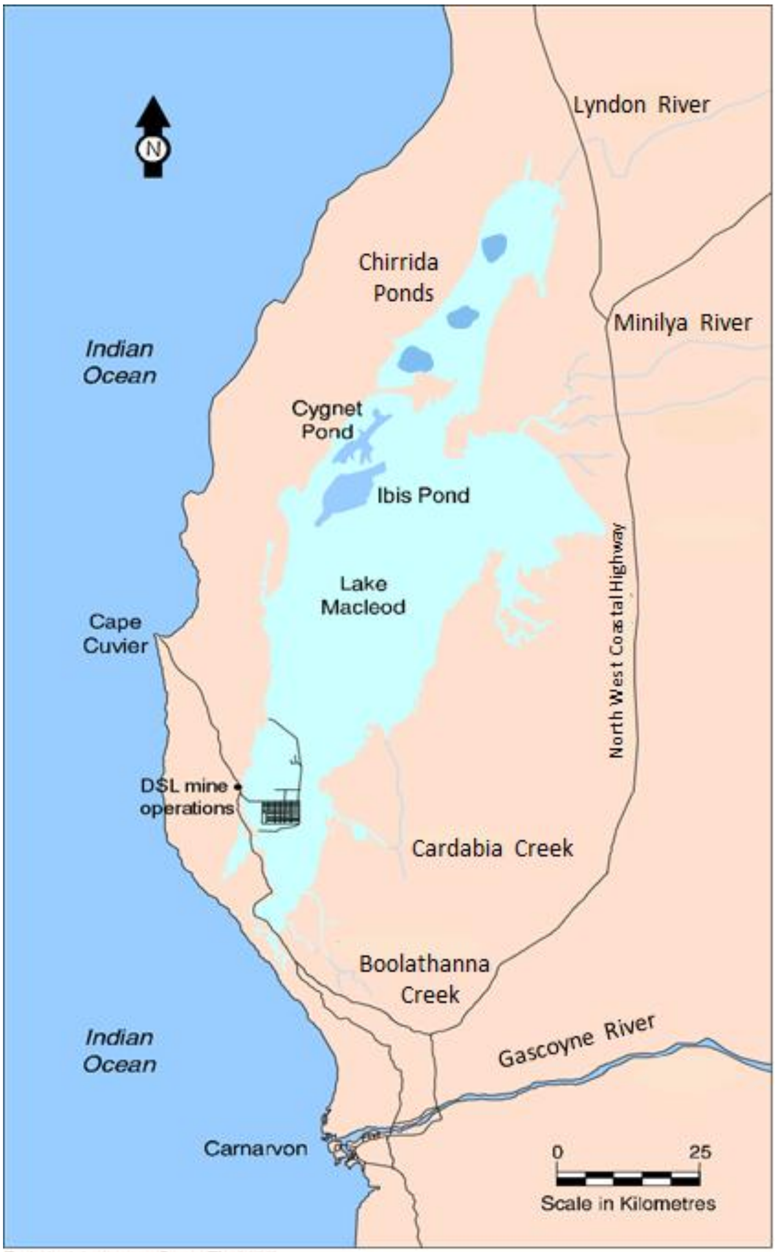

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Figure 5: Lake MacLeod evaporite basin including permanent water bodies Chirrida, Cygnet and Ibis Ponds and Dampier Salt Limited (DSL) mining operations (adapted from; Streamtec Pty Ltd 2000).

2.3.3 Vegetation

The Lake MacLeod mangrove stand is one of the largest of the eight known inland mangrove stands worldwide (Ellison 1997; Ellison and Simmonds 2003). Like mangrove stands in temperate and semi-arid climates of Australia (Johnstone 1990), *Avicennia marina* is the dominant overstorey species at Lake MacLeod. It occurs with a range of Samphire species, *Tecticornia, Sarcocornia* and *Chenopodium* genera. The taxonomic identities of these genera are currently under investigation (K. Shepherd pers. comm., Nov. 2012). Mangrove and Samphire vegetation commonly occur together, with Samphire shrubs found around the base of the mangrove trees, although they can be found independently across the lake bed.

The vegetation growing within Lake MacLeod lakebed is highly variable in structure, form and composition. There is generally a fringing band of vegetation surrounding each lagoon, pond or channel, commonly a larger closed to open forest. Here, the trees are reasonably tall, some *A. marina* reaching 3 - 4 m in height with large trunks and dense canopies. The associated pneumatophore beds are dense and relatively tall, with the Samphire vegetation occurring as a dense understorey (Johnstone 1990; Ellison and Simmonds 2003). Behind this narrow band of trees, vegetation structure, form and composition varies considerably, either low open Samphire scrubland, scarcely scattered shorter to dwarfed *A. marina* supported by Samphire shrubs*;* or bare saltpan (Ellison and Simmonds 2003). With greater distance from the permanent water bodies, the pneumatophores are generally sparser and much shorter. These structural features appear to be dependent upon the occurrence of a constant supply of water.

2.4 Coastal Environment of Carnarvon

2.4.1 Location and Significance

Carnarvon is adjacent to the World Heritage Area of Shark Bay, the Shark Bay Marine Reserve and Woomeral Special Purpose Zone to the south, as well as Ningaloo Marine Park to the north. The coast line immediately surrounding Carnarvon is low lying and has been in the present form for approximately 6000 years as sea level along the West Australian coast has been relatively stable since then (Lambeck and Nakada 1990). The limestone coast line supports an extensive mangrove stand with *A. marina* occurring along the sandy low lying coast, river mouth, channels and wetlands.

2.4.2 Hydrology

The dominant hydrological processes on the coast are river discharge and tidal flows. The difference in tide range is from 0.3 m to a maximum of 1.7 m, usually there are two high tides a day and less commonly one (tide-forecast 2013). The Gascoyne River is large and the catchment area vast. It flows irregularly, typically after extreme events during the tropical cyclone season, although rainfall during the south west temperate winter season is regular and lower flows are recorded during this time.

2.4.3 Vegetation

Vegetation within the Gascoyne region is predominantly low open woodlands dominated by *Acacia sp.* with understorey vegetation including *Eremophila sp.*, *Cassia sp.* shrubs with hummock grasses and an array of salt bushes including rich communities of Samphires (Burbidge, McKenzie *et al.* 2000). Coastal mangrove stands surrounding Carnarvon consist of one species, *Avicennia marina* and these can occur as woodland to stunted shrubland stands (Johnstone, Burbidge *et al.* 2000). Individual trees found at the water’s edge on the coastline or riverbanks are large (> 5 m) with dense canopies and smaller, dwarfed and sparsely spread trees occurring further inland. The coastal and riverine stands display typical community-pattern zonation found within tropical and subtropical mangrove stands, although the zones appear to be much narrower with more distinct demarcation between zones (Bunt 1999; Vilarrubia 2000; Martin, Bruhn *et al.* 2010).

2.5 Site selection

2.5.1 Rationale for locations and sites

The aim of this study was two-fold: firstly to examine the patterns in mangrove dominated vegetation and how those patterns are related to hydrological and environmental conditions at inland mangrove stands; and secondly to compare the ecophysiological traits of the mangrove *A. marina* between coastal and inland mangrove stands. Four sites were selected in both inland and coastal environments that covered a range of hydrological conditions relating fresh and salt water supply (Table 1 & Table 2).

Table 1: Inland study area description based on hydrological, geomorphological and topographical characteristics of Lake MacLeod sites.

Site characteristics		**Inland marine – Cygnet Pond**	**Inland marine – Chirrida Pond**
Geomorphology & Topography		Deep ponds & Marsh areas. Low-lying barrier south of the pond (1) Channel to Ibis Pond (2)	Northern cluster of ponds. Middle cluster of ponds. Southern cluster of ponds (4)
Mangrove presence		Monospecific *A. marina.* All ponds have mangroves, spatial extent varies dependent upon local geomorphology. (2)	Monospecific *A. marina*. Almost all ponds in this region have a narrowband of mangrove trees surrounding the individual water bodies. (2, 4)
Salinity		Similar to seawater at vents with a gradient to hypersaline with distance from vents (2)	Similar to seawater at vents with a gradient to hypersaline with distance from vents (2)
Hydrology	River flow	Rarely 1 in 6 - 5 year event (1, 2)	Very rare, 1 in 10 year event (1, 2)
	Residence time of river water flow	Moderate/high depending on event (2)	Minor/Moderate depending on event (2)
	Tidal exchange	Indirect, small (cm) variation in fluctuation (1)	Indirect, small (cm) variation in fluctuation (1)
	Seepage	Southern Cygnet Seepage face facilitates saltwater intrusion from the western side; spill sheet flow is generally in an eastern/southern direction (1, 3)	Isolated ponds fed by saltwater via Northern Cygnet Seepage Face on the western side (1)

(1), Shepherd, 1991; (2), Ellison, 1997; (3), Russell, 2004; (4), Google Earth

2.5.2 Inland sites

One site in Lake MacLeod was in Cygnet Pond Goat Bay (23° 58 179’’ S, 113° 36 372’’ E) and the remaining three were in the Chirida Ponds; Whistler Pond (23° 50 825” S, 113° 41 960” E); Pete’s Pond (23° 46 976’’ S, 113° 45 764’’ E); and Neil’s Pond (23° 48 667’’S, 113° 41 579’’ E). These sites span the lake bed from far north (Pete’s Pond) to the most southern site (Goat Bay) (Figure 6 a & b). As the hydrological regime occurring at Lake MacLeod is extremely complex, varying extensively from north to south, the sites included comprise the most suitable suite of wetlands representative of the hydrological patterns present. There is no tidal exchange at these sites, but sea-water is delivered from vents into the ponds. Due to the large size of Cygnet Pond, a large wind fetch can be generated and wind waves facilitate the movement of water out of

Cygnet Pond onto surrounding sediment and mangrove and salt-marsh habitat. River water rarely flows into Cygnet or the Chirrida Ponds. However, when it does it is less rare in the Chirrida Ponds (1 in 10 years) vs. Cygnet Pond (1 in 5 years). When freshwater reaches Cygnet Pond, it has a longer residence time than the Northern Chirrida Ponds.

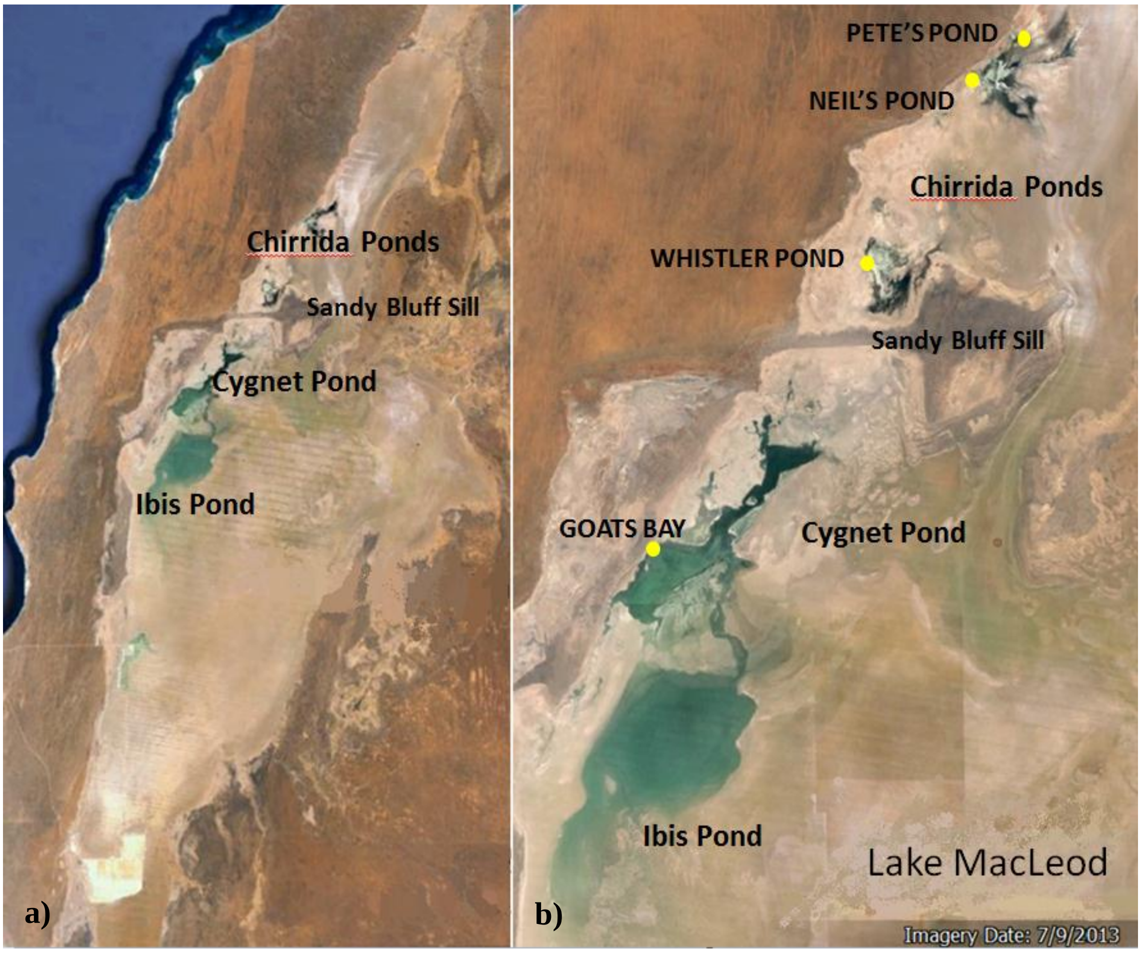

Figure 6: a) The greater Lake MacLeod with Ibis, Cygnet and Chirrida Ponds and Sandy Bluff Sill, the geomorphological feature separating Northern and Southern regions of the lake. b) Location of the inland sites Pete's Pond, Neil's Pond, Whistler Pond and Goat Bay.

2.5.3 Coastal sites

Two sites were selected at fringing coastal mangrove stands, south of Carnarvon (Figure 7) and away from the direct influence of a fresh-water river (Coastal site 1 - 113° 40 837" E, 25° 03 224" S, and Coastal site 2 - 113° 43 843" E, 25° 07 264" S)(Table 2). Both these sites are within the Brickhouse Station lease and the band of mangroves up to 200 m wide with a seaward and landward edge (Figure 7b). Two sites were selected at coastal riverine mangrove stands associated with the Gascoyne River Mouth, one at the false mouth of the Gascoyne River (113° 39 143” E, 24° 53.266” S) within Carnarvon township, next to the port, and one slightly north of Carnarvon town site at One Arm Tree Point (113° 37 738” E, 24° 51 716” S) (Figure 7b). The main difference between these two sets of sites was the freshwater influence at the riverine sites.

Table 2: Coastal study area description based on hydrological, geomorphological and topographical characteristics.

Site characteristics		**Coastal fringing - Carnarvon**	**Coastal Riverine - Carnarvon**
Geomorphology & Topography		Elevation begins at sea level and gradually increases in a perpendicular landward direction (1).	Varied from low flat areas with gradual increases in elevation to sharp increases (riverbank) in elevation to gradual increases.
Salinity		Seawater to hypersaline depending upon location within intertidal zone and tidal patterns (1).	Almost fresh to brackish to saline dependent upon distance from the river mouth.
Mangrove presence		Dominated by *A. marina* supported by *Aegialitis annulata* (2).	Dominated by *A. marina* supported by *Aegialitis annulata* (2).
Hydrology	River flow	Nil, direct rainfall has a moderate/low impact.	Regular and low – winter*, episodic and extreme – summer*.
	Tidal exchange	Regular daily flushing water fluctuation up to 1.80 metres in height.	Regular daily flushing water fluctuation up to 1.80 metres in height.
	Residence time of river water flow	Nil	Moderate

(1 Nybakken and Bertness 2005); (2 Pedretti and Paling 2001) * South West Western Australian weather patterns

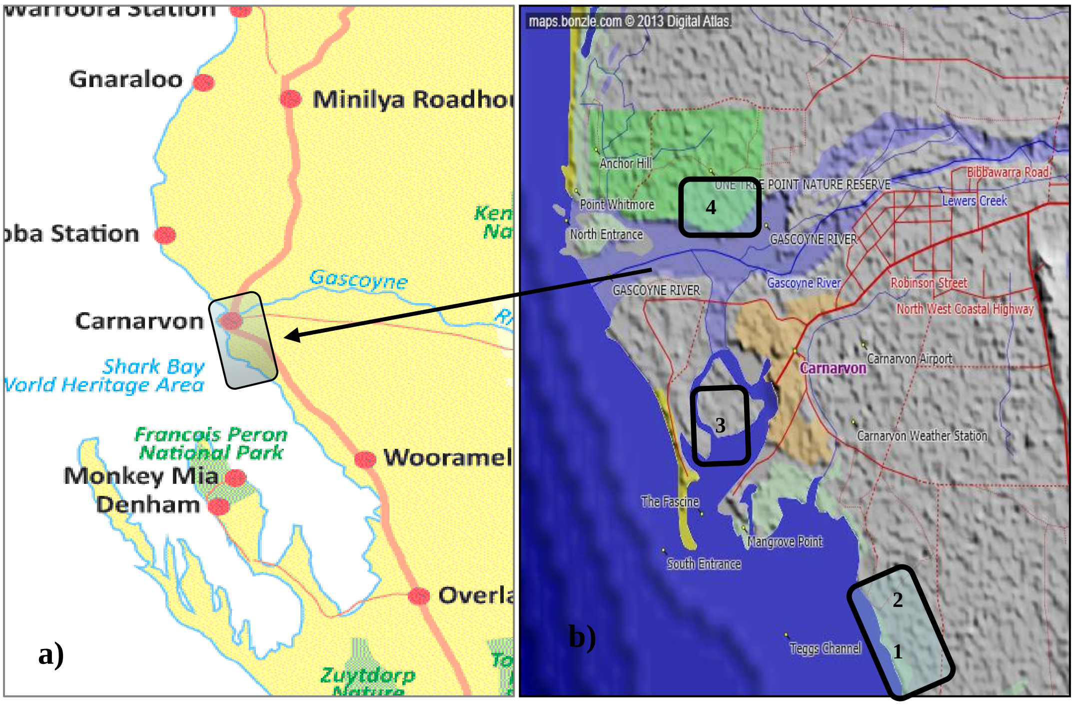

Figure 7: a) All coastal and riverine sites are found within the shaded area surrounding Carnarvon Township. b) The shaded boxes indicate the locations of the coastal and riverine sites: One Arm Tree Point (4), Gascoyne River Mouth (3) and the two coastal sites (1 & 2).

3 Chapter three – Inland mangrove vegetation distribution and structure relative to local environmental conditions.

3.1 Introduction

Globally, inland mangrove systems are rare with only eight recorded worldwide (Ellison 1997). They originate from sea level (Shepherd 1991; Ellison 1997) and geomorphological changes to the basin (Van Steenis 1984; Thomas, Logan *et al.* 1992) and/or coastline so that an embayment becomes separated from the ocean (Stoddart, Bryan *et al.* 1973; Lugo 1981; Van Steenis 1984; Ellison 1997; Ellison and Simmonds 2003). The eight identified inland mangrove systems also have unique hydrological regimes, ranging from hypersaline to brackish/freshwater conditions (Ellison 1997). These differences in hydrological regimes are largely related to climate and the relative importance of freshwater inflow. For example, tropical inland mangrove stands found at Anchialine Ponds, Bermuda (Thomas, Logan *et al.* 1992) are limestone based with connections to the ocean whereas mangroves situated on Inagua Bahamas (Lugo 1981), Tuvalu Island in the South Pacific (Woodroffe 1987) and northern and southern Irian Jaya (Van Steenis 1984; Ellison and Simmonds 2003), have no apparent connection to the ocean and rely entirely on rainfall and/or river inputs. In contrast, temperate or semi-arid habitats where rainfall is lower and evaporation is high the systems are likely to present hypersaline conditions through evapoconcentration. As Lake MacLeod is the only inland mangrove system found outside the tropics, one may expect the regime of freshwater inflow and particularly evaporation to define mangrove distribution and structure.

The quality of water inflow and outflow contributes to local hydrological conditions and is a key influence on vegetation patterns (Feller, Lovelock *et al.* 2010). Unlike coastal and riverine mangroves, inland systems receive minimal or no tidal influence and reduced throughflow of surface water such as in riparian systems. This reduced flushing of the root zone in combination with evapoconcentration can lead to hypersaline conditions (Paliyavuth, Clough *et al.* 2004). Where inland systems are connected to the ocean via submarine caves (Thomas, Logan *et al.* 1992) or an underground karst network (Logan 1982) marine inflow is possible due to hydrostatic pressure, however the tidal range is small (centimetres).

Limited tidal range and hypersaline conditions have been associated with a narrower distribution of mangroves (Feller, Lovelock *et al.* 2010) and the trees often exhibit a smaller growth form than the same species found within coastal habitats, i.e. lower tree height, canopy cover and basal area as well as xeromorphic leaf traits (Beard 1967; Stoddart, Bryan *et al.* 1973; Lugo 1981; Van Steenis 1984; Thomas, Logan *et al.* 1992; Ellison and Simmonds 2003). The reported range in height varies from 1 to 7 metres, depending on the local hydrological regime. Typically, where rainfall is low and evaporation high, the resultant high salinity represses mangrove growth, production and reproduction (Naidoo 2010).

The Lake MacLeod ecosystem has a very complex and crudely understood hydrological regime (Ellison 2003). It is represented by an extensive basin comprised largely of a dry lake bed with brackish-saline flats that surround permanent saline ponds and lagoons maintained by seawater sourced from an underground karst network (Johnstone 1990). This system supports *A. marina* stands under conditions of low rainfall, no tidal influence and high evaporation rates. Although the tidal range may only be a few centimetres, evaporation rates in the basin are high and this causes a relatively continual inflow of seawater (Phillips, Butcher *et al.* 2005). There is irregular and episodic rainfall which can cause flooding at Lake MacLeod, usually one in 5 – 10 years and typically occurs as a result of summer cyclones (Streamtec Pty Ltd 2002).

Mangroves at Lake MacLeod appear to only persist where consistent water sources are present via an underground limestone karst system. Essentially, Lake MacLeod is an expression of the hydrogeological saline groundwater system present in the area, which is separate from the regional fresh groundwater system that does not appear to upwell into the lake (Russell 2004). The balance between hydrostatic pressure and evaporation generates a relatively consistent supply of seawater (Russell 2004) through openings called ‘vents’ where water supply and salinity is relatively consistent. With increasing distance from the vents, surface and soil water become hypersaline primarily via evapoconcentration. Exceptions to this pattern occur due to the variable characteristics and location of ‘vents’ along the western side of the larger lagoon areas of Lake Macleod and within the smaller ponds within the ‘Northern Pond’ area above Sandy Bluff Sill (Figure 6) (Shepherd 1991). In addition, there are smaller (ranging from centimetres to metres) seeps that discharge seawater constantly and often support mangrove vegetation similar to that surrounding the larger bodies of water (Figure 8).

Some seeps however may be devoid of mangroves and Samphire and only support a thick cyanobacteria mat (Figure 8; Shepherd 1991).

Figure 8: Photos of vents found at distances from the main water body. (Left) A vent provides this small pool of water with a constant supply of seawater, thus allowing taller mangrove trees to exist. (Right) A small seep opening, found in a bare area of saltpan, that supports an algal mat.

This persistent discharge of seawater from vents into spill sheets and saltpans combined with high evaporation, may strongly influence water availability and salinity and define mangrove distribution and structure. The characteristics of the lake make it an ideal candidate to specifically address the objective of this chapter, which is:

To identify the environmental parameters associated with variability in the distribution and structure of the mangrove-dominated vegetation at Lake MacLeod.

3.2 Materials and Methods

3.2.1 Sampling Design

To address the objective of this study, a survey of the mangrove dominated vegetation, including Samphire and the associated environmental variables, was undertaken in February and July 2012. This occurred at four locations in Lake MacLeod as detailed in Chapter 2 (Figure 6). Goat Bay is part of Cygnet Pond below Sandy Bluff Sill and Whistler, Neil’s and Pete’s Ponds are components of the southern, middle and northern clusters of ponds within Chirrida Pond (in that order) above Sandy Bluff Sill (Figure 9). The four sites represented a range of hydrological conditions found at Lake MacLeod (Table 3).

Table 3: Hydrological characteristics of the four sampling locations within Lake MacLeod.

	Goat Bay	**Whistler Pond**	**Neil's Pond**	**Pete's Pond**
Geomorphology & Topography	Deep ponds & Marsh areas. Low lying barrier south of the pond (1). Channel to Ibis Pond (2).	Southern cluster of ponds (3).	Middle cluster of ponds (3).	Northern cluster of ponds (3).
River flow	1 in 5 - 6 year event (1, 2).	1 in 10 year event (1, 2).	1 in 10 year event (1, 2).	1 in 10 year event (1, 2).
Residence time of river water flow	Moderate/high depending on event (2).	Minor depending on event (2).	Minor/Moderate depending on event (2).	Moderate depending on event (2).

(1 Shepherd, 1991) (2 Ellison, 1997) (3 Google Earth)

To examine the variability in mangrove-dominated vegetation presence and structure associated with hydrological (water quantity and quality) conditions at each of the sampling locations, a gradsect design was employed (Austin and Heyligers 1991). A gradsect design determines sample location by change in elevation. This method was selected as elevation influences hydrological conditions experienced by vegetation therefore maximising the probability of capturing differences in vegetation characteristics within and between locations (Austin and Heyligers 1991; Wessels, Van Jaarsveld *et al.* 1998).

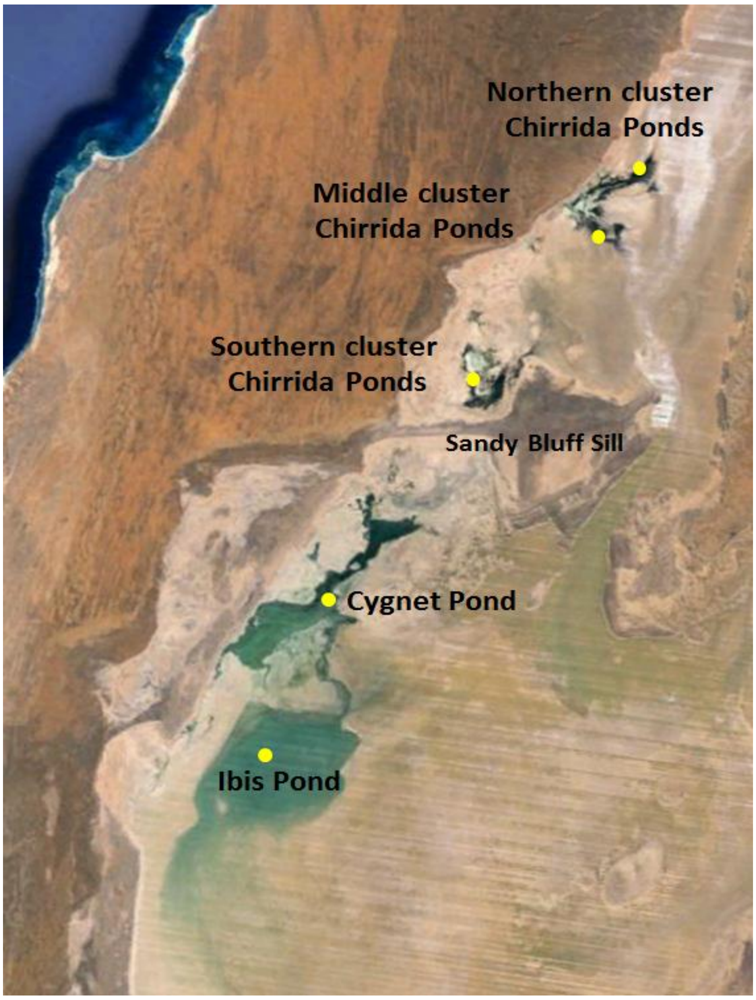

Figure 9: Location of permanent individual ponds which represent the greater Lake MacLeod.

At each location, three replicate gradsects were arranged perpendicular to the pond edge (Martin, Bruhn *et al.* 2010). Plots (10 m x 10 m) were located from the edge of the pond, with plot one covering the first 10 m from the pond edge and subsequent plots placed along the gradsect where a 10 cm change in elevation (negative or positive) occurred, or every 20 m, whichever occurred first. Elevation was measured using an automatic level (Leitz/Sokkisha, C3E) and staff. The minimum length of each gradsect was 100 m, or 20 m beyond the last mangrove tree. Each plot was defined on the basis of relative elevation and distance from the pond edge (Figure 10). Due to the gradsect design, the number of plots in each varied, from 4 - 7, with four being the most common outcome.

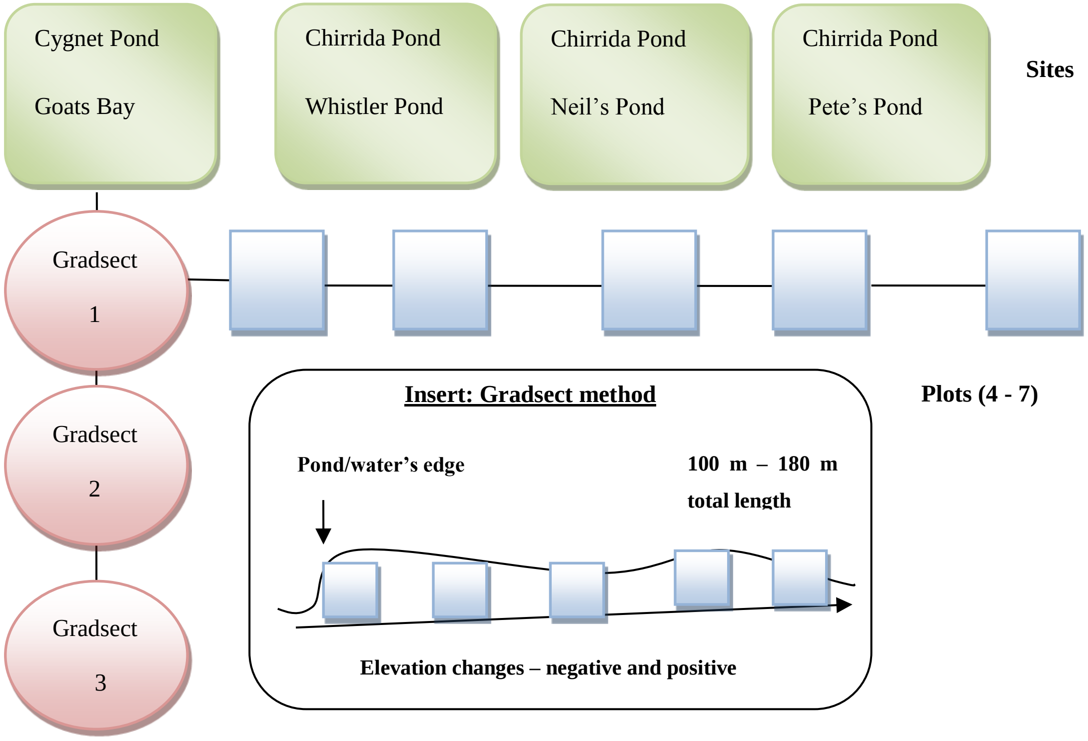

Figure 10: Schematic displaying the sample design used at sites within Lake MacLeod. Insert: Gradsect method utilises changes in sediment elevation to determine plot placement. The sampling design and method is structured to best capture the key environmental parameters accounting for variability in mangrove dominated vegetation characteristics.

3.2.2 Vegetation Sampling

The following mangrove vegetation variables were measured in each plot:

Samphire cover

Samphire cover was estimated visually as a percentage cover of the 100 m^2 plot. This percentage was then converted to m^2.

Mangrove trees

Tree density

The mangrove trees were counted in each plot and expressed as a number per plot (100 m^2).

Canopy cover (CC)

Canopy cover of each mangrove tree was measured by recording the diameter of the widest part of the canopy, and the perpendicular diameter in the same horizontal plane, to the nearest mm. Canopy cover (m²) was then calculated for each tree using equation 1.

$$\text{Canopy cover} = \pi(A \times B) \qquad \text{(Equation 1)}$$

A - Widest diameter; B - perpendicular diameter

Two variables were then determined for each plot; total canopy cover (m²), by summing the canopy cover of all trees in a plot and average canopy cover (m²) by averaging all trees in a plot.

Basal area (BA)

Basal area per plot was estimated by measuring the diameter of the trunk of each mangrove tree at 30 cm above either ground level or the basal plate, with a diameter tape to the nearest mm. Where trees had multiple trunks, each trunk was measured and added together (Clough 1998) and, where there was an exposed basal plate the widest point across the plate was measured (Clough, Dixon *et al.* 1997) . Basal area (m²) was calculated for each tree using equation 2.

$$\text{Basal area} = \left(\frac{D}{2}\right)^2 \times \pi \qquad \text{(Equation 2)}$$

D - Diameter

Once again two variables were determined for each plot as described above, total and average.

Height

Height was estimated using a measuring staff; the maximum height of the tree was recorded to the nearest mm and expressed in metres. Two variables were determined for each plot; maximum and average tree height (m).

Number of dead branches

Dead branches were counted on each mangrove tree and expressed as average and total per plot.

Mangrove pneumatophore density and height

A smaller 25 cm x 25 cm quadrat was placed in nine locations within the larger 100 m² plots (Figure 11) in which mangrove pneumatophores were counted, summed and expressed as number per m^{-2}. The tallest pneumatophore in each quadrat was also measured and expressed as average maximum pneumatophore height per plot (mm).

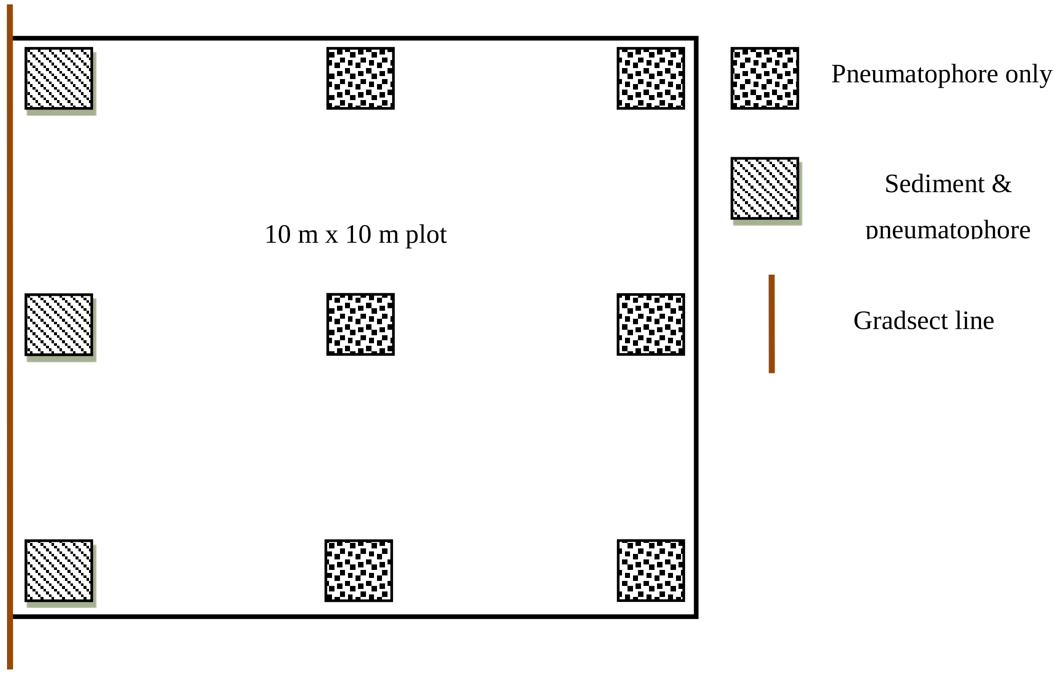

Figure 11: Sampling locations (quadrats) for pneumatophore and sediment variables within each plot.

Litter

Litter cover was estimated as a percentage cover and converted to m² per plot. Maximum depth of the litter layer was measured to the closest mm and expressed as the maximum litter depth per plot.

3.2.3 Sediment and Water Sampling

Sediment elevation relative to the water level of the pond and distance from the pond edge were recorded for all plots. In addition, the following environmental variables were measured:

Sediment sampling

All sediment variables were estimated from three quadrats in each plot (Figure 11). Sediment cores (5 cm diameter, metal) were taken to a depth of up to 10 cm. Shallower core depths were necessary at some sites due to consolidated layers in the sediment. Each sediment core was stored in a plastic bag and placed on ice in a portable cooler.

Samples were frozen on return to the laboratory until further analysis. Sediment cores were collected and variables measured in February and July 2012 to capture seasonal effects of rainfall and evaporation.

Sediment moisture content

Sediment moisture content (SMC, %) was determined on defrosted sediment cores after oven drying at 105ºC (>24 hours), and calculated using equation 3.

$$SMC = \left(\frac{WW - DW}{DW}\right) \times 100 \qquad \text{(Equation 3)}$$

WW - wet weight; DW – dry weight (Buurman, van Lagen et al. 1996)

As there were no consistent seasonal differences in SMC, data were expressed as an average and range per plot.

Sediment electrical conductivity and pH.

Sediment electrical conductivity (EC, mS cm^{-3}) and pH (with and without $CaCl_2$) of 1:5 water extracts (Al-Busaidi, Cookson *et al.* 2005; Lara and Cohen 2006) was measured using an Orion 5-Star portable Multimeter Kit (pH/ORP/ISE/DO/Conductivity; Thermo electron Corporation). As there were no consistent seasonal differences in EC or pH, data were expressed as an average and range per plot.

Sediment clay content

Sediment clay content (%) was estimated using field texture analysis (McDonald and Isabell 1984). The field texture grade categorised the clay content of each quadrat sample and was expressed as average % clay content per plot.

Sediment organic matter content

Organic matter content (OM, %) was determined by undertaking a loss on ignition (LOI) method (Buurman, van Lagen *et al.* 1996). A crucible two thirds full of sediment was placed into a furnace and ignited at 500°C for 2 hours. The mass lost represents the OM (%) within the sample it was calculated using equation 4.

$$OM\ content = 100 \times \frac{(OS - IS)}{OS} \qquad \text{(Equation 4)}$$

OS - mass of oven dried sediment; IS *– mass of ignited soil*

3.3 Data analysis

To identify for variability in vegetation attributes and how this related to sediment and water characteristics, all variables (Table 4) were analysed using a Canonical Analysis of Principal Coordinates (CAP) which is a constrained ordination (Primer-E 2009). A permutation test was run with a maximum number of permutations set at 9999 using Permanova+ (Anderson, Gorley *et al.* 2008)

Table 4: Vegetation and environmental variables used in the data analysis for identifying environmental and vegetation relationships.

Data type	**Variable**	**Code**	**Unit/plot (100m^2)**
Vegetation	Mangrove tree density	MD	density
	Mangrove tree canopy cover	TCC/ACC	m^2
	Mangrove tree basal area	TBA/ABA	m^2
	Mangrove tree height	MH	m
	Dead branches on mangrove tree	TDB/ADB	count
	Pneumatophore density	PD	count
	Pneumatophore max. height	PH	mm
	Samphire cover	SC	m^2
	Litter cover	TLC	m^2
	Litter depth	LD	mm
Environmental	Distance from pond	Distance	m
	Sediment elevation	Elevation	mm
	Sediment moisture content	SMC	%
	Sediment moisture content diff.	SMC differ	%
	Sediment electrical conductivity	EC	mS/cm
	Sediment electrical conductivity diff.	EC differ	mS/cm
	Sediment pH	pH	pH
	Sediment clay content	Clay content	%
	Sediment organic matter content	OM	%

The results of the permutation test revealed the strength of these canonical relationships and highlighted the main environmental variables that have an association with the observed variation in the vegetation variables. To further investigate the relationships between hydrological drivers and sediment variables, the significance of the linear regression was determined using Pearson’s correlation coefficient in SPSS Statistics V19.0, with the significance level set at $p < 0.05$.

The plots were placed into five hydrological categories based on sediment elevation and distance from permanent water source. Significant differences between groups in sediment variables: SMC, EC, pH, OM and key vegetation variables: Mangrove tree height, canopy cover, basal area, average dead branches, density and Samphire cover were analysed using One-way ANOVA SPSS Statistics V19.0, with ANOVA and LSD Post hoc significance level set at $p \leq 0.05$. Finally, plots were grouped based on vegetation type and the coefficient of variance (%) was determined for sediment variables SMC, EC, pH and OM.

3.4 Results

3.4.1 Multivariate analysis of mangrove vegetation and environmental variables.

There was a significant canonical correlation between the vegetation and environmental variables within Lake MacLeod ($p = 0.0089$). The canonical analysis of principal coordinates (CAP) revealed that the correlation eigenvalues (λ) for axes one and two were high at 0.6896 and 0.4755 respectively (Figure 12). Pearson correlation values indicate that the environmental variables responsible for the spread of data points along CAP axis one are average SMC (0.836), distance from pond (-0.386) and average sediment OM content (-0.244). Mean sediment EC (-0.667), and the temporal difference in sediment EC (February and July) (0.469) are responsible for the spread of data points along CAP axis two (Figure 12). A negative value indicates that the variable decreases along the axis whereas a positive value indicates it increases along the axis.

Mangrove tree density, average height, and total canopy cover as well as pneumatophore density and maximum height, correlated positively with axis one (Figure 12). Total Samphire cover, litter cover and the average dead number of branches per tree all correlated with axis two. Samphire cover increased whereas total litter cover and average number of dead branches decreased along CAP axis two (Figure 12).

Based on the output of the CAP, the following patterns are evident:

1. Mangrove tree height, total canopy cover, and pneumatophore density and maximum height increased with SMC.
2. Dead branches per mangrove tree and total litter cover increased with sediment EC.
3. Plots with greater Samphire cover had greater seasonal variation (range) in sediment EC.
4. Mangrove tree canopy cover, height and basal area increased with decreasing sediment EC and increasing SMC.
5. With greater distance from the pond, mangrove tree density, pneumatophore density and maximum height all decrease. Relative elevation did not correlate with vegetation characteristics.

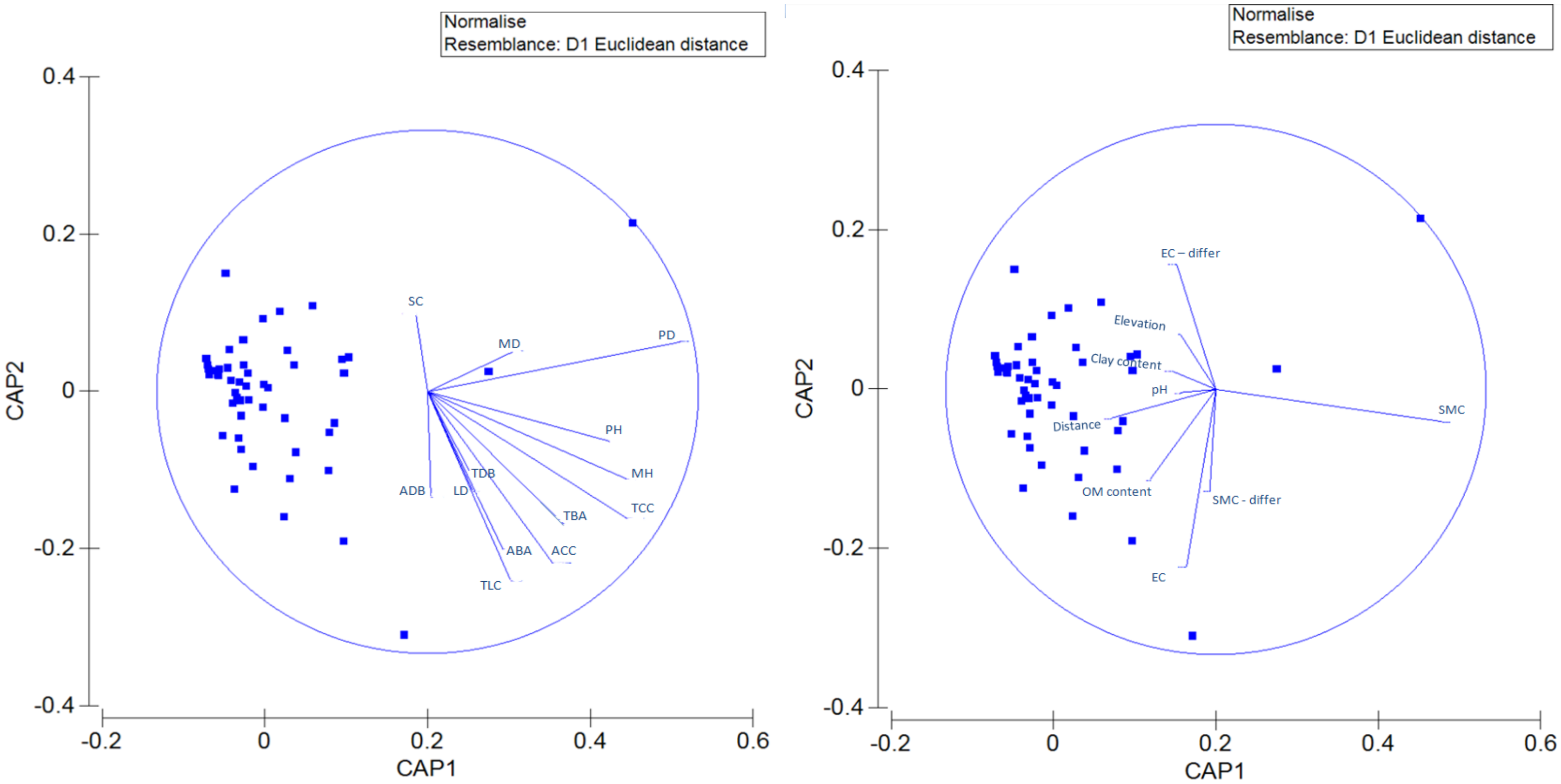

Figure 12: Canonical analysis of principal ordinations of mangrove-dominated vegetation and environmental variables. Each point represents a plot. Left: Vegetation variables overlayed; SC – total Samphire cover, MD – Mangrove tree density, PD - pneumatophore density, PH – average maximum pneumatophore height, MH – average mangrove tree height, TCC - total mangrove tree canopy cover, TBA - total mangrove tree basal area, ACC – average mangrove tree canopy cover, TDB - total dead branches on mangrove trees, ABA – average mangrove tree basal area, LD - maximum litter depth, TLC - total litter cover and ADB – average dead branches on mangrove trees. Right: Environmental variables overlayed; SMC – average sediment moisture content, SMC differ - temporal difference in SMC, EC – average sediment electrical conductivity, OM content – average organic matter in sediment, Distance - from the pond edge, pH – average sediment pH, Clay content – clay content in sediment, Elevation – relative sediment elevation in relation to the level of the water surface and EC differ - temporal difference in sediment EC.

3.4.2 Hydrological categories and sediment attributes

The influence of hydrologically relevant variables i.e. elevation and distance from pond, on environmental conditions is investigated in this section.

SMC is higher within ~80 m of the pond edge and on average is lower further away from a pond, although there is variation between ponds. SMC was high at plots within ~30 m from the pond edge and ranged between 25% - 45%. At relative elevations between 0 – 500 mm, the SMC varied from 20% - 40%. At elevations greater than 500 mm, high SMC was restricted to close to the pond edge. SMC of elevated, but more distant plots were always low (Figure 13).

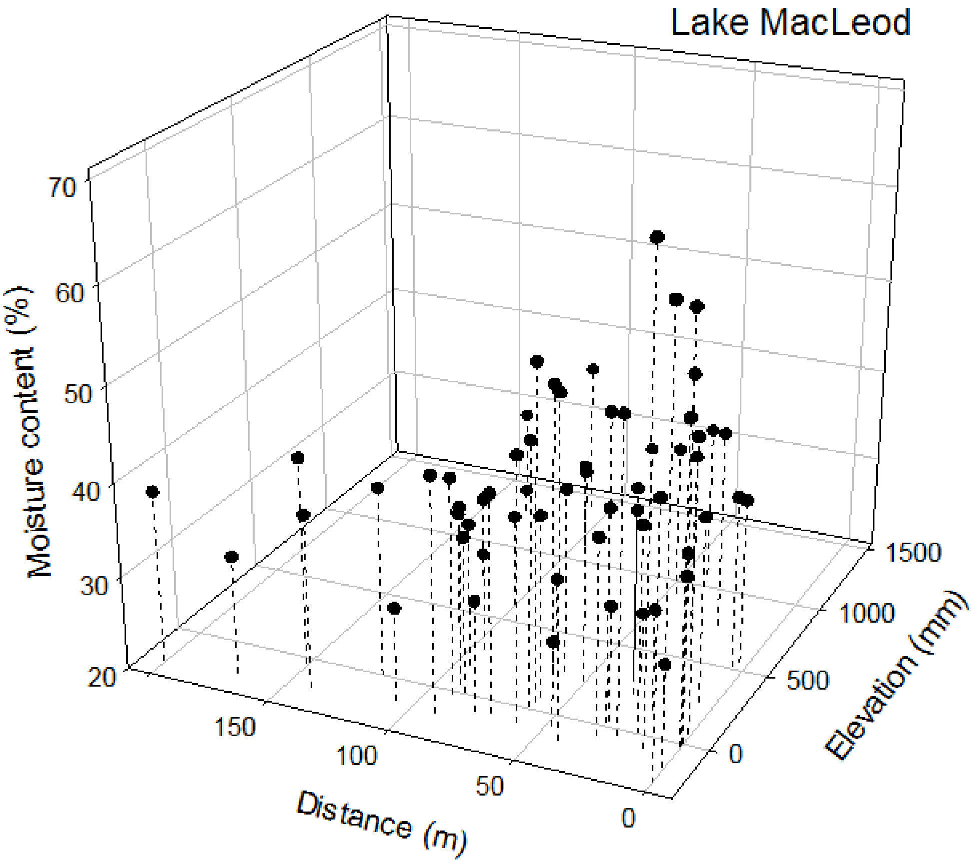

Figure 13: 3D scatterplot revealing relationships between sediment moisture content, relative sediment elevation and distance from pond.

There was marked variability in sediment EC across the Lake MacLeod plots (Figure 14). Sediment EC was generally lower at plots near the pond edge and increased with elevation, irrespective of distance.

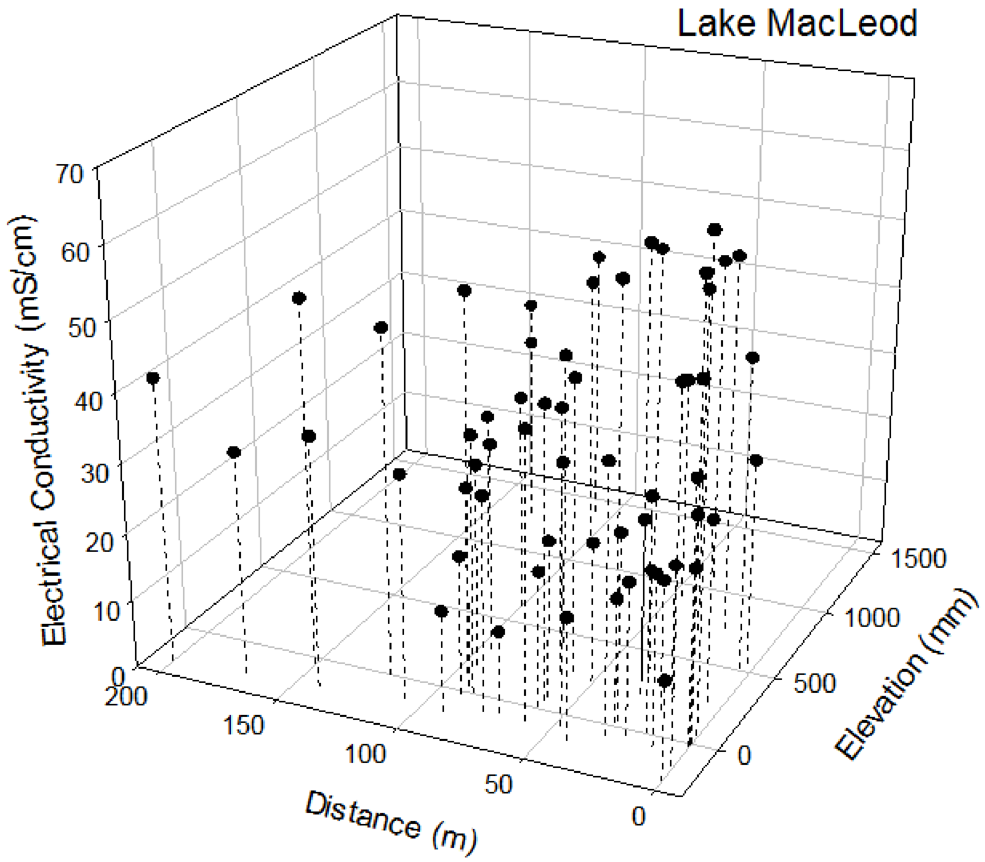

Figure 14: 3D scatterplot indicating the relationship between sediment EC, relative elevation and distance from pond.

Sediment pH was lower at the pond edge and increased with elevation (Figure 15).

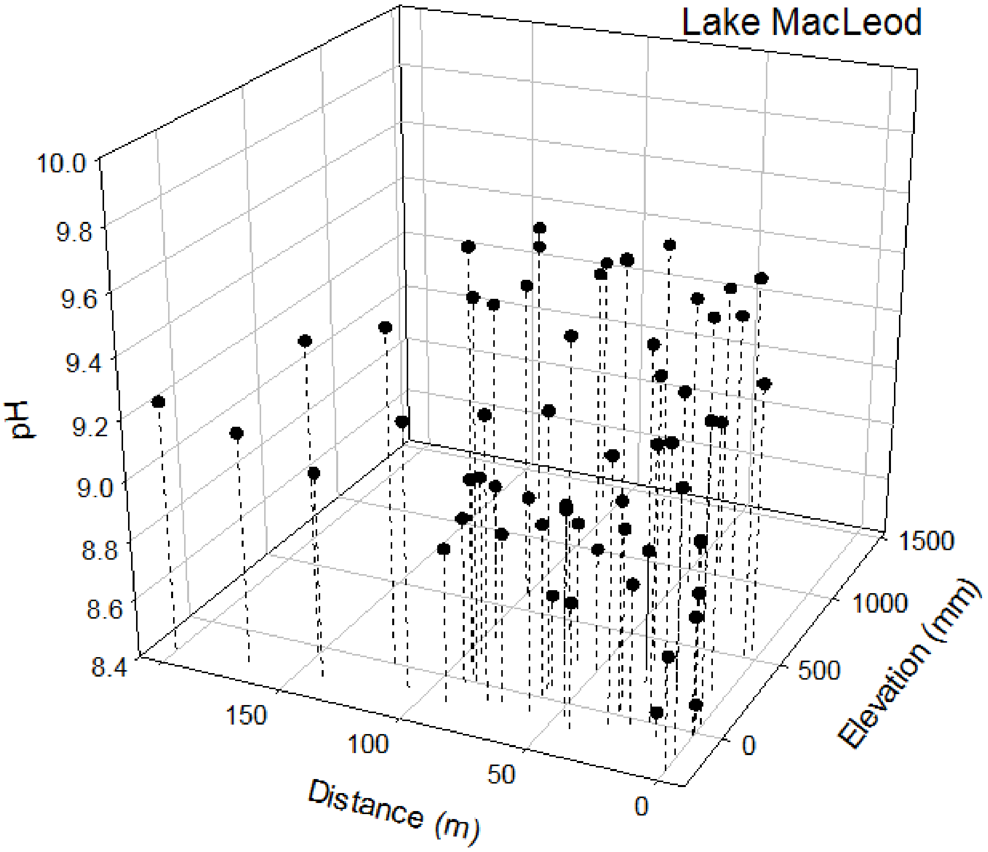

Figure 15: 3D scatterplot indicating the relationship between sediment pH, relative elevation and distance from pond.

Overall, sediment OM increased with increasing distance and elevation. Consistent patterns were observed at > 500 mm elevation where sediment OM was highest (Figure 16).

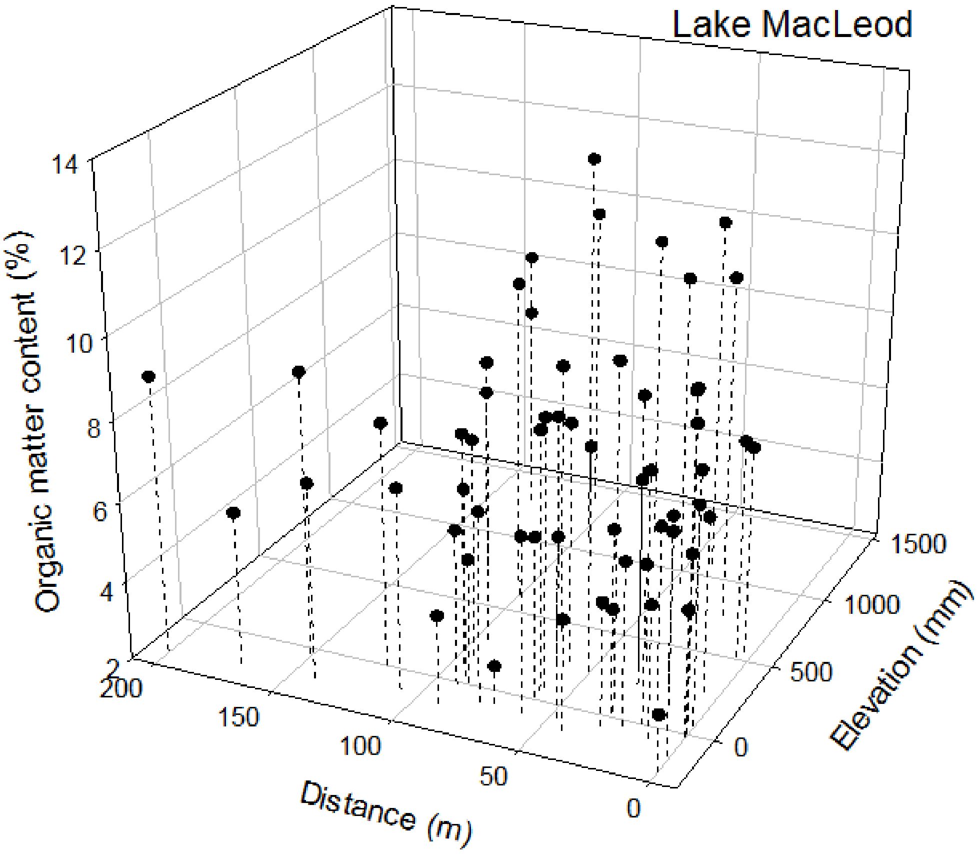

Figure 16: 3D scatterplot indicating the relationship between sediment OM content, relative elevation and distance from pond.

The complexity of the relationships between hydrological 'drivers' (elevation and distance relative to pond) and sediment variables within the Lake MacLeod system highlights the importance of depicting interaction between multiple variables when categorising plant habitat.

There was no consistent relationship between distance from pond and elevation (Figure 17). At Goat Bay relative sediment elevation increased with distance from pond whereas this relationship was variable at Whistler Pond and Neil's Pond. Sediment elevation did not change with distance at Pete's Pond. All plots ranged from 243 mm below pond water surface to 1501 mm above, with distances up to 200 m from the pond at Goat Bay and Whistler Pond and 100 m from the pond at both Neil's and Pete's ponds. Five different categories of hydrological conditions were identified based on the relative elevation and distance from pond (Figure 17).

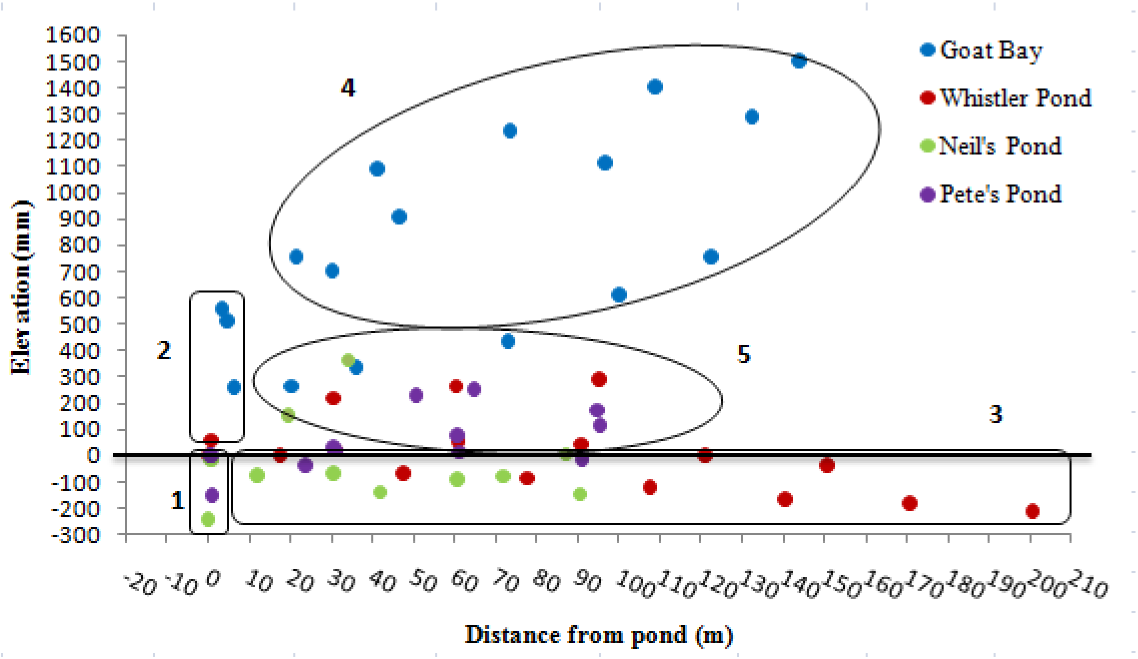

Figure 17: The position of individual plots based on distance from the pond edge and elevation relative to pond water level. Groupings (categories) are based on similar elevation and distance characteristics: 1) At or below pond water surface height, close to pond [NL] (4 plots); 2) Above pond water surface height, close to the pond [NH] (4 plots); 3) At or below pond water surface height, away from pond [FL] (21 plots); 4) Increasing elevation with increasing distance from the pond [FH] (11 plots); and 5)Above pond water surface height, away from pond, but elevation not increasing with distance from pond [FF] (15 plots).

Plots with low elevation close to pond (NL) had high mean SMC and variable sediment EC. Sediment pH was lowest in NL plots and OM content was variable. Plots with high elevation close to pond (NH) had high average sediment EC and pH with relatively consistent OM content. Plots with low elevation away from pond (FL) are extremely varied in nature; on average sediment EC was lower than seawater, but the range was vast. These plots had reasonably high SMC with a broad range of values recorded and extremely varied sediment pH and OM content. The plots with high elevation away from pond (FH) had sediment EC close to seawater and low average SMC, while average sediment OM content and pH were high. Plots that were above the pond water surface height and away from pond, but elevation not increasing with distance from pond, (FF) varied in sediment EC, but the average was just higher than seawater (Table 5).

Table 5: Mean (±SE) and range values of sediment variables for plots in each hydrological category. Subscript letters signify significant differences between hydrological categories (similar letters denote no difference) according to 1-way ANOVA and LSD post-hoc test (Significance level of 0.05).

			Environmental variables			
			SMC (%)	EC (mS/cm)	pH	OM (%)
Hydrological category	NL	Mean	$53.71 \pm 1.87_{ac}$	$41.25 \pm 2.80_{a}$	$8.93 \pm 0.04_{a}$	$7.32 \pm 0.42_{a}$
		Range	37.71 – 65.77	14.43 – 63.88	8.49 – 9.27	3.44 – 10.25
	NH	Mean	$41.84 \pm 1.71_{bcd}$	$45.43 \pm 5.0_{a}$	$9.44 \pm 0.05_{b}$	$7.44 \pm 0.19_{a}$
		Range	37.59 – 50.62	26.76 – 68.35	9.28 – 9.63	6.39 – 8.22
	FL	Mean	$48.65 \pm 2.1_{ac}$	$30.32 \pm 2.94_{a}$	$9.08 \pm 0.06_{c}$	$6.13 \pm 0.42_{b}$
		Range	38.42 – 70.02	12.05 – 52.61	8.48 – 9.43	2.97 – 9.09
	FH	Mean	$31.72 \pm 1.03_{bd}$	$38.07 \pm 1.57_{a}$	$9.36 \pm 0.01_{b}$	$8.88 \pm 0.33_{c}$
		Range	22.32 – 41.22	25.22 – 54.49	9.26 – 9.46	4.97 – 11.91
	FF	Mean	$39.54 \pm 2.79_{bd}$	$36.98 \pm 1.95_{a}$	$9.11 \pm 0.06_{c}$	$8.21 \pm 0.2_{a}$
		Range	23.18 – 55.13	19.11 – 42.73	8.86 – 9.39	6.25 – 9.00

SMC in plots within FH were significantly different to hydrological categories NL ($p < 0.001$) and FL ($p < 0.05$). Sediments at lower elevations (NL & FL) were also significantly different to FF ($p < 0.001$). Sediment EC within plots across all hydrological categories were not significantly different; there was high variability within each category. Sediment pH within plots grouped in NL hydrological category was significantly different to all other hydrological categories ($p < 0.005$). Sediment pH within plots grouped in hydrological categories NH and FH were significantly different to plots grouped in FL and FF ($p < 0.0001$). OM content within sediments was significantly different between FL and FH and all other hydrological categories ($p < 0.05$).

3.4.3 Mangrove vegetation attributes in each hydrological category

Vegetation present at Lake MacLeod consisted of both mangrove trees and Samphire, with greatest densities occurring close to the pond edge at lower elevations [NL]. However, mangrove tree density was also high at distances further from the pond at high elevation [FH], particularly where small vents/seepages occurred. Samphire vegetation dominated those plots which occurred above pond water surface height and at greater distances from pond (or small seepages) and where mangrove trees were least common [FF].

Mangrove trees found within plots close to the pond at low elevations [NL] were taller, with greater basal area and canopy cover than plots found anywhere else in the study site. This category is also where the average number of dead branches found on mangrove trees was highest. Plots close to the pond, but at higher elevation [NH], had trees similar in height to trees found in NL, but they had lower total basal area and canopy cover. Plots at a greater distance from the pond [FL & FH] had mangrove trees that were shorter with smaller total basal area and canopy cover. Trees within plots above pond water surface height and away from the pond, but elevation not increasing with distance from pond [FF], were short ($\leq$ 1m) with small canopies and basal areas. This hydrological category at Lake MacLeod supported sparsely scattered small mangrove trees with a high cover of Samphire vegetation (Figure 18).

Mangrove tree BA was significantly lower with greater distance from pond edge, trees growing in hydrological category NL were significantly different to trees in FF ($p < 0.001$) and FH ($p < 0.05$). The other significant differences in BA was between trees in hydrological categories NH and FL and FF ($p < 0.01$ & $p < 0.05$, respectively) (Figure 18). Mangrove tree height was significant different across many of the hydrological categories, trees growing in NL, NH and FL were significantly different to FH and FF ($p < 0.001$), but trees in the NL category were significantly taller than in FL ($p < 0.05$) (Figure 18). Mangrove tree CC was significantly different between trees in hydrological categories with low elevation and close to pond edge NL ($p < 0.001$), NH ($p < 0.001$) and FL ($p < 0.001$) and plots with greater distance from pond edge FH and FF (Figure 18). Average dead branches on mangrove trees were not significantly different between hydrological categories, but on average trees in NL had more dead branches than any other category (Figure 18). Hydrological category FF significantly differed in mangrove tree density to hydrological categories NL and FH ($p < 0.05$). Hydrological categories NL and FF significantly differed in Samphire cover to plots in categories NH ($p < 0.05$) and FL ($p < 0.05$) (Figure 18).

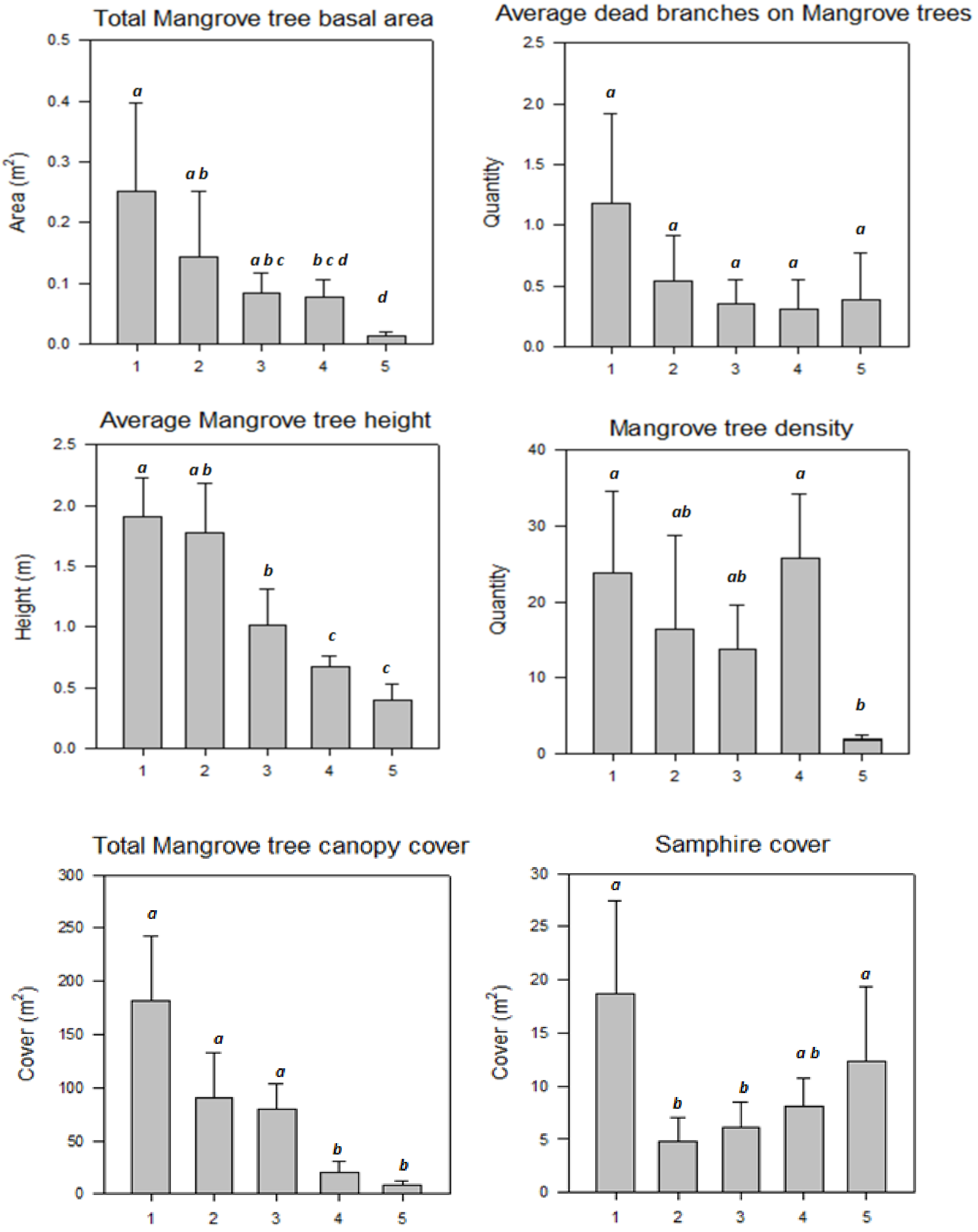

Figure 18: Mangrove tree and Samphire vegetation variables describing Lake MacLeod vegetation importance and presence based on hydrological categories present. 1. NL - Low elevation close to pond [n=4], 2. NH - High elevation, close to pond [n=4], 3. FL - Low elevation, away from pond [n=21], 4. FH - High elevation, away from pond [n=11], 5. FF - Mid elevation, mid distance from pond [n=15]. Subscript letters signify significant differences between hydrological categories (similar letters denote no difference) according to 1-way ANOVA and LSD post-hoc test (Significance level of 0.05).

3.4.4 Association between specific vegetation types and sediment conditions.

Associations between environmental variables and the presence of vegetation, Mangrove only, Samphire only and Mangrove + Samphire plots are presented in Figure 19. Most of the plots sampled within the study gradsects contained both Mangroves and Samphires. In contrast, plots that were bare or contained just Mangrove or Samphire were less common (Appendix 1.1).

Plots containing Mangrove only vegetation had the smallest range in SMC with a coefficient of variation (CV) value of 14.8%. Plots with Samphire only (CV of 25.9%) had no outliers but variation was high and plots with no vegetation had low variation with a CV value of 17.3%. The plots containing Mangrove and Samphire vegetation included the maximum range of SMC when inclusive of points outside the 10th and 90th percentile, this group of plots contained many outliers. The CV value of 28.4% supports this variation (Figure 19).

Plots with both vegetation types present had the broadest range of sediment OM content with many outliers above and below the 10th and 90th percentile range (CV of 28.2%), but it was the plots with mangrove trees only which had the highest CV value of 33% (Figure 19). Sediment pH was consistent across all plots ranging from alkaline (~8.4) to highly alkaline (~9.9). This consistency is supported by the following low CV values; Bare plots CV of 3.1%, Mangrove trees only CV of 3.9%, Samphire shrubs only CV of 3.2% and plots with both Mangrove and Samphire vegetation had a CV of 3%. Coefficient of variances for average sediment EC was high across all vegetation group types. The broadest range was in plots which contained Mangrove trees only with a CV value of 41% and lowest in plots with Samphire vegetation only (CV of 33.8%). A broad range of sediment EC was identified within plots that had both vegetation types (CV of 36.4%), with many outliers presented in the data.

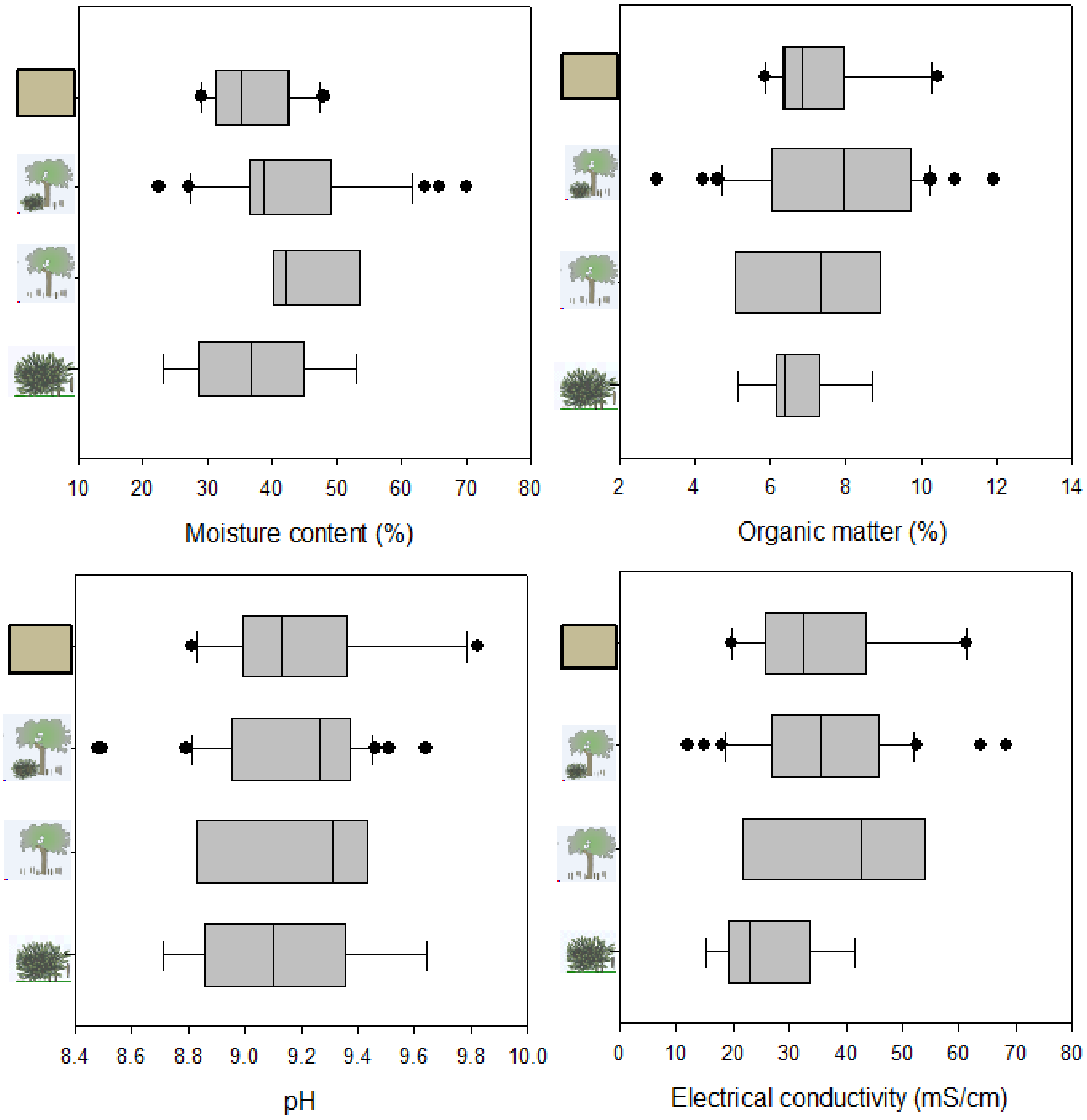

Figure 19: Vegetation type groups (Samphire [n=9], Mangrove trees [n=8], Samphire and Mangrove [n=32] and bare [n=10]) and key environmental variables relating to sediment condition (mean moisture content, mean organic matter content, mean pH and mean electrical conductivity) at sites within Lake MacLeod. Box plot lower line is the 25th percentile, the middle line represents the median, the upper line is the 75th percentile and error bars represent the 10th and 90th percentile. Black dots represent plots outside this range.

3.5 Discussion

This chapter examines the relationship between environmental conditions and mangrove dominated vegetation characteristics at Lake MacLeod. Significant associations between hydrological and sediment characteristics were revealed. The inland mangrove system at Lake MacLeod has highly variable environmental factors both spatially and temporally, (Figure 20) contributing to the variability observed in hydrological conditions, sediment properties and vegetation characteristics. The dominant factors associated with variability in mangrove vegetation presence and structure were relative elevation and distance from a consistent water source. The interaction between these factors represents subtle hydrological and sediment differences that influence mangrove vegetation.

The apparent environmental variables influencing vegetation characteristics were sediment variables such as SMC and OM content, average and seasonal range in sediment EC and the hydrological variable distance from pond (Figure 12). Distance from a consistent (continuous discharge) water source and elevation in relation to the water source are two well documented factors contributing to hydrological condition, and ultimately mangrove presence and importance within mangrove dominated stands (Paliyavuth, Clough *et al.* 2004; Naidoo 2010). Overall, relative elevation increased slightly with increasing distance from the pond, although no consistent pattern was identified between these factors. This inconsistency prompted grouping of plots into hydrological categories based on each plot's position according to relative elevation and distance from the pond edge; these categories were useful for exploring the complex relationships influencing vegetation characteristics.

Typically, hydrological conditions within mangrove stands vary along an environmental gradient; differences in vegetation attributes along the gradient depend on elevation, slope and frequency of flooding. In Australian coastal mangrove systems, habitats closer to permanent water and at lower relative elevations typically have higher average SMC and sediment EC is equivalent to that of seawater (52 mS/cm) or lower with less fluctuation (Kenneally 1982). With increasing distance from permanent water and higher elevation, SMC and sediment EC have been shown to be lower due to increased influence from freshwater inflow (Medina and Francisco 1997; Naidoo, Hiralal *et al.* 2011). In the analysis of hydrological categories (habitats) at Lake MacLeod, it was revealed that SMC was highest at low elevations close to discharging ponds [NL] and at low elevations away from ponds [FL]. At low elevations away from the pond edge, high SMC and surface water can persist due to the existence of smaller vents and seepages distributed throughout the greater lakebed. SMC decreased with increasing elevation both near and (typically) far from discharging ponds. [FH & FF]. Regular daily water movement is also common, caused by local trade winds that push water into parts of the lake bed at lower elevation (Shepherd 1991).

Variability in sediment EC can also be attributed to the local climate, micro-elevation and the complex geomorphology and topography found at Lake MacLeod (Figure 20). Average sediment EC was highest near the ponds (NH) where consistent seawater discharge and evapoconcentration occurs, due to the extreme variability there were no significant differences between hydrological categories (Table 5). With subtle increases in elevation near the ponds, sediment EC increased most likely due to extenuated capillary rise and evaporation of seawater. Lowest average sediment EC was found at greater distances from the ponds at low elevations [FL & FF] where the influence of seasonal and episodic freshwater inflow may reduce concentration of salts in the surface sediments.

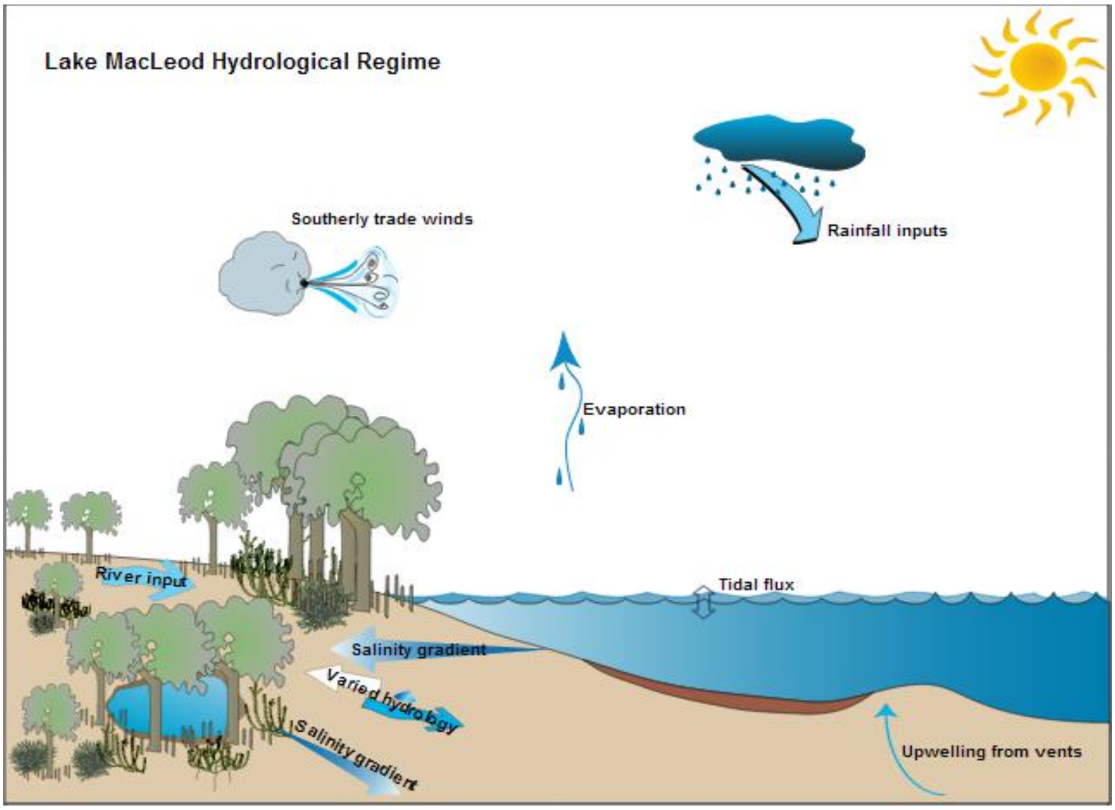

Figure 20: A conceptual diagram displaying the key environmental drivers that may contribute to the hydrological regime currently observed at Lake MacLeod.

Sediment OM content had a significant relationship with elevation but not with distance from pond and reflects the presence of vegetation, as litter accumulation, entrapment of sediment and shallow roots raise sediment elevation with time (Saintilan and Williams 1999).

Mangrove vegetation distribution and structure reflect habitat heterogeneity

The presence of mangrove and Samphire vegetation is dependent upon the extent of flooding (Matthijs, Tack *et al.* 1999). In the case of coastal and riverine mangroves, denser and taller stands occur under conditions of consistent flooding by marine water (Dawes, Siar *et al.* 1999; Matthijs, Tack *et al.* 1999; Naidoo 2010). The width of the mangrove fringe is known to reflect tidal influence and elevation characteristics (Saenger 1982; Matthijs, Tack *et al.* 1999; Feller, Lovelock *et al.* 2010). At Lake MacLeod, mangrove tree cover, basal area and height were highest close to ponds and consistent discharge of marine water. However, due to the absence of significant tidal variation, the width of the 'high biomass' mangrove fringe surrounding the ponds was comparatively narrow. Samphire cover was also highest close to the pond perimeter.

Elevation above and distance from consistent water supply is known to reduce mangrove stand biomass in other inland (Lugo 1981; Thomas, Logan *et al.* 1992; Vilarrubia 2000) and coastal mangrove systems (Dawes, Siar *et al.* 1999; Paliyavuth, Clough *et al.* 2004; Lara and Cohen 2006). At Lake MacLeod, with increasing distances away from ponds mangrove cover, basal area and height decreased as the influence of drying and episodic freshwater inflow increased. In some habitats such as Goat Bay, the fringe of mangroves was wider and density remained high with increasing distance and elevation, although cover, basal area and height decreased with distance from pond edge. This is probably due to the influence of easterly wind-driven waves extending the width of the wetted perimeter of the pond. This is representative of other inland mangrove stands such as Inagua (Lugo 1981), Madora salt marshes (Beard 1967) and Barbuda (Stoddart, Bryan *et al.* 1973).

Salinity gradients and their influence on mangrove stand structure and condition has been previously reported (Menge and Sutherland 1987; Hogarth 1999; Matthijs, Tack *et al.* 1999; Ajmal Khan and Aziz 2001; Lara and Cohen 2006; Feller, Lovelock *et al.* 2010) and suggest that sediment EC is a key environmental determinant of mangrove habitat. At Lake MacLeod, sediment EC did indeed associate with vegetation attributes as reflected in the CAP analysis. Biomass attributes such as cover and basal area increased with sediment EC and both were associated with close proximity to pond edge. Of note is the correlation between EC and number of dead branches found on mangrove trees. The greatest extent of mangrove canopy dieback was recorded at plots close to the pond edge where sediment EC was also elevated. However, one should be cautious about interpreting this canopy dieback as a function of higher sediment EC. Mangroves at the pond edge are also at the lowest relative elevation and therefore subjected to greater frequency and duration of inundation. Significant freshwater inflow and prolonged flooding of mangroves have been reported at Lake MacLeod (Ellison 2001) and it is highly likely the observed canopy dieback is a result of interaction between prolonged submergence of pneumatophores (Ellison 2009) and elevated sediment EC. The effect of both variables is unlikely to be simultaneous but cumulative over time. *A. marina* habitat salinities have been reported to be 5 mS/cm - 85 mS/cm (Gordon 1993; Sobrado 1999) and Lake MacLeod sediment EC represents the complete range of salinities with the higher end of this range occurring commonly (47.1 – 75.4 mS/cm) (Streamtec Pty Ltd 2003).

Consistency of marine water supply appears to be a key environmental variable responsible for the presence and persistence of mangrove vegetation at Lake MacLeod. Ellison & Simmonds (2003) suggested that frequency, quantity and quality of water supply influenced Lake MacLeod vegetation condition. The environmental gradients identified at Lake MacLeod in the current study support this suggestion and represent the interaction between discharge of marine water, evapoconcentration and infrequent freshwater inflow from the catchment. The absence of tidal fluctuation limits the extent of hydrological and sediment characteristics that are optimal for mangrove growth, as represented by structural attributes. Consistency of marine discharge therefore appears to be critical for maintaining a narrow hydrological envelope that supports optimal mangrove productivity in this inland mangrove system. How the optimal productivity at Lake MacLeod compares to reported high productivity coastal systems is unknown, however Medina and Francisco (1997) suggest that with increasing salinity (e.g. through evapoconcentration of consistent marine discharge) and reduced frequency of freshwater inflow, mangrove productivity will be comparatively low. The following chapter focuses on this comparative assessment of mangrove productivity and water use efficiency.

4 Chapter Four – Ecophysiological condition and morphological features of *Avicennia marina* growing in a semi-arid climate

4.1 Introduction

Avicennia marina has the broadest global distribution of all mangrove species; from tropical - temperate and high rainfall - semi-arid climates (Figure 21). It occupies a diversity of habitats within the intertidal zone and can tolerate both variable and a wide range of hydroedaphic conditions (Duke 2006). This means that the species *A. marina* can be exposed to a wide range of environmental conditions, which vary over daily, seasonal or annual cycles such as; water availability (Paliyavuth, Clough *et al.* 2004), salinity (Medina and Francisco 1997; Naidoo 2006), irradiance (Ball and Sobrado 1998), temperature (Stewart and Popp 1987) and nutrients (McKee, Feller *et al.* 2002; Martin, Bruhn *et al.* 2010). Across this range of environmental conditions *A. marina* exhibits a broad range of morphological features (Clough 1984; Naidoo 2010), anatomical characteristics (Suarez and Medina 2006) and ecophysiological responses (Sobrado 1999; Wei, Yan *et al.* 2008; Feller, Lovelock *et al.* 2010; Naidoo, Hiralal *et al.* 2011).

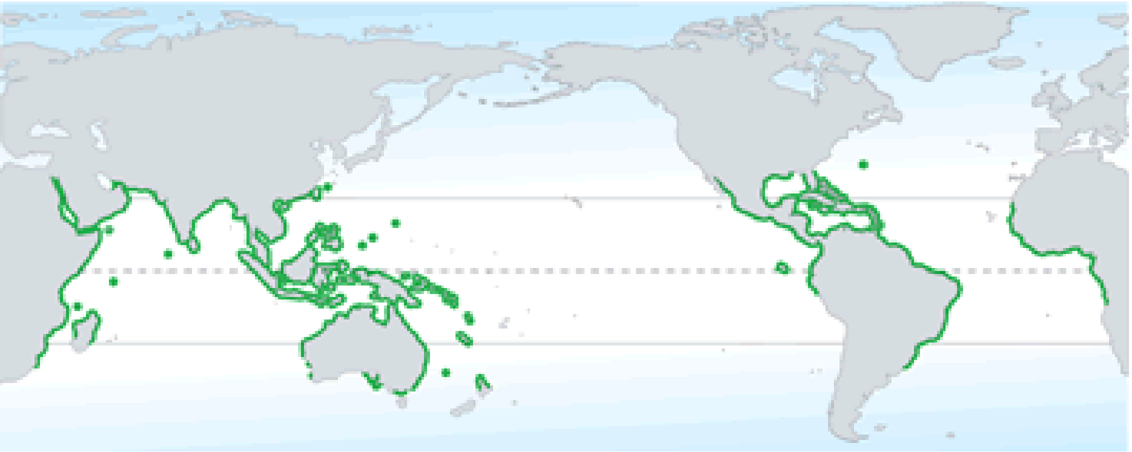

Figure 21: Global distribution of Avicennia. Green areas indicate presence (MangroveWatch, Australia).

4.2 Avicennia marina

Avicennia has been identified as the most salt tolerant mangrove genus, tolerating brackish to hypersaline conditions (Hutchings and Saenger 1987; Sobrado 1999). There are various structural (Naidoo 2006), physiological (Stewart and Popp 1987) and biochemical processes (Naidoo, Hiralal *et al.* 2011) that mangroves use to regulate uptake and accumulation of salt (Popp, Polania *et al.* 1993). *A. marina* regulates salt movement primarily via uptake of salt and then secretion from leaves (Clough 1984), although other physiological processes are also involved in salt management (Liang, Zhou *et al.* 2008).

4.3 Plant responses to salinity and water stress

Although many environmental conditions influence plant traits, this study focussed primarily on salinity and soil moisture, so this will be the focus of the following discussion. Higher salt stress is often associated with water stress, and due to this relationship, these stressors are often divided into two components; ionic effects within cells and stress derived from osmotic relations at the leaf and root level (Yeo 1983). These stresses affect intrinsic photosynthetic capacity leading directly to reduced productivity (Medina and Francisco 1997). Research indicates that these stressors and responses are not independent; with growth and productivity affected by a complex mix of environmental factors (Krauss, Lovelock *et al.* 2008).

Mangrove trees demonstrate variability in their water-use efficiency and photosynthetic rates and this depends upon the climate and hydrological environment in which they are growing. Photosynthetic rate is primarily regulated by irradiance but factors such as salinity and water stress are also important (Lovelock and Ball 2002). For example, down-regulation of photosynthesis occurs under hypersaline conditions (Naidoo, Hiralal *et al.* 2011). This occurs due to the changes in concentration of ions in the leaf cells, in particular; K^+, Na^+, Cl^- (Ball, Chow *et al.* 1987; Suarez and Medina 2006), which put extra pressure on intrinsic processes (Krauss, Lovelock *et al.* 2008). For example Naidoo et al. (2011) found that under chronic hypersalinity and low soil water potential, there were high soil concentrations of Cl^-, Na^+, K^+, Ca^{2+}, and Mg^{2+}. These hydroedaphic conditions induced higher concentrations of Na^+ and Cl^- within leaf material and reduced uptake of K^+, Ca^{2+} and Mg^{2+} leading to an ion imbalance within the leaves. Due to the changes in leaf ion content under different salinity and soil water conditions, ion content is a reliable indicator of the local hydroedaphic conditions (Ball and Farquhar 1984).

Mangrove tree growth is dynamic, rates can change across scales of months to years, therefore numerous measures are used to represent various scales of growth (Alongi 2002). Climate and local hydrological regimes, particularly irradiance, temperature (Clough 1993) , salinity and water stress (Naidoo 2006) and sediment quality influence the production and growth of mangrove stands (Clough 1992). Rate of shoot growth is a commonly used short-term measure of plant productivity (Ball 1988b). Salinity stress and low water potential generally results in a decline in plant productivity, which is directly, but not solely linked to a decrease in photosynthetic capacity (Ball 1988b; Gonzalez-Mendoza, Espadas y Gil *et al.* 2011). These stressors also influence the morphology of leaves. Naidoo (2010) established that *A. marina* exposed to irregular tidal inundation and hypersaline conditions developed thicker leaves with higher specific leaf weight (SLW) and lower specific leaf area (SLA). These morphological features are strategies to reduce water loss, which results in a decline in photosynthetic rate and therefore reduced growth (see summary; Table 6).

Variation in the biomass and form of trees is also influenced by environmental conditions, particularly soil moisture and salinity. For example *A. marina* displays a range of structural forms from tall to dwarf trees, attributed to environmental differences not genetic variation (Lin and Sternberg 1992a; Medina and Francisco 1997; Naidoo 2006; Naidoo, Hiralal *et al.* 2011). Typically aboveground biomass is reduced in semi-arid climates at higher elevations and with increased distances from permanent water sources (Lin and Sternberg 1992a; Naidoo 2010). The total aboveground biomass is often considered an estimate of long-term productivity of a mangrove forests (Clough and Scott 1989).

4.4 Interactions with water-use efficiency, photosynthesis and productivity

Medina & Francisco (1997) proposed that the rates of photosynthesis, productivity and water-use efficiency (WUE) of a number of mangrove species including *Avicennia* were influenced by the interactions between salinity and freshwater supply. They presented this model over two different climate types with contrasting annual rainfall; humid and arid, and included three different hydrological regimes; fringing mangroves on an arid coast, fringing mangroves on a humid coast and riverine mangroves on a humid coast.

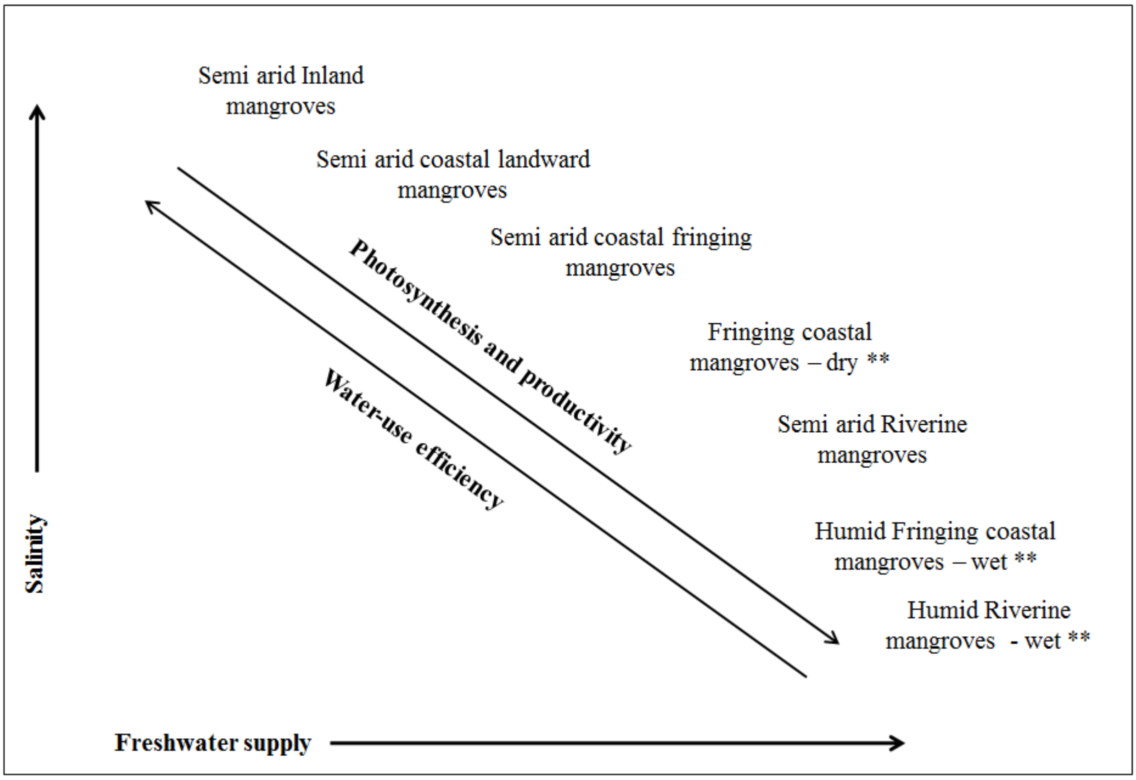

*Figure 22: A prediction of where the different mangrove stands from this study would be positioned within the E. Medina & M. Francisco's hypothetical model. This version displays the interactions between salinity and water availability with both factors relating directly to hydrological regime at sites. (Medina and Francisco 1997). ** indicates the stands from Medina & Francisco's study, wet (average annual rainfall - 1892 mm) and dry (average annual rainfall - 643 mm).*

Their model predicts that as there is an inverse relationship with salinity and freshwater supply, mangroves exposed to greater salinity and less freshwater would have a higher water-use efficiency and lower photosynthetic rate and productivity compared to those exposed to higher amounts of freshwater and lower salinity. This is attributed to the fact that photosynthesis and WUE are interrelated: as WUE increases the rate of photosynthesis slows, resulting in reduced growth (Alongi 2009). This model does not make predictions for inland mangrove systems or riverine mangroves in arid climates. Here, we predict that compared to all other hydrological regimes inland systems would have less freshwater supply and greater salinity; as they are isolated from rivers with the fresh water and flushing that these bring, additionally they are not exposed to tidal flushing but have a continual supply of salt-water entering ponds and a high evaporation rate. Therefore, mangroves growing in these habitats would have greater water-use efficiency and lower photosynthesis and productivity compared to all other habitats with different hydrological regimes (Figure 22, Table 6). In contrast, coastal riverine mangroves in arid climates would be intermediate to arid fringing mangroves and humid mangroves as they would have relatively more fresh water input and flushing, both from river and tidal flow compared to coastal fringing mangroves in arid climates.

Table 6: Typical responses to environmental conditions within a range of hydrological habitats which mangroves exist. Arid fringing, Humid fringing and Humid riverine characteristics are derived from the Medina and Francisco model (Figure 22). Arid inland and Arid riverine are predictions. Subscripts refer to additional references which support the Medina and Francisco model or guided the predictions.

Variables	**Arid**			**Humid**	
	Inland	**Fringing**	**Riverine**	**Fringing**	**Riverine**
WUE	very high [2,7,16,17]	high [2,7,16,17]	moderate [7,15,2]	low [7,15,17, 16]	very low [7,15,2]
Photosynthesis	very low [9,18,12,1,8]	low [9,18,12,1,8]	moderate [18,12,13,1]	high [18,12,13,1]	very high [18,12,13,1]
Growth (short-term)	very low [7,4]	moderate/low [7,4]	moderate [7,4]	high [7,4]	very high [7,4]
Above ground biomass (long-term)	very low/low [9,11,1]	moderate [9,1]	high [11,1]	high [11,1]	very high [11,1]
Specific leaf weight	very high [10,18]	high [10,7,18]	moderate [10,7,18]	low [7,18]	very low [7,18]
Specific leaf area	very low [10,8]	low [10,8,7,17]	moderate [7]	high [7,17]	very high [7]
Tree height	very low [9,8,11,10]	moderate [17,9,8,10,16]	high [7,11,5]	very high [11,5,17,10,16]	very high [7,11,5]
Leaf Chloride content	very high [19]	high [19]	moderate [19]	low [19]	very low [19]
Photochemical efficiency	very low [9, 10]	low [9, 10,14]	moderate [14,13]	high [13]	very high [14,13]

[1] (Suarez and Medina 2006); **[2]** (Ball and Sobrado 1998); **[3]** (Krauss, Lovelock *et al.* 2008); **[4]** (Martin, Bruhn *et al.* 2010); **[5]** (Lara and Cohen 2006); **[6]** (Lugo, Cintron *et al.* 1982); **[7]** (Medina and Francisco 1997); **[8]** (Naidoo 2010); **[9]** (Naidoo 2006); **[10]** (Naidoo, Hiralal *et al.* 2011); **[11]** (Ross, Ruiz *et al.* 2001); **[12]** (Ball and Farquhar 1984); **[13]** (Gonzalez-Mendoza, Espadas y Gil *et al.* 2011); **[14]** (Sobrado and Ball 1999); **[15]** (Wei, Yan *et al.* 2008); **[16]** (McKee, Feller *et al.* 2002); **[17]** (Lin and Sternberg 1992a); **[18]** (Lugo, Medina *et al.* 2007); **[19]** (Popp 1984).

Here we build on the Medina Francisco model by predicting, not only photosynthesis, productivity and water-use efficiency but additional traits that have been shown to be involved in the plant processes associated with salinity and water stress such as photosystem efficiency, leaf ionic composition, specific leaf size and weight and tree structure (Table 6).

Due to the salinity levels, freshwater delivery and flushing conditions expected across these habitats, we predict that mangrove stands will express traits across a gradient from inland, to arid coastal fringing, to arid coastal riverine and then to humid coastal fringing and humid coastal riverine, which are not part of this study, but have been presented previously by Medina & Francisco (1997). Like the variables water-use efficiency, photosynthesis and productivity, other plant traits such as specific leaf area and weight and tree height would also vary across this gradient, from the smallest, densest leaves at the inland sites up to larger and less dense leaves at the humid riverine sites. Chloride content of leaves is also expected to reflect increased salinity exposure with greater chloride content at the inland sites, followed by coastal fringing and then coastal riverine. Finally plants are likely to be most stressed at the inland sites due to high salt exposure and would have the lowest photosynthetic efficiency here.

This study will fill a number of gaps. Firstly we will assess the relationship between water-use efficiency, photosynthesis and productivity of the stress tolerant mangrove *A. marina* at arid inland, coastal fringing and coastal riverine habitats. Two of these habitats, inland and semi-arid coastal riverine have not been investigated before and will add to the model of Medina and Francisco (1997). Secondly, we will examine the relationship between key vegetation traits that vary with salinity and sediment conditions among inland and coastal mangrove stands in semi-arid environments.

This study has two main investigations. Firstly to compare the productivity, water-use efficiency, morphological features and physiological attributes of mangrove *A. marina* growing within a semi-arid climate at both coastal and inland locations. The following hypothesis was tested:

- There is no significant difference in the water-use efficiency, photosynthesis, productivity and other key ecophysiological traits of the mangrove *Avicennia marina* in a semi-arid inland marine habitat compared to a coastal habitat.

Secondly, to examine the relationship between the environmental and hydrological conditions and the ecophysiological features of the mangrove *Avicennia marina* in semi-arid inland, coastal and riverine habitats.

4.5 Materials and Methods

4.5.1 Sampling Design

Four sites were sampled in Lake MacLeod which constituted the inland region and four locations were sampled along the coast and in the Gascoyne River, which constituted the coastal region. At the inland sites, the same plots as described in Chapter 3 were sampled. There were three gradsects running perpendicular to the pond edge with between four – seven plots (10 x 10 m) (Chapter 3; Figure 10). At the coastal sites, there were two sites selected along the river edge (Riverine mangroves) and two along the coast (Coastal mangroves). At the riverine mangroves sites, there was a narrow band of mangrove trees along the river edge. Here three plots along the river edge were sampled, with each plot ~ 20m apart from the next. Whereas at the coastal mangrove sites, each stand of mangroves was ~ 100 m wide and three plots were sampled along the water's edge and three at the back of the mangrove stand, farthest from the water's edge (See Chapter 2 for more details). Due to the larger trees at these sites, it was not always possible to sample 4 trees in a 10 x 10 m area, so the plots were slightly larger to allow sampling of four trees in a similar proximity. Within both the inland and coastal regions, a number of hydrological categories or conditions were sampled. The inland categories were defined in Chapter 3 and were pooled across the four inland ponds that were sampled, as detailed below:

Inland

1. At/below pond water level, close to pond (NL, 9 plots)
2. Above pond water level, close to pond (NH, 7 plots)
3. At/below pond water level, away from pond (FL, 4 plots)
4. Increasing elevation with increasing distance from pond (FH, 22 plots)
5. Above pond water level, away from pond, but elevation not increasing with distance from pond (FF, 16 plots)

The four coastal locations were divided into three hydrological categories

1. Coastal close to water (N, 2 sites x 3 plots)
2. Coastal away from water (F, 2 sites x 3 plots)

3. Riverine (RN, 2 sites x 3 plots)

[N] - close to the permanent water source [F] - at a distance from the permanent water source [L] - relative elevation below the surface water level [H] - relative elevation above the surface water level [FF] - relative elevation above surface water level but not increasing with distance.

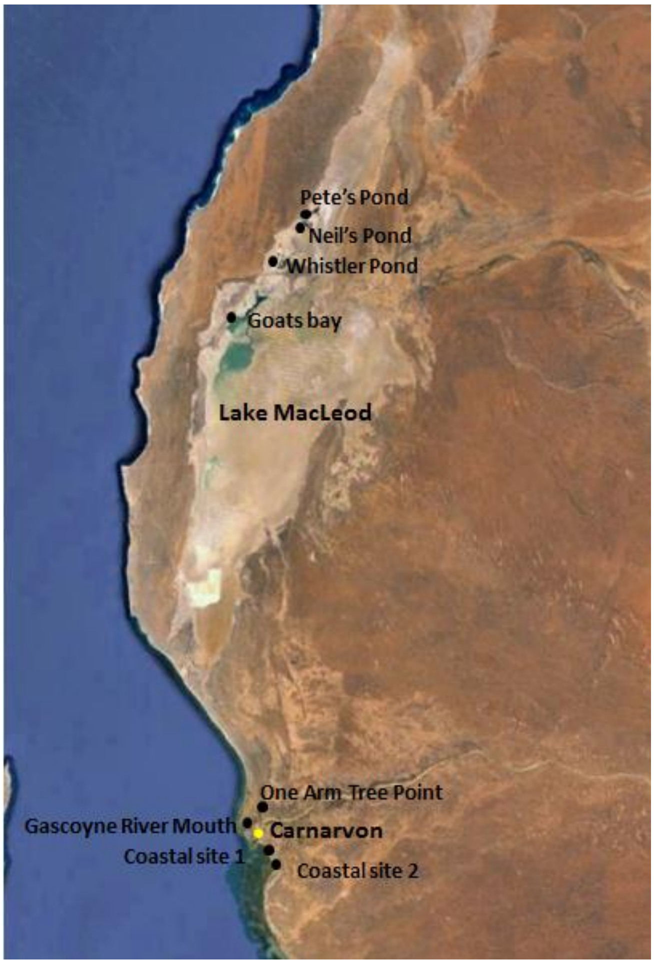

Figure 23: Location of sites and plots within both inland and coastal regions

Within each plot a maximum of four trees were measured for a suite of ecophysiological traits and environmental conditions. Not all plots at the inland region had four mangrove trees within them, therefore numbers of trees in plots varied from one to four (Appendix 1.2). The ecophysiological assessment was carried out from the 16th – 23rd of July 2012.

4.5.2 Field sampling

In February 2012, during the first major data collection described in Chapter 3, up to four trees in each plot were tagged for productivity estimates (See details below). Five months later all previously attended plots were revisited with the following sampling undertaken. A photograph was taken of each plot and sediment sampling carried out for soil moisture content (SMC), sediment salinity (EC), pH and organic matter content (OM) following the methods described in Chapter 3 (3.2.3; Figure 11).

4.5.3 Mangrove sampling

Eight ecophysiological and morphological measures were taken for each mangrove tree (Table 7). These are detailed below.

Photosynthetic rates and photosynthetic health

Pulse Amplitude Modulated (PAM) fluorometry was used to estimate the electron transport rate (ETR), a proxy for photosynthetic rate, and the photosynthetic efficiency, a measure of the photosynthetic health of the plant. The Diving-PAM fluorometer (Walz GmbH, Effeltrich, Germany) employs a red light-emitting diode (LED) as the measuring light. An internal halogen lamp provides the actinic illumination for rapid light curve (RLC) and dark adaptation routines. Ambient light was measured using the micro-quantum sensor (Walz GmbH, Effeltrich, Germany) that had been calibrated using a Li-Cor quantum sensor (Li-Cor, Lincoln, NE, USA) and is displayed as µmol quanta m^{-2} s^{-1}. Data transfer and analysis was performed using the PC software WinControl Version 3.21(Walz GmbH, Effeltrich, Germany). Both fluorometry routines were measured between 8:30am – 11:30am in order to avoid photoinhibition influences and standardise as much as possible among sites.

Relative electron transfer rate

From each tagged *A. marina* tree, two of the youngest leaves associated with each tag were selected from the exterior of the canopy, either facing north, northeast or northwest. A specialized leaf clip was placed on each leaf, one third up the lamina from the junction of the petiole on the right-hand side of the midvein. RLCs were measured using a preinstalled eight-step routine where the actinic illumination increased with each successive step (Heinz Walz GmbH, 1998). Initial irradiance intensity (LC-INT) and width (LC-WIDTH) were set to 1 and 10 seconds respectively. Due to field logistics two PAMS were used and the same settings were set on each, but the intensity of light emitted from each PAM at each RLC step was slightly different. The irradiance (PPFD) for each step was as follows 90, 145, 210, 360, 520, 860, 1360 and 2340 µmol quanta m^{-2} s^{-1} for PAM 1 and 47, 125, 190, 325, 395, 660, 860 and 1315 µmol quanta m^{-2} s^{-1} for PAM 2. Relative ETR from each RLC step was calculated using equation 5.

$$rETR = quantum\ yield\ x\ PPFD\ x\ 0.5\ x\ ETR\ factor \qquad \textit{(Equation 5)}$$

The actual absorbance of incident light in leaves was not measured and the ETR factor was set to 0.84, hence it is a relative measure (Schreiber, Gademann *et al.* 1997).

Data were exported to Sigmaplot 12 (Systat Software 2012) where 'regression wizard' was used to fit a curve to the rapid light curve data and estimate the maximum relative electron transfer rate (rETRmax) following Ralph and Gademann (2005) (Equation 6). Only curves which reached a maximum and either maintained that maximum or declined were used in the estimation of $rETR_{max}$, all other data are discarded.

$$rETR_{max} = P_s \left(\frac{\alpha}{\alpha+\beta}\right)\left(\frac{\beta}{(\alpha+\beta)}\right)^{\frac{\beta}{\alpha}} \qquad \textit{(Equation 6)}$$

β - characterises the slope of the RLC where PSII declines. α – is the initial slope of the RLC before the onset of saturation. P_s *is a scaling factor defined as the maximum potential rETR.*

From each tree the average of the two readings was calculated.

Photosystem II health (PSII)

The maximum quantum yield of photosystem II is observed after the dark adaptation routine. This was also performed on two of the youngest leaves from marked branches as described above. Leaves were dark-adapted for 30 minutes and then the potential quantum yield of PSII measured (Ralph and Gademann 2005). From each tree the average of the two readings was calculated.

Growth and productivity

During the February 2012 field trip up to four mature *A. marina* were tagged, labelled and a GPS location recorded within each plot. On each tagged tree four apical shoots were selected from the exterior of the canopy, either facing north, northeast or northwest and a plastic coated wire was loosely wrapped around the stem just below the apical node (branch tag) (Lovelock, Fellar *et al.* 2007).

Collection

On completion of the PAM fluorometry routines, marked branches were removed from the tree, put into labelled paper bags and placed into chilled coolers before being frozen until laboratory analysis began. Foliage samples were cut from the tree directly below the branch tag with the foliar sample including the original apical leaves and any new growth.

Measurement of growth

Growth was estimated as total shoot production. All leaves and stems produced over the tagging period (February – July) were washed in deionised water and blotted dry. Leaves and stems from each tagged shoot were put into labelled paper bags, placed into the oven to dry at 70ºC for 48 hours and then weighed. Total shoot production was calculated as g.dry weight/shoot/day:

$$SP = \frac{total\ shoot\ DW}{number\ of\ tagged\ days} \qquad (Equation\ 7)$$

SP - total shoot production; DW – dry weight

The average growth per tree was calculated, this measure represents short-term growth and represents a portion of the growth period. The average was based on 2 - 4 measures depending on the number of tags recovered.

Long-term productivity

Above ground biomass was used to estimate long-term mangrove tree productivity. Using coefficients for the allometric relationship between *A. marina* leaf, stem and branch dry weight (kg) (W) and stem diameter (cm) (D), above ground biomass was estimated (Clough, Dixon *et al.* 1997). It was calculated using:

$$log\ (W) = A + B\ x\ log\ (D) \qquad (Equation\ 8)$$

A and B are constants in the equation. This allometric relationship allows for the multi-stemmed nature of A. marina.

The stem diameters were measured for each tagged tree following the methods described in Chapter 3 (3.2.2; page 28).

Tree height

The height of each tagged tree was measured following the methods described in Chapter 3 (3.2.2; page 28).

Leaf anatomical features

Foliage samples collected from tagging were used for leaf anatomical feature analysis. The youngest most mature leaves were selected with the petiole cut from the leaf, if there were two opposing leaves this was performed on both leaves. Leaf lamina thickness (mm) was measured with digital callipers on the right hand side adjacent the midvein at the base of the leaf. Leaf length (mm) was measured from the apex to the base of the leaf blade (minus the petiole) and width (mm) was recorded at the widest part of the leaf blade. Windias 2.0 PC program (1995 – 2000) supported by a CCD camera was used to measure leaf area, which is expressed as mm^2 (Delta-T Devices Ltd.). Each individual leaf was dried in an oven at 55°C for one week and weighed to determine the specific leaf weight (SLW, $g.cm^{-2}$):

$$SLW = \frac{DW\ (g)}{leaf\ area\ (cm)} \qquad \text{(Equation 9)}$$

DW – dry weight (Witkowski and Lamont 1991)

Leaf area (cm^2) and specific leaf weight were averaged for each tree.

Water-use efficiency analysis

Carbon isotope readings were used as a proxy for water-use efficiency as leaf carbon isotope ratios ($\delta^{13}C$) indicate a time specific WUE of a plant, i.e. it can indicate the water transpired for each unit of carbon fixed (Farquhar, Ehleringer *et al.* 1989). Changes in the $\delta^{13}C$ ratio indicate preferential uptake of ^{12}C above ^{13}C, this isotope fractionation occurs during CO_2 uptake (Farquhar, Ehleringer *et al.* 1989). Carbon isotope ratios are commonly related to environmental condition (Macfarlane, Warren *et al.* 1999), particularly water quantity and salinity concentrations (Lin and Sternberg 1992a; Medina and Francisco 1997). Whilst the method is seen as a reliable approach to determine WUE, it has only been studied sparingly on mangrove trees in the field (Medina and Francisco 1997; McKee, Feller *et al.* 2002; Wei, Yan *et al.* 2008). The dried leaves used for leaf morphology analysis were pooled for each tree and ground in a Retsch oscillating mill (MM 200) at 30 hertz for 4 minutes or until the leaf material was pulverized. The carbon isotope ratio ($\delta^{13}C$, ‰) was determined by continuous flow isotope mass spectroscopy (Europa Scientific, 20-20 IRMS, Crewe, UK) with 2 mg of material using the laboratory standard Vienna PeeDee belemnite (V-PDB).

Mangrove leaf ion analysis

The dried, ground samples described above were prepared for Chloride (Cl^-) ion analysis. Leaf material (100 mg) was placed into 10 ml plastic eppendorf tubes with ~9 ml of HNO_3 to make a 10 ml solution. The solution was inverted numerous times ensuring it was mixed thoroughly. The samples were placed in a preheated oven to 80°C for 1 hour and inverted once during the heating process. After an hour the samples were removed from the oven and allowed to cool, then inverted again after cooling. All solid material was allowed to settle and from the middle of the solution 0.5 ml was pipetted into 50 ml of acid buffer solution (Appendix 1.3). The concentration of Cl^- within mangrove leaf material was measured with a Corning 956 Chloride Analyzer, units are displayed as mg/L.

Sediment analysis

Sediment cores from each plot were analysed as described in (Chapter 3; 3.2.3) and the following variables derived: soil moisture content (SMC; %), Sediment EC (mS/m), pH and Organic matter content (OM, %).

4.6 Data analysis

To test if there were differences in the water-use efficiency, photosynthesis and productivity as well as other key vegetation variables (Table 7) between Inland and Coastal mangroves a PERMANOVA routine was run in Permanova+ for Primer (Anderson, Gorley *et al.* 2008) with a maximum number of permutations set at 9999. To address the second question, the relationship between *A. marina* ecophysiology and morphological features and sediment conditions across Inland and Coastal sites, all variables within Table 7 were included in a CAP, the multivariate constrained ordination (Primer-E 2009). In addition, the hydrological categories were overlayed on the CAP outputs to examine the patterns in the vegetation due to hydrological categories.

Table 7: Avicennia marina and environmental variables, measured at Lake MacLeod. These are used in data analysis to identify relationships between environmental and ecophysiological and morphological features of Avicennia marina. Average for vegetation is calculated per tree and for environment is calculated per plot.

Data Type	Variable	Code	Unit
Vegetation			
Water-use efficiency	Avg. carbon isotope ratio	$\delta^{13}C$	δ^{13}Carbon (‰)
Photosynthesis	Avg. maximum electron transfer rate	$rETR_{max}$	
Productivity	Avg. growth shoot^{-1} day^{-1}	SP	(sqrt) g.dry weight/shoot/day
Productivity	Total aboveground biomass	A/GB	(log) dry weight (kg)
Leaf morphology	Avg. specific leaf weight	SLW	g.dry weight/cm^2
Leaf morphology	Avg. specific leaf size	LS	cm^2
Leaf salt content	Leaf chloride content	TCC	mg/L
Photosynthetic health	Avg. photochemical efficiency	DA	yield (F_v:F_m ratio)
Environmental			
	Avg. sediment moisture content	SMC	%
	Avg. sediment pH	pH	pH
	Avg. sediment electrical conductivity	EC	mS/cm
	Avg. organic matter content	OM	%

To further investigate the relationships between environmental variables and vegetation data, significant variables from the CAP analysis were analysed in a uni-variate manner using Sigmaplot 12 (Systat Software 2012). The regression wizard was used to identify the best model; both polynomial linear and quadratic equations were fitted and the highest r^2 value determined the best fit. The significance of the fitted model was determined in SPSS Statistics V19.0, with significance level set at $p < 0.05$. The variables to test as determined from the CAP analysis were SMC with $rETR_{max}$, WUE, DA and EC with TCC, LS, A/GB, SP and pH with SLW, WUE, LS, A/GB, SP. In addition the relationship between SMC and EC were also assessed. Only the significant relationships with an r^2 greater than 10% were displayed.

Finally, although the CAP analysis identified differences between coastal and inland mangroves stands, there was also structuring evident due to the hydrological categories (i.e. trees from similar hydrological categories grouped together). To investigate these relationships further, the environmental and vegetation variables were plotted by hydrological category. Sediment variables and key vegetation variables (WUE, ETR_{max}, Growth and Biomass) were summarised within each hydrological category using box plots in Sigmaplot (Systat Software 2012). The box plots displayed; median, 25th and 75th percentile, error bars and black dots representing outliers.

The mangrove tree variables such as; DA, ETR_{max}, $\delta^{13}C$, A/GB, SLW, LS and TCC in each hydrological category were analysed using One-way ANOVA SPSS Statistics V19.0. LSD post hoc tests with the significance level set at $p \leq 0.05$ was carried out on the significant results to determine which hydrological categories were significantly different for each variable. If assumptions could not be met in the One-way ANOVA, variables were tested in PERMANOVA (Primer-E 2009) with the significance level set at $p \leq 0.05$; this was only required for SP.

4.7 Results

4.7.1 Coastal vs. Inland vegetation

A significant difference between Inland and Coastal mangrove trees is evident when comparing the vegetation variables relating to morphological and ecophysiological characteristics (PERMANOVA $p = 0.0001$). The main vegetation variables accounting for the separation of coastal and inland mangrove trees are associated with axis one of the CAP analysis (Figure 24). These include mangrove leaf size (LS), total aboveground biomass (A/GB) and total shoot production (SP) which are greater at the coastal sites, and total leaf chloride content (TCC) along with average specific leaf weight (SLW) which are greater at the inland sites (Figure 24). Other variables such as water-use efficiency ($\delta^{13}C$), relative maximum ETR ($rETR_{max}$) and photosynthetic health (DA) do not explain the separation of coastal and inland sites. They are associated with axis 2 of the CAP analysis and are more related to the separation of hydrological categories, particularly at the coastal sites (Figure 24).

4.7.2 Key environmental variables and the influence on mangrove morphological and ecophysiological characteristics

There was a significant canonical correlation between the environmental and vegetation variables at inland and coastal stands ($p = 0.0001$). Pearson correlation values suggest the environmental variables responsible for the spread of data points along CAP axis one are average sediment pH (-0.640) and average sediment EC (-0.541). Average sediment EC (-0.377), and SMC (0.800) are responsible for the spread of data points along CAP axis two (Figure 24). This correlates such that coastal sites have a lower sediment salinity and pH than inland sites as they are separated along axis one, and the hydrological categories, particularly at the coastal sites are separated by variables such as soil moisture and sediment salinity (Figure 24).

By overlaying the vectors on the CAP the following patterns are evident. As average sediment pH increases, average SLW and average $\delta^{13}C$ also increase. As average SMC increases there are increases in average $rETR_{max}$, average $\delta^{13}C$ and average DA. Trees exposed to higher sediment EC had higher TCC within the leaves. As average sediment pH and average sediment EC decrease average mangrove LS, total A/GB and total SP increase (Figure 24).

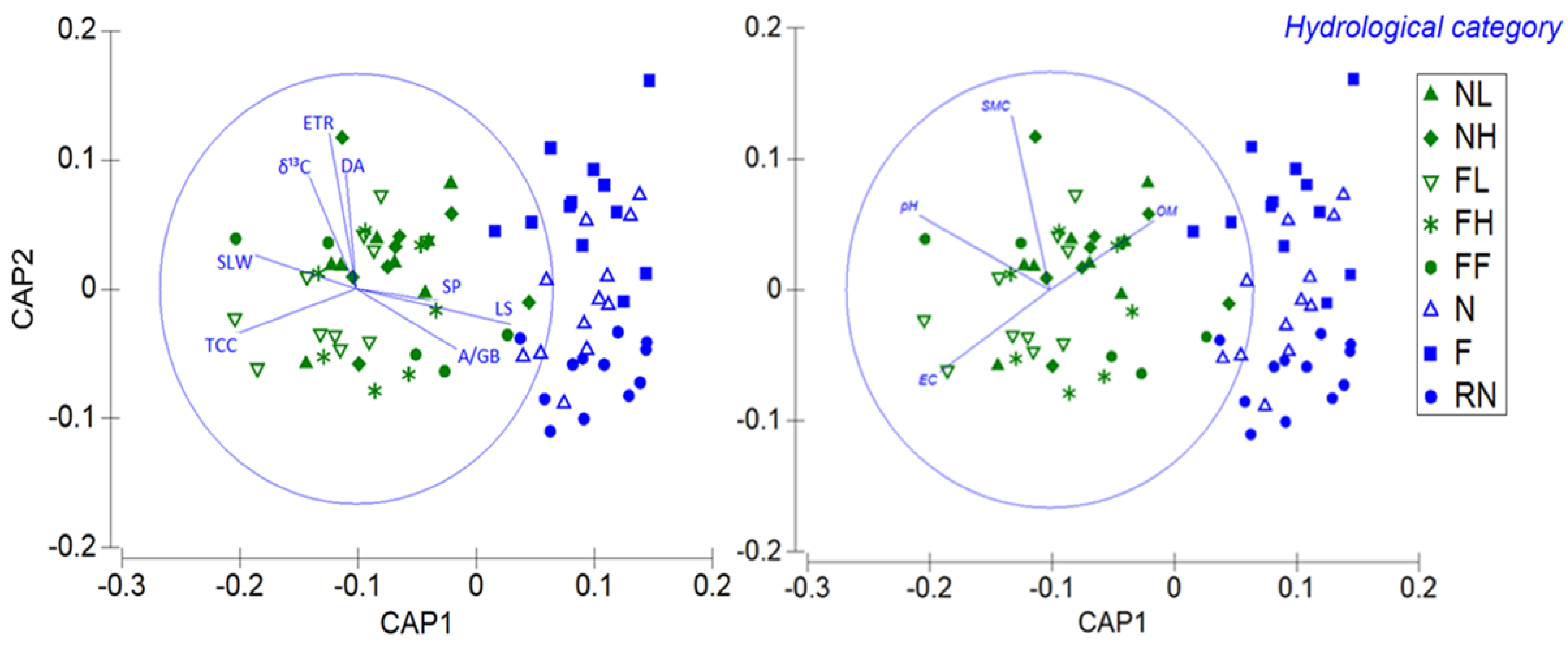

Figure 24: Ordination (Canonical analysis of principal ordinations; CAP) used to discriminate which environmental variables are responsible for differences in the morphology and ecophysiology of vegetation at Lake MacLeod. Points represent features of individual trees. Right: Environmental variables overlayed; SMC – average sediment moisture content, EC – average sediment electrical conductivity, OM content – average organic matter in sediment and pH – average sediment pH. Left: Mangrove tree variables overlayed; SLW – average specific leaf weight, $\delta^{13}C$ – average carbon isotope ratio, ETR - average maximum electron transfer rate, DA – average photochemical efficiency, SP – total shoot production per day, LS – average specific leaf size, A/GB - total aboveground biomass and TCC – total leaf chloride content.

4.7.3 Uni-variate analysis exploring relationships between environmental variables and Mangrove characteristics

To further examine the relationships among the key variables explaining the patterns in the environmental and vegetation data from the CAP analysis, uni-variate plots were examined. The strongest uni-variate relationships occur between sediment EC and LS (r^2 0.5194, $p < 0.0001$), as sediment EC increases the LS decreases following a quadratic relationship (Figure 25) and sediment pH and LS (r^2 0.5395, $p < 0.0001$), as sediment pH increases LS decreases, following a quadratic relationship. There is also a significant linear relationship with sediment EC and TCC (r^2 0.1124, $p < 0.0001$), explaining 11% of the variation found in this data. There was a broad range of leaf TCC, from 61 – 579 mg/L (Figure 25). Finally, there is a statistically significant quadratic relationship between sediment pH and SLW (r^2 0.2164, $p < 0.0001$), explaining 21.6% of the variation (Figure 25).

There was no significant uni-variate relationship between sediment pH and EC and vegetation variables such as A/GB, SP, WUE, DA and rETRmax. SMC did not have significant uni-variate relationships with any of the vegetation variables.

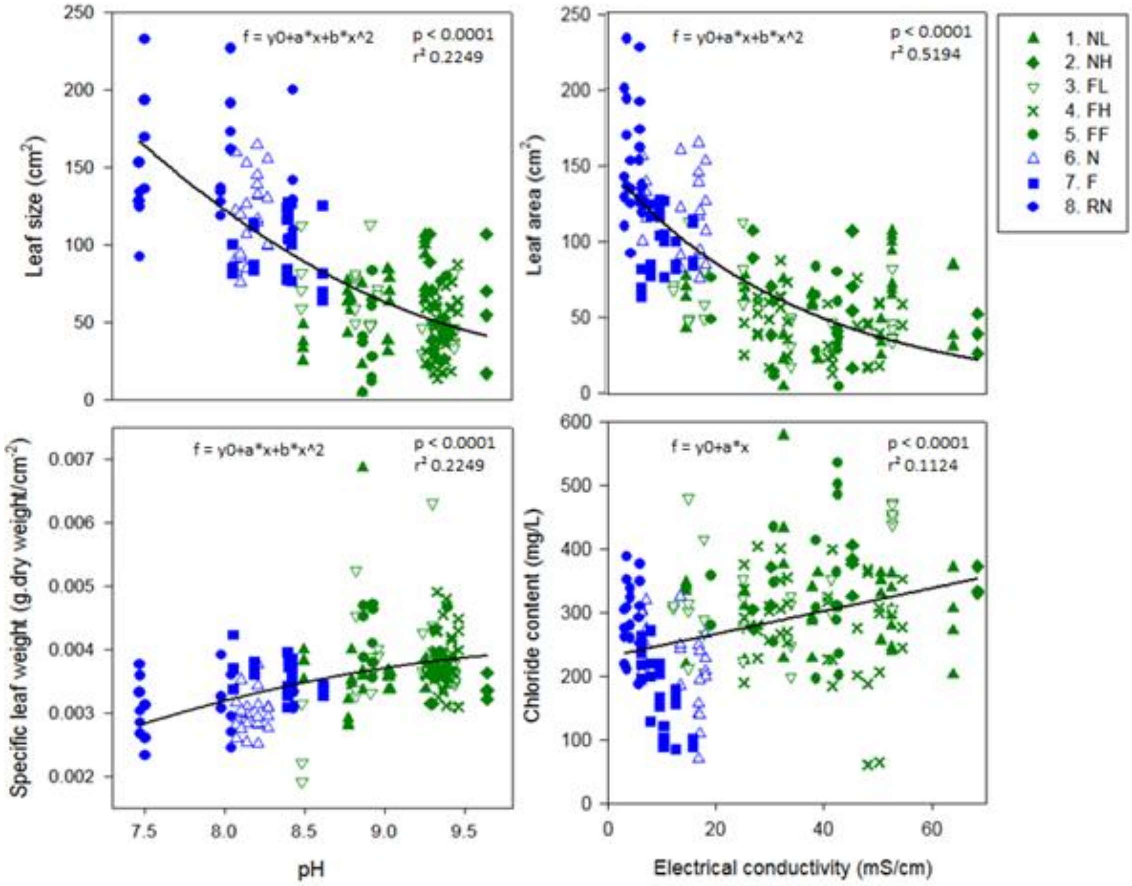

Figure 25: Uni-variate analysis between sediment EC and specific leaf size (LS) [top right], and total leaf chloride content (TCC) [bottom right]; and sediment pH and specific leaf weight (SLW) [bottom left] and specific leaf size (LS) [top left]. NL – close to the pond below zero elevation, NH – close to pond above zero elevation, FL – increased distance from pond below zero elevation, FH – increased distance from pond above zero elevation, FF - increased distance from pond level elevation, N – close to ocean, F – away from the ocean, RN – close to ocean riverine sites.

4.7.4 Environmental conditons across hydrological categories

There were significant differences in environmental conditions in the sediment between hydrological categories (SMC: $p < 0.01$, EC: $p < 0.001$, pH: $p < 0.0001$, OM: $p < 0.0001$). Sediment EC was significantly lower at all coastal hydrological categories compared to all inland hydrological categories (Table 8). There was a trend of lower EC at the riverine sites compared to the coastal fringing sites however, this was not significant. For Soil moisture content (SMC) there was not a clear distinction between the coastal and inland hydrological categories (Table 8). SMC was significantly lower at the riverine sites (RN), followed by coastal sites (N, F) and the inland category away from the pond at high elevations (FH). This was followed by the inland categories FF and NH, then FL and the highest SMC was at the hydrological category NL, near to the pond at lower elevation. There were significant differences in pH values at hydrological categories between all inland and all coastal categories with lower pH at the coastal location (Table 8). There were also significant differences within inland categories, with pH highest at NH and FH, intermediate at FF and lowest at FL and NL. There were significant differences in pH at the coastal categories with the highest pH recorded at the coastal landward edge, intermediate values at the coastal seaward edge and lowest values at the riverine category. There was a significant distinction between coastal and inland categories in organic matter content, with the highest amount of organic matter recorded at the coastal location. Additionally there were differences within the categories at both inland and coastal locations (Table 8). For the inland location the lowest organic matter content was at FL, followed by NL, then NH and FF, with the greatest content at FH. At the coastal sites, the lowest organic matter content was recorded at the riverine and coastal landward edge categories, with both significantly different from the coastal seaward edge.

Table 8: Average quality of the sediment within plots grouped in each hydrological category based on key sediment variables such as soil moisture content (SMC), electrical conductivity (EC), pH and organic matter content (OM). Data is average and standard error measures from both sampling times (February and July 2012). Subscript letters signify differences between hydrological categories (similar letters denote no difference) according to 1-way ANOVA and LSD post-hoc test (Significance level of 0.05).

			Environmental variables			
			SMC (%)	EC (mS/cm)	pH	OM (%)
Hydrological category	NL	Inland	$53.71\pm1.87_{abc}$	$41.25\pm2.80_{a}$	$8.93\pm0.04_{a}$	$7.32\pm0.42_{abce}$
	NH		$41.84\pm1.71_{abcdef}$	$45.43\pm5.0_{a}$	$9.44\pm0.05_{b}$	$7.44\pm0.19_{abde}$
	FL		$48.65\pm2.1_{abce}$	$30.32\pm2.94_{a}$	$9.08\pm0.06_{a}$	$6.13\pm0.42_{ac}$
	FH		$31.72\pm1.03_{bdefg}$	$38.07\pm1.57_{a}$	$9.36\pm0.01_{b}$	$8.88\pm0.33_{bde}$
	FF		$39.54\pm2.79_{bcdef}$	$36.98\pm1.95_{a}$	$9.11\pm0.06_{ab}$	$8.21\pm0.2_{abde}$
	N	Coastal	$31.72\pm3.05_{bdefg}$	$13.1\pm1.0_{b}$	$8.16\pm0.01_{cde}$	$43.58\pm2.17_{f}$
	F		$31.11\pm2.18_{bdefg}$	$10.35\pm0.65_{b}$	$8.34\pm0.04_{ce}$	$21.71\pm1.58_{g}$
	RN		$21.91\pm1.17_{dfg}$	$4.69\pm0.28_{b}$	$7.85\pm0.08_{cd}$	$19.73\pm0.71_{g}$

4.7.5 Ecophysiological condition of mangrove *Avicennia marina* across hydrological categories

There were no consistent patterns in water-use efficiency ($\delta^{13}C$) between coastal and inland sites with the highest and lowest water-use efficiency (WUE) recorded at hydrological categories at the coastal location. WUE was significantly higher for the coastal fringing mangroves at the landward edge (F), and significantly lower for the coastal fringing mangroves at the seaward edge (N) and the riverine mangroves (RN) (Figure 26). At the inland sites WUE was found to be intermediate across all hydrological categories, with all trees having similar median $\delta^{13}C$ values, but significantly different to the coastal categories (Figure 26).

There were no consistent patterns in maximum rETR, a proxy for photosynthetic rate, between coastal and inland sites (Figure 26). Maximum rETR was highest at the coastal fringing mangroves on the landward edge (F), lowest at the coastal riverine site (RN) and intermediate across all other hydrological categories (Figure 26). Notably inland trees close to the pond and at high elevation (NH) displayed a wide range of rates.

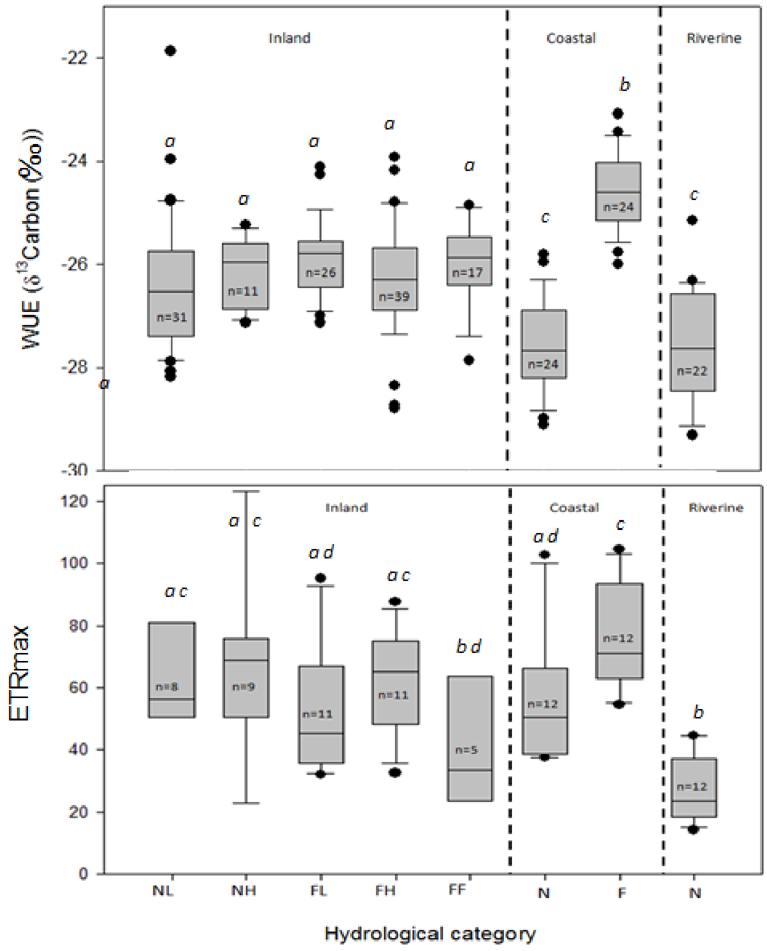

Figure 26: Water-use efficiency and relative maximum electron transfer rate (rETRmax) through photosystem II of Avicennia marina; trees are grouped into hydrological categories. NL – close to the pond below zero elevation, NH – close to pond above zero elevation, FL – increased distance from pond below zero elevation, FH – increased distance from pond above zero elevation, FF - increased distance from pond level elevation, N – close to ocean, F – away from the ocean, RN – close to ocean riverine sites. The lower and upper lines of the box plot represent the 25th and 75th percentile respectively and the middle line represents the median of the data. The error bars below and above the box represent the 10th and 90th respectively and black dots are the outliers. Subscript letters signify significant differences between hydrological categories (similar letters denote no difference) according to 1-way ANOVA and LSD post-hoc test (Significance level of 0.05).

Aboveground biomass was significantly higher at coastal riverine and coastal fringing mangrove stands on the seaward and landward edge, along with inland mangroves in hydrological category NH. Aboveground biomass was significantly lower at FH and FF than all other categories (Figure 27).

The highest shoot production occurred on coastal riverine and coastal fringing trees on the seaward edge. These were significantly different to all other hydrological categories ($p < 0.05$) except inland plots close to the pond at high elevations (NH). Coastal mangroves on the landward edge (F) were similar to all inland hydrological categories, where significantly lower and more variable shoot production occurred (Figure 27).

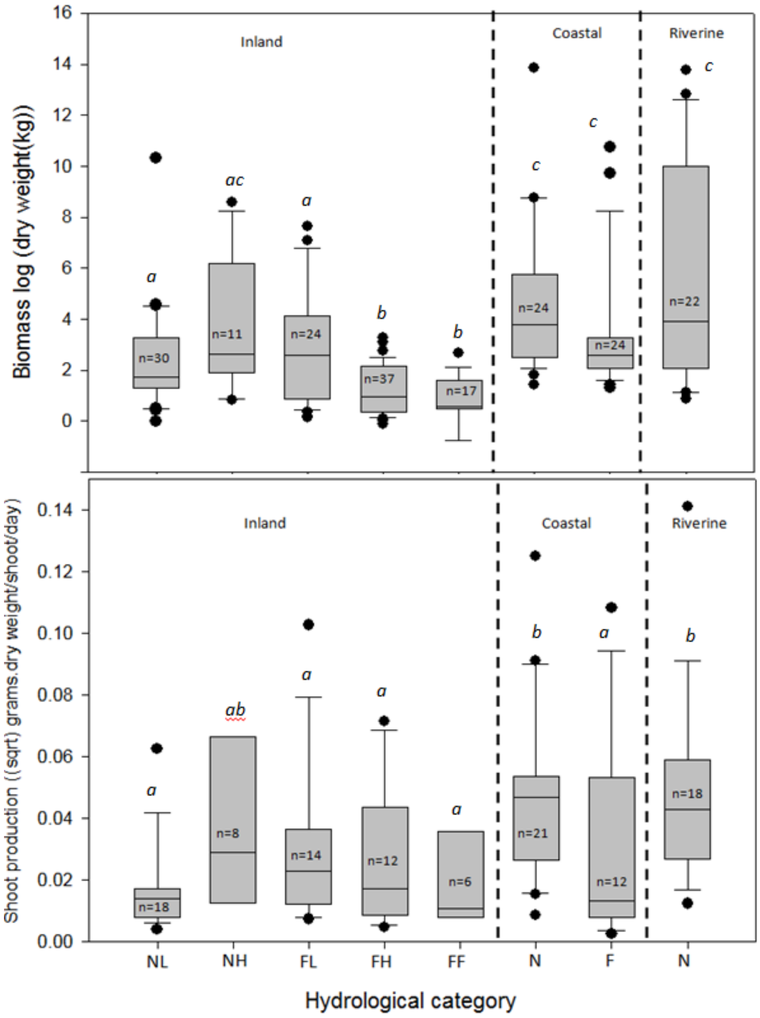

Figure 27: Aboveground biomass of Avicennia marina log(dry weight(kg)) and shoot production (grams dry weight /shoot/day) of A. marina, trees are grouped into hydrological categories. NL – close to the pond below zero elevation, NH – close to pond above zero elevation, FL – increased distance from pond below zero elevation, FH – increased distance from pond above zero elevation, FF - increased distance from pond level elevation, N – close to ocean, F – away from the ocean, RN – close to ocean riverine sites. The lower and upper lines of the box plot represent the 25th and 75th percentile respectively with the middle line representing the median of the data. The error bars below and above the box represent the 10th and 90th percentile respectively and black dots represent outliers. Subscript letters signify significant differences between hydrological categories (similar letters denote no difference) according to 1-way ANOVA and LSD post-hoc test (Significance level of 0.05).

4.7.6 Vegetation traits of mangrove *Avicennia marina* across hydrological categories

Individual leaf size (LS) was significantly larger at coastal riverine sites [RN], followed by coastal fringing sites [N] and landward edge sites [F] respectively. All of these hydrological categories produced leaves significantly larger than the inland categories. Here, trees growing at low elevation and close to the pond edge [NL] displayed significantly larger LS than trees at a greater distance and higher elevation [FH & FF] (Table 9). Although trees growing in hydrological category NH displayed average LS similar to trees within NL the variation was vast, and therefore there was not a significant difference (Table 9). Specific leaf weight (SLW) was significantly greater at inland hydrological category FF and significantly lighter at the coastal hydrological categories N and RN. SLW displayed by coastal fringing trees on the landward edge were significantly different to all other trees except those growing close to the pond at higher elevations than the pond water level (NH) (Table 9). Total leaf chloride content (TCC) was significantly higher in trees growing inland in hydrological categories NH ($p < 0.05$), FF ($p < 0.01$) and FL ($p < 0.05$) and significantly lower at coastal categories N and F ($p < 0.005$) (Table 9). Mangrove trees at coastal hydrological categories N and RN were significantly taller ($p < 0.0001$) than all other trees, and those growing at FH and FF were significantly smaller ($p < 0.0001$). Coastal fringing trees growing on the landward edge [F] were statistically similar to mangrove trees growing in hydrological categories NL, NH and FL (Table 9). Average photochemical efficiency (DA) was significantly lower at hydrological categories FF and RN compared to all other categories ($p < 0.05$) (Table 9).

Table 9: Comparison of mangrove Avicennia marina vegetation traits across all hydrological categories. Subscript letters signify differences between hydrological categories (similar letters denote no difference) according to 1-way ANOVA and LSD post-hoc test (Significance level of 0.05).

		Dark adaptation (yield) (DA)	Cl^{-} (mg/L) (TCC)	Mangrove tree height (m)	LS (cm^2)	SLW ($g\ cm^{-2}$)
Inland	NL	$0.69 \pm 0.02_{a}$	$314.9 \pm 13.3_{a\ e}$	$2.40 \pm 0.2_{a}$	$60.42 \pm 4.61_{a}$	$0.0037 \pm 1.2E\text{-}04_{ac}$
	NH	$0.71 \pm 0.02_{a}$	$345.1 \pm 12.02_{a}$	$2.15 \pm 0.3_{a}$	$61.17 \pm 10.21_{b}$	$0.0035 \pm 8.2E\text{-}05_{ab}$
	FL	$0.72 \pm 0.01_{a}$	$331.3 \pm 17.05_{a}$	$2.15 \pm 0.22_{a}$	$57.52 \pm 4.67_{b}$	$0.0037 \pm 1.6E\text{-}04_{ac}$
	FH	$0.70 \pm 0.02_{a}$	$279.3 \pm 12.73_{b}$	$0.89 \pm 0.07_{b}$	$46.33 \pm 3.08_{b}$	$0.0039 \pm 6.7E\text{-}05_{cd}$
	FF	$0.65 \pm 0.02_{b}$	$342.6 \pm 24.9_{a}$	$0.81 \pm 0.1_{b}$	$44.48 \pm 5.75_{b}$	$0.0041 \pm 1.0E\text{-}04_{d}$
Coastal	N	$0.70 \pm 0.01_{a}$	$222.1 \pm 13.36_{c}$	$3.37 \pm 0.15_{c}$	$119.94 \pm 5.32_{c}$	$0.003 \pm 6.0E\text{-}05_{e}$
	F	$0.72 \pm 0.01_{a}$	$161.2 \pm 12.14_{d}$	$1.88 \pm 0.1_{a}$	$98.78 \pm 4.07_{c}$	$0.0036 \pm 5.3E\text{-}05_{ab}$
	RN	$0.66 \pm 0.01_{b}$	$284.9 \pm 11.55_{b\ e}$	$3.14 \pm 0.17_{c}$	$153.06 \pm 7.86_{d}$	$0.0031 \pm 8.9E\text{-}05_{e}$

4.8 Discussion

4.8.1 General information

Review of the literature has failed to find similar studies comparing WUE, productivity and ecophysiological traits of *A. marina* mangrove trees across inland and coastal mangrove stands which are exposed to very different hydrological regimes. Previous research from tropical and semi-tropical locations experiencing higher rainfall than this study region found that as sediment salinity increases mangrove trees became more WUE and less productive (Medina and Francisco 1997; Naidoo 2010), and Wei et al. (2008) noted that further research is required to understand the responses of mangroves across a broader range of salinities. This is the intention of this research, focusing at the higher range of salinities combined with low rainfall.

4.8.2 Comparison of environmental conditions at inland and coastal sites

We predicted that inland sites would be more saline than coastal sites, and this was clearly demonstrated based on sediment salinity. As expected, riverine mangroves were exposed to the freshest conditions (~ 5 mS/cm), followed by fringing coastal mangroves (10-13 mS/cm) and then inland mangroves, which were significantly more saline (42-68 mS/cm). In addition soil moisture content was elevated at inland sites compared to coastal sites. The occurrence of *A. marina* persisting in soils with characteristically elevated salinities and high moisture content has been explained by Naidoo et. al. (2011). Under these conditions, low and irregular tidal flushing combined with high evaporation rates, as is the case at Lake MacLeod, results in hypersaline sediment conditions. At Lake MacLeod, seawater under hydrostatic pressure enters the ponds through subterranean vents and as seawater input is continuous, excess spills over onto the surrounding lake bed. The high evaporation rate experienced results in the maximum salinity levels recorded at mangroves immediately adjacent to the ponds.

4.8.3 Comparison of water-use efficiency, photosynthesis and productivity at inland, coastal fringing and coastal riverine sites

We predicted that due to elevated salinity levels, reduced freshwater supply and lack of tidal flushing at inland sites, water-use efficiency would be greater and photosynthesis and productivity reduced compared to coastal sites. This was partly supported in this study, as significant differences in the vegetation characteristics of inland and coastal sites were detected. These differences were explained by long-term productivity as estimated by above-ground biomass of mangrove trees, and short-term productivity, as measured by shoot production, with lower productivity recorded at inland sites. Despite these general patterns being supported (Figure 24); there was complexity in these patterns related to the specific hydrological conditions the mangrove trees were growing under. Here patterns in shoot production and above-ground biomass of coastal fringing mangroves growing on the landward edge were more similar to inland mangroves, however these results are not unexpected, as Lin & Sternberg (1992a) found that small or dwarf mangroves are commonly found on the landward edge of coastal stands, where height, canopy size and productivity are much lower than the nearby fringing mangroves growing on the seaward edge.

Long-term productivity (A/GB) was significantly lower at inland sites where trees were growing furthest from the ponds but not at low elevations [FH & FF]. Here the average sediment EC was on average close to sea water, but the range was large (19 % - 54.5 %) and SMC was low (Table 8). These environmental conditions can be attributed to limited access to a constant supply of water as they are furthest from the water supplied via flow over the edge of ponds, and are not close to seepage directly from the sediment. If there was sub-surface seepage, then the soil moisture content would likely be higher. Another indication that it is water supply that is most important, rather than sediment salinity, is that mangrove tree A/GB was similar at inland hydrological category [NH] and coastal categories [RN], [N] and [F]. These categories varied extensively in sediment EC i.e. the riverine trees were growing in almost fresh conditions (avg. 4.69 mS/cm) and the inland trees in hypersaline conditions (avg. 45.43 mS/cm), but all these categories had a relatively consistent supply of seawater, either due to tidal flushing and/or river flow at the coastal sites, and pumping from the vents at the inland sites. Water supply, irrespective of salinity is an important driver of long-term productivity of mangrove trees and *A. marina* is tolerant of a broad range of salinities.

Short-term productivity (SP) also showed a general trend of greater productivity at coastal sites compared to inland sites, but the relationship was also influenced by the hydrological conditions. The lowest production rates were observed at the coastal fringing mangroves on the landward edge and all inland sites. The inland hydrological category close to the pond at a high elevation (NH) was the one exception; here the short-term production was similar to coastal fringing and riverine trees. This hydrological category had the highest average salinity of all hydrological categories, but the moisture content was slightly lower than other categories close to the pond edge. This lower moisture content may be beneficial, as coping with waterlogging can be costly to productivity as energy is invested into the pneumatophores in order to maintain water uptake and gas exchange i.e. longer pneumatophores are needed to reach above the water (Ball 1988a) which has negative consequences for growth. In addition, Naidoo (1985) revealed that water uptake is lowered in waterlogged situations as opposed to well-drained soils, so if water-uptake is reduced, plants need to be more water-efficient and there can be negative implications for productivity (Medina and Francisco 1997). However, as there is a constant water supply, but possibly reduced waterlogging, shoot production is enhanced (Vilarrubia 2000). The other hydrological categories close to the pond edge were permanently inundated (e.g. NL) and shoot production was lower, here waterlogging may have impacted productivity.

Water-use efficiency and photosynthetic rates did not follow our predictions, and were not consistently different between inland and coastal sites. WUE was lower at two of the coastal habitats, fringing on the seaward edge and riverine (~ -28 ‰), compared to the inland hydrological categories (~ -26 ‰). However, the outlier was the coastal fringing mangroves on the landward edge; these trees were the most WUE (~ -24.5 ‰) of all studied. The sediment data that we have does not provide any insights to explain this. The salinity at this habitat was much lower than the inland sites (10 mS/cm vs. 30 - 45 mS/cm). The SMC was similar to some hydrological categories at the inland sites (31%), so reduced soil moisture content cannot explain this result either. The low WUE in these coastal mangroves on the landward edge of the mangrove stand may be related to the frequency of inundation of water, i.e. water supply. Average tidal range in this area is from 0.3 m to 1.80 m and there is a mixed tidal pattern due to tidally driven water movement and ocean surges (Eliot, Gozzard *et al.* 2012). We would have expected that the trees were regularly flushed by the tidal movement. However, we observed a barrier between the seaward and landward edge trees, which is likely to have reduced tidal flushing and frequency of inundation. This barrier was a small elevated sediment mound. This topographic feature most likely inhibited tidal flushing leading to more water-use efficient trees.

We predicted that photosynthetic rates (ETR_{max}) would be higher at the coastal riverine sites, followed by the coastal fringing and then the inland sites. In fact, the opposite was observed; the lowest ETR’s were recorded at the riverine sites. This is unusual as the sediment salinity and soil moisture was lowest here compared to all other sites. So it is unlikely that these factors are responsible for the lower photosynthetic rates. One possible explanation is that the trees were stressed due to another factor. The maximum quantum yield, an indicator of the health of the photosystem can be inhibited by other stressors such as toxicants particularly herbicides (Ralph, Smith *et al.* 2007). The photosystem health was depressed at the riverine site (0.66 ± 0.01); healthy photosystems would be expected to be 0.8 (Cheeseman, Herendeen *et al.* 1997). The flood that occurred in December 2010 as a result of a tropical storm was 2 to 7 times larger than any previous events, this event was subsequently followed by smaller flooding events in January and February 2011. These events caused significant damage to infrastructure and substantial sediment loss within the region, particularly in the rangelands and Carnarvon horticultural area (Waddell, Thomas *et al.* 2012). The catchment condition prior to these events was deemed poor as a result of dry conditions and overgrazing which exacerbated erosion and hence the sediment loads within the flood were extreme (Waddell, Thomas *et al.* 2012). Horticultural and pastoral activities contribute to increased toxicants within these sediment loads which could possibly impact photosynthetic capacity of the aquatic and littoral vegetation of the Gascoyne River (Waddell, Thomas *et al.* 2012). Interestingly, the hydrological category from the inland site with the lowest maximum quantum yield also had the lowest ETR. This category was furthest from the pond water supply and at similar elevation to the pond water level (FF). It also had the lowest A/GB but not the driest or most saline sediments. It is not clear which environmental conditions are driving lower photosynthetic capacity and shoot production in these inland areas, but it does support previous studies where low photosynthetic rate is correlated with lowest growth and biomass (Ball and Sobrado 1998; Gonzalez-Mendoza, Espadas y Gil *et al.* 2011).

4.8.4 Comparison of other vegetation traits at inland, coastal fringing and coastal riverine sites

Most of the *A. marina* vegetation traits followed our predictions. For instance leaf size and tree height were greater at coastal sites compared to inland sites and specific leaf weight and leaf chloride content were greater at inland sites versus coastal sites (Table 9). All vegetation traits of *A. marina* growing at the coastal landward mangrove stands displayed statistically similar traits to the inland mangroves, except total leaf chloride content. These trees displayed the lowest average TCC which is supported by the sediment EC (10.35 ± 0.65 mS/cm) (Table 8). This contrasting result is possibly due to sediment deposits increasing elevation within the stands preventing regular tidal flushing; with effective root flushing occurring only when ocean surges coincide with a high tide or during larger storm events (Eliot et al., 2012). The absence of river flow means that the only other water input these trees experience is from direct rainfall which is variable and low. It is therefore assumed that it is a lack of water quantity rather than quality that is responsible for the coastal landward edge mangroves displaying vegetation traits similar to the inland mangroves.

4.8.5 Application of the Medina and Francisco model to inland mangrove systems

The Medina & Francisco model uses the environmental variables of freshwater supply and salinity, which vary across climatic zones and habitats. This model uses the increase in freshwater supply as a way of separating hydrological regimes. In the current study all mangroves except the coastal riverine trees received little freshwater input; therefore the hydrological categories used did not fit into this model linearly. It was an access to permanent water sources that impacted the physiological responses of the mangroves rather than water quality. This was evident by the significantly higher sediment salinities identified at the inland system compared to coastal sites. In general freshwater inputs within this climatic region are reduced. Although variable, the maximum and most direct water input is experienced at riverine sites, followed by coastal seaward and landward trees receiving indirect input via rainfall and inland trees receiving water during extreme events (Table 3).

Both productivity measures, short (SP) and long-term (A/GB) production fit within the models concept, with inland and coastal landward edge trees having lower production rates and the riverine and fringing coastal trees having higher production rates (Table 10). Here photosynthetic rates did not support production rates, with mixed results produced. Therefore the photosynthetic rate of these mangroves does not support the Medina & Francisco model. Photosynthetic processes are among the most sensitive indicators of environmental stress as these processes are impacted by the slightest changes in environmental condition around roots influencing biochemical and physiological processes (Ball 2009). The inland mangrove trees were expected to display the highest WUE based on the model, this was not the case. The most WUE mangroves were growing at the coast on the landward edge of the stand (Table 10). This is likely due to distance from a permanent water source and lack of root zone flushing. The inland trees were exposed to a more constant supply of water than the landward coastal trees supporting a conclusion that within a semi-arid climate constant access to a water supply rather than quality (i.e. freshwater supply) is more important.

Results from this study confirm that mangrove trees in hydrological categories either experiencing regular tidal flushing, occurring at lower elevations or near permanent water sources; were taller with larger specific leaf area and lower specific leaf weight. These traits agree with predictions indicating that *A. marina* acclimates to conditions with changes in morphology (Table 10).

The predictions for total leaf chloride content and photosystem efficiency were not met; with results mixed across all hydrological categories. However, total leaf chloride content corresponded with salinity measures in the sediment; with increased sediment salinity coinciding with increased chloride content except for mangroves in hydrological categories NL and FH (Table 9). Photochemical efficiency of all mangroves in this study was unexpected; except for mangroves growing inland at hydrological category FF these were similar to the trees growing at the coastal sites and riverine mangroves had the lowest efficiency. This mix of results indicates that *A. marina* has the ability to adjust and grow in a semi-arid climate and morphological features and ecophysiological responses displayed evidence of this.

Table 10: The key vegetation traits displayed on Avicennia marina growing in the various hydrological categories identified in the sites. WUE – water-use efficiency; rETR$_{max}$ – relative maximum electron transfer rate; DA – photochemical efficiency; SP – shoot production; A/GB – above-ground biomass; tree height - individual mangrove tree height; SLW – specific leaf weight; SLA – specific leaf area; TCC – total leaf chloride content. Grey shading indicate where patterns within the variable followed expectations.

	Hydrological Categories							
	Inland					**Coastal**		**Riverine**
	NL	**NH**	**FL**	**FH**	**FF**	**N**	**F**	**RN**
WUE	Medium	Medium	Medium	Medium	Medium	Low	High	Low
rETR$_{max}$	High	High	Medium	High	Low	Medium	V. High	V. Low
DA	Low	Medium	Medium	Medium	V. Low	Medium	Medium	V. Low
SP	Low	Medium	Low	Low	Low	High	Low	High
A/GB	Medium	High	Medium	Low	V. Low	V. High	High	V. High
Tree height	High	Medium	Medium	V. Low	V. Low	V. High	Low	V. High
SLW	Medium	Medium	Medium	High	High	Low	Medium	Low
LS	Medium	Medium	Medium	Low	Low	High	High	V. High
TCC	Medium	High	High	Medium	High	Low	V. Low	Medium

5 Chapter Five – Study synthesis

5.1.1 Environmental conditions and *Avicennia marina* vegetation characteristics at Lake MacLeod

I examined the relationship between sediment environmental conditions and the presence and structure of the vegetation dominated by the mangrove *A. marina* at Lake MacLeod, Western Australia. This is a unique inland marine system located in a semi-arid climate with incredibly high levels of evaporation. The system is fed by underground channels that constantly pump seawater into the inland lake where water can either pool and form small bodies of water, or seep into the sediment without forming ponds. Sediment salinity at Lake MacLeod was incredibly high, a maximum of 105 mS/cm was measured, one of the highest recorded sediment salinities for *A. marina* mangrove stands worldwide (Van Steenis 1963; Beard 1967; Lugo 1981; Thomas, Logan *et al.* 1992). Sediment moisture was also higher than coastal sites. Most mangroves are found near the edge of the ponds, and extend up to 20 meters away from the ponds and grow with saltmarsh vegetation. Globally, *A. marina* tolerates a broad range of environmental conditions (Sobrado and Ball 1999) and is found in many different climatic zones. This study is unique in examining the relationship between vegetation structure and environmental conditions at this extreme and unique environment of low rainfall, high evaporation, minimal freshwater input and constant seawater supply.

Typically in coastal mangroves, the sediment moisture and EC varies along distance and elevation gradients away from the consistent water source (Kenneally 1982; Ball and Sobrado 1998). Soil salinity maximums are usually found furthest from the main water source and at higher elevations. The patterns for soil moisture content are the reverse, with greater soil moisture closer to the water source and at lower elevations. However, these patterns may vary under a number of conditions, specifically when there is reduced water input or limited flushing of the root zone and/or low rainfall with high evaporation rates. Under these conditions, the maximum sediment EC could be located closer to the water source (Hutchings and Saenger 1987). Interestingly, spatial patterns in sediment salinity and moisture within Lake MacLeod did not follow the typical gradients identified at coastal mangrove stands.

We predicted that sediment salinity and moisture content would vary with distance from the pond, such that moisture content would decrease with greater distance from the permanent water source, and salinity would increase due to high evaporation. However the patterns identified at Lake MacLeod were more complex. We identified five different hydrological categories related to distance from the pond and elevation relative to the pond water level. The most saline and highest SMC was found close to the ponds at low and high elevations, due to the continuous flow of seawater into the ponds, lack of freshwater input and the high evaporation rates. Sediments were driest further from the pond edge, except where sediment elevations were low and sediment salinity was slightly higher than seawater (36.98 – 38.07 mS/cm). This suggests that water reaches these sediments through seepage of water or exposure to wind driven water from across the lake bed. In addition, the presence of smaller permanent vents and seeps occurring at distances from the larger water bodies are responsible for the complexity in sediment conditions.

Both sediment salinity and moisture content were strongly associated with the vegetation presence and structure. *A. marina* is clearly tolerant of hypersaline conditions providing there is a consistent supply of water, irrespective of whether it is fresh or salty. Generally *A. marina* tree height, canopy cover, basal area and density were greatest in narrow bands around the permanent ponds where sediment salinity and moisture were highest. This is similar to other inland mangrove systems (Lugo 1981; Thomas, Logan *et al.* 1992). Clearly it is the consistent supply of seawater that supports the existence of larger trees. Interestingly, the number of dead branches per tree was also highest within this zone, potentially due to the extreme hypersaline conditions. Further from ponds where the sediment is less saline and moist, trees were shorter, of lower biomass but had similar shoot production rates to other areas. It is likely that terminal buds die off, which promotes additional branching and aids development of shorter multi-branched mangrove trees (Lin and Sternberg 1992b).

5.1.2 Comparison of water-use efficiency, photosynthesis and productivity of mangrove *Avicennia marina* growing in coastal, riverine and inland stands.

Medina & Francisco’s (1997) model predicts an inverse relationship between WUE and productivity (as well as photosynthetic rates) across a freshwater supply gradient, where WUE decreases and productivity increases with greater freshwater supply. Their model was based on tropical and semi-arid fringing mangroves. I examined this relationship across new habitats, semi-arid riverine and inland mangrove stands. It was predicted that inland mangrove trees would display higher WUE and lower photosynthesis and productivity than trees at coastal and riverine sites, as they would be exposed to higher salinity, have less flushing and less freshwater input (Medina and Francisco 1997; Naidoo 2010).

The coastal landward edge trees were significantly more WUE than any other trees in the study, suggesting that when there is a combination of climatic and hydroedaphic stresses, as opposed to salinity stress alone, *A. marina* becomes more WUE. The trees growing within Lake MacLeod displayed an intermediate WUE, which was significantly higher than the coastal seaward and riverine trees and significantly lower than the coastal landward trees. Even though the main water supply at Lake MacLeod is saline, it is the constant supply of water that is influencing the WUE of these inland trees. Therefore, at all these semi-arid mangrove stands, moisture availability is more important than salinity for WUE. On average WUE of *A. marina* within this study was similar to former research, although individual tree response extended the range of WUE previously measured (Lin and Sternberg 1992b; Medina and Francisco 1997; McKee, Feller *et al.* 2002). For example, Wei et al. (2008) studied *A. marina* growing in a sub-tropical climate with salinities ranging from 14% – 19%: these trees were less WUE (avg. -28.82 ‰) than the semi-arid coastal riverine (avg. – 27.55 ‰) and fringing trees (avg. – 27.58 ‰) from the present study.

The variability of natural ecosystems makes it difficult to compare the productivity levels measured with other research, but the current results do follow a similar pattern to the Medina & Francisco (1997) model. Mangrove trees with higher long-term productivity (A/GB) and greater short-term productivity (SP) were closest to permanent water sources at Lake MacLeod, or were growing where the frequency of inundation was regular through tidal flushing at the coastal sites. SP and A/GB in coastal landward edge mangrove trees displayed similar patterns to trees growing at Lake MacLeod close to the pond edge at higher elevations. SP on these trees was highly variable (many did not grow at all). Previous studies indicate that salinity is among the environmental variables that influences mangrove tree production (Clough 1984; Clough 1992). The hypersaline conditions within inland sediments confirm the importance of salinity to mangrove production, yet this is in contrast to the coastal landward trees where sediment salinity was significantly lower (10.35 ± 0.65 mS/cm). The long-term production (A/GB) patterns displayed by trees within this study are supported by other field studies (Lin and Sternberg 1992b; Vilarrubia 2000; Naidoo 2010). Where there is lower sediment EC, the A/GB is highest; this was found at the coastal fringing and riverine sites. Except at Lake MacLeod, the greatest A/GB was surrounding the ponds where sediment salinity is highest. These contrasting results indicate that distance from a permanent water source, and not salinity, is the key factor driving short and long-term production of mangroves at Lake MacLeod and coastal locations.

The photosynthetic rate ($rETR_{max}$) and photochemical efficiency (DA) of *A. marina* measured during this study were not significantly different between inland and coastal trees, but $rETR_{max}$ was significantly different between the hydrological categories. The photosynthetic response patterns displayed by these mangrove trees were unexpected and complex. Unusually $rETR_{max}$ of mangrove trees at the riverine site were significantly lower than all other trees. These trees were clearly stressed as photochemical efficiency (DA) was also low; displaying a similar photochemical efficiency to mangroves growing inland at greater distances from the pond edges and at elevations above the water level. This finding is difficult to explain without collecting further information that was beyond the scope of the present study. Based on surrounding land use (extensive horticulture and pastoral) and extreme flooding events that occurred prior to the commencement of this study, it is possible the introduction of toxicants (i.e. herbicides) into the river system is placing extra stress on the riverine trees (Waddell, Thomas *et al.* 2012). Ralph et. al. (2007) revealed that fluorescence parameters can be used to identify plant stress caused by herbicides and other pollutants, which may be applicable to future studies in this area.

5.1.3 Knowledge gained from this study

This research has improved our understanding of the extreme conditions that the mangrove *A. marina* can grow in, and the environmental drivers responsible for the structure of vegetation dominated by *A. marina* in a unique inland lake system. Lake MacLeod is an inland saline system that has supported *A. marina* mangrove stands for ~5300 years (Logan 1987); therefore this species is clearly capable of persisting under extreme conditions. These mangrove trees display a range of ecophysiological features, particularly related to mangrove tree height, canopy cover, basal area, leaf area and weight, growth and water-use efficiency which are indicative of mangroves growing within stressful conditions. These results support Youssef & Saenger’s findings (1999) that good correlations exist between salinity and mangrove presence and structure; however the present study demonstrates that it is not the only factor driving mangrove production. It is evident that there is an interaction between a number of environmental variables that explain the patterns in mangrove stand characteristics (Ball 1988b). Water availability was clearly the most important environmental factor contributing to the persistence of *A. marina* at inland and coastal stands within a semi-arid climate.

Across habitats from coastal riverine, to coastal fringing and to inland mangrove habitats, there were a number of processes influencing water supply. On the coast seawater is exchanged with tidal movement, but in the inland system there is a constant supply due to the positive pressure from the vents. In both areas, trees furthest from this water supply were most water-use efficient. Freshwater is supplied through irregular rainfall and river flow, therefore the coastal habitats are likely to receive more freshwater due to the river flow. This was clearly demonstrated by the lower salinity and greater productivity in these habitats compared to inland systems. The key difference between inland and coastal systems is the more constant supply of seawater at the inland system, compared to the irregular but greater supply of freshwater in coastal habitats.

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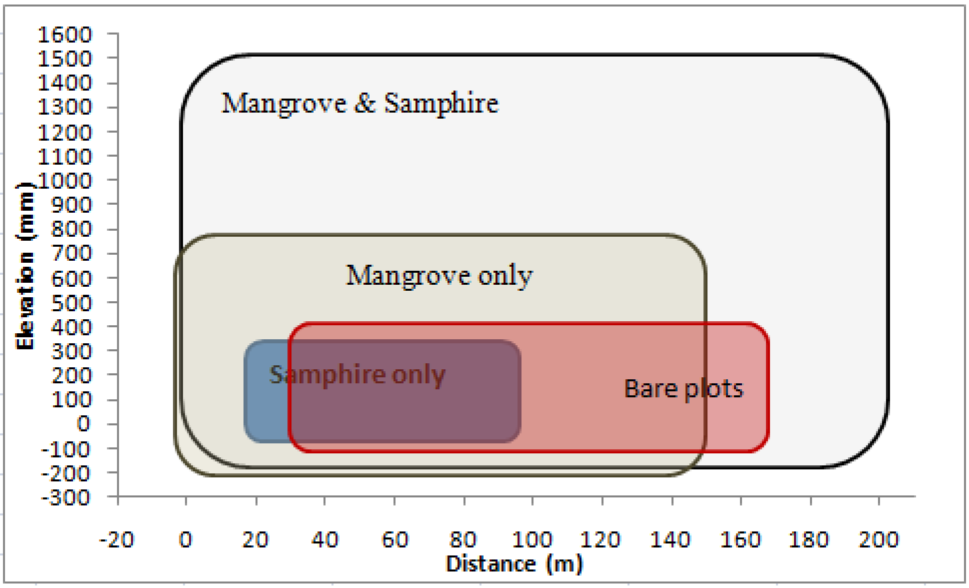
7 Appendix 1



Appendix 1.1: Indication of where individual plots and the vegetation type were found at Lake MacLeod, based on relative sediment elevation and distance from the pond edges.

Appendix 1.2: Design outline for all sites, numbers of trees tagged in each plot.

Site	Gradsect/plot	Trees	Gradsect/plot	Trees	Gradsect/plot	Trees
Goat Bay	1.1	2	2.1	4	3.1	2
	1.2	2	2.2	4	3.2	3
	1.3	0	2.3	4	3.3	4
	1.4	3	2.4	3	3.4	2
	1.5	4	2.5	4	3.5	3
	1.6	4		2	3.6	

Site	Gradsect/plot	Trees	Gradsect/plot	Trees	Gradsect/plot	Trees
Whistlers	1.1	4	2.1	4	3.1	3
Pond	1.2	0	2.2	0	3.2	0
	1.3	3	2.3	0	3.3	3
	1.4	3	2.4	0	3.4	0
			2.5	0	3.5	0
			2.6	0	3.6	4
			2.7	2		

Site	Gradsect/plot	Trees	Gradsect/plot	Trees	Gradsect/plot	Trees
Neil's	1.1	4	2.1	4	3.1	3
Pond	1.2	4	2.2	1	3.2	0
	1.3	4	2.3	0	3.3	0
	1.4	2	2.4	4	3.4	0

Site	Gradsect/plot	Trees	Gradsect/plot	Trees	Gradsect/plot	Trees
Pete's	1.1	4	2.1	4	3.1	4
Pond	1.2	0	2.2	0	3.2	0
	1.3	0	2.3	0	3.3	0
	1.4	3	2.4	0	3.4	0

Site	Gradsect/plot	Trees	Gradsect/plot	Trees	Gradsect/plot	Trees
Coastal 1	1.1	4	2.1	4	3.1	4
	1.2	4	2.2	4	3.2	4

Site	Gradsect/plot	Trees	Gradsect/plot	Trees	Gradsect/plot	Trees
Coastal 2	1.1	4	2.1	4	3.1	4
	1.2	4	2.2	4	3.2	4

Site	Gradsect/plot	Trees	Gradsect/plot	Trees	Gradsect/plot	Trees
Riverine GRM	1.1	4	2.1	4	3.1	4

Site	Gradsect/plot	Trees	Gradsect/plot	Trees	Gradsect/plot	Trees
Riverine OATP	1.1	2	2.1	4	3.1	4

Appendix 1.3: Contents of acid buffer solution, these amounts make up 500ml of solution.

Ingredient	ml
Thymol blue gelatine indicator (TBGI)	6.25
Nitric Acid (conc.)	5
Acetic Acid (conc.)	10
Chloride standard (200ppm)	2.5
Extran 300	0.5